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TESSMANNIANTHUS, AN ARBORESCENT GENUS OF MELASTOMATACEAE NEW TO PANAMA[1]

Frank Almeda[2]

ABSTRACT

Recent collecting activity in montane cloud forests of western and central Panama has led to the discovery of two new species of *Tessmannianthus*, a little-known genus of trees previously recorded from Colombia, Ecuador, and Peru. *Tessmannianthus carinatus* and *T. gordonii* are described, illustrated, compared, and contrasted with similar species. A key to the new taxa and a synoptic history of the genus are also provided.

In a paper describing new Peruvian flowering plants collected by the late Günther Tessmann, Markgraf (1927) proposed the new genus and species *Tessmannianthus heterostemon*, to accommodate one of the tallest known trees (30–45 m) among neotropical Melastomataceae. Markgraf's circumscription of *Tessmannianthus* emphasized its unique androecial characters. The connectives on the larger set of dimorphic stamens are modified dorsally into biauriculate, ventrally upturned appendages. The smaller anther sacs are longitudinally bifurcate distally and have connectives that are prolonged dorsally at the base into bilobed or deflexed, bifid appendages. These characters, together with the pentamerous flowers, trilocular capsular fruits, and prevailingly lepidote indument, define *Tessmannianthus* as a natural alliance worthy of generic rank.

For nearly fifty years *Tessmannianthus* was thought to be a monotypic genus. Wurdack (1975) described *T. cenepensis* and transferred the enigmatic *Miconia calcarata* Gleason to *Tessmannianthus*, enlarging the genus to three species and extending its range from Peru northward to Colombia.

Because of its arborescent habit, rainy season flowering, and evidently limited number of individuals in any one population, *Tessmannianthus* has

[1] I thank John J. Wurdack for sharing information about *Tessmannianthus*, Gordon McPherson for returning to collecting localities to gather flowering material, and curators of the following herbaria who sent specimens as gifts or loans: F, MO, NY, US.

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escaped the attention of most collectors. Each of the species is known from fewer than six collections, and open flowers of *T. cenepensis* and mature seeds of *T. heterostemon* remain unknown.

The discriminating collecting efforts of Gordon McPherson in Panama have yielded the first collections of the two new species described here. Among the six merianioid genera of Melastomataceae now known from Panama (Gleason, 1958; D'Arcy, 1987), *Tessmannianthus* is likely to be confused only with *Graffenrieda*. The latter is distinguished by a calyptriform or irregularly rupturing calyx, dorsally arcuate stamens, and anther connectives modified into acute dorso-basal spurs. The Panamanian species of *Tessmannianthus* do not appear to be closely related to one another. They are, nevertheless, readily separated from all other Central American melastomes by the following characters: the small (4–7.5 × 2–6 mm) clawed petals are retrorsely erose-ciliolate; the larger ventrally arcuate anthers open by a pair of ventrally inclined confluent pores; and each of the bifurcate anther sacs in the smaller stamens opens by a dorsally inclined pore.

KEY TO *TESSMANNIANTHUS* IN PANAMA

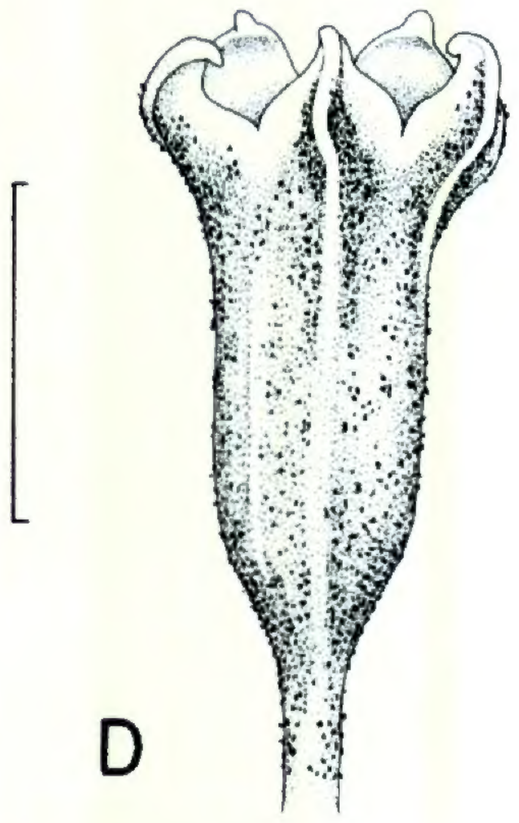
1a. Upper leaf surfaces sulcate, the elevated nerves on lower leaf surfaces moderately covered with a caducous mixture of shaggy-dendritic (pinoid) and lepidote hairs; hypanthia (at anthesis) 7–8 mm long to the torus; calyx lobes beset with a carinate keel that forms an incurved clawlike apical tooth; petals distally puberulent abaxially; larger anthers 9.5–10 mm long ... 1. *T. carinatus*

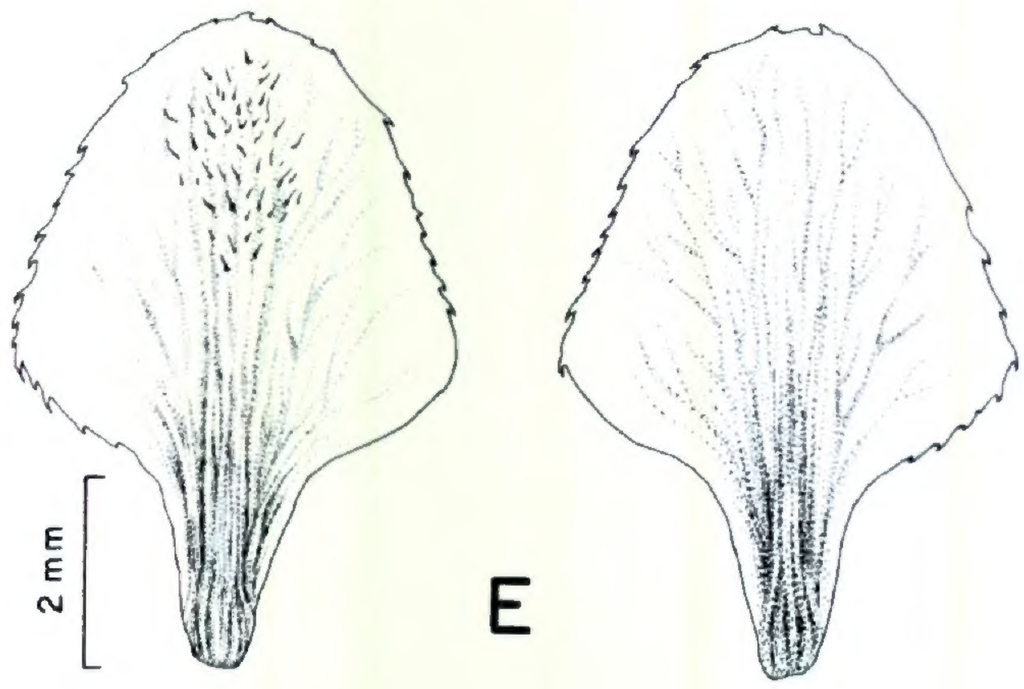
1b. Upper leaf surfaces essentially flat, the elevated nerves on lower leaf surfaces moderately to sparingly covered only with lepidote hairs; hypanthia (at anthesis) 3(–3.5) mm long to the torus; calyx lobes beset with an inconspicuous blunt subapical tooth; petals glabrous abaxially; larger anthers 4.5 mm long ..... 2. *T. gordonii*

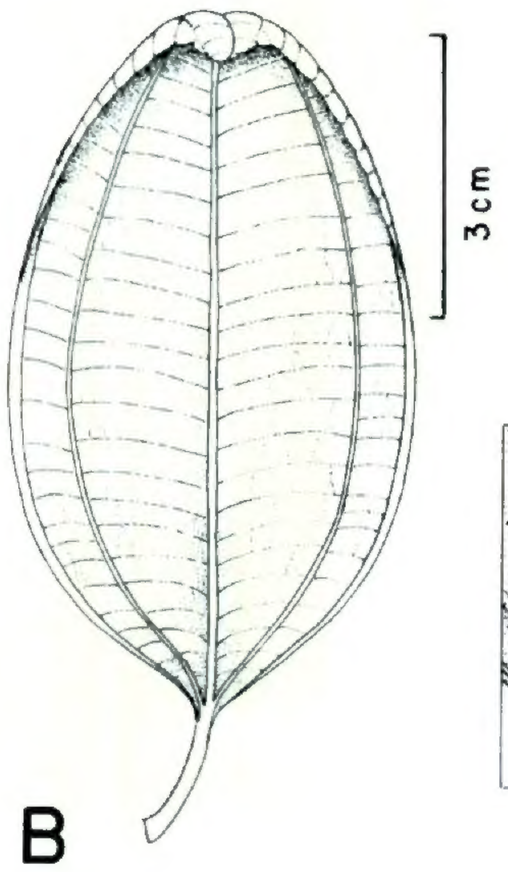
Tessmannianthus carinatus Almeda, sp. nov. TYPE: Panama. Panamá: Cerro Jefe region, ca. 9°15′N, 79°30′W, forest near summit, ca. 850 m, 24 Aug. 1986 (fl), *McPherson 9980* (holotype, CAS; isotypes, MO, PMA, not seen). Figure 1.

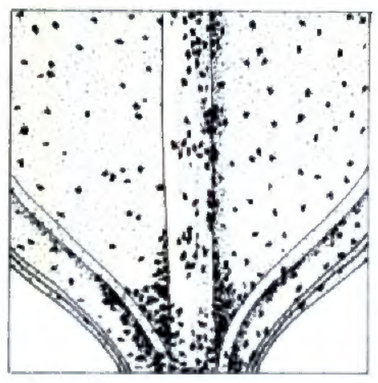
Ramuli primum quadrangulati demum teretes sicut folia novella foliorum subtus venae primariae inflorescentiaque dense vel modice pilis pinoideis ca. 0.5 mm longis et squamis lepidotis modice intermixtis. Petioli 0.5–1.4 cm longi; lamina 4.3–8.5 × 1.7–4.4 cm elliptica vel elliptico-ovata apice breviter (2–3 mm) gradatimque acuminato basi obtusa, 5-nervata (pari inframarginali tenui neglecto) nervis secundariis ca. 2.5–4 mm inter se distantibus subtus elevatis, coriacea et integra. Panicula 3–5.5 cm longa multiflora; flores 5(–6)-meri, pedicellis (ad anthesim) 3–6 mm longis. Hypanthium (ad torum) 7–8 mm longum; calycis tubus 1.5 mm longus, lobis 2.5 × 3 mm late ovatis, dentibus exterioribus callosis acutis ca. 1 mm eminentibus. Petala 7–7.5 × 5.5–6 mm obovato-suborbicularia ca. 2–2.5 mm unguiculata extus apicaliter modice puberula. Stamina dimorphica glabra; antherae ad basim in staminibus maioribus et staminibus minoribus biauriculatae. Ovarium triloculare et ca. ⅔ inferum. Fructus maturus ignotus.

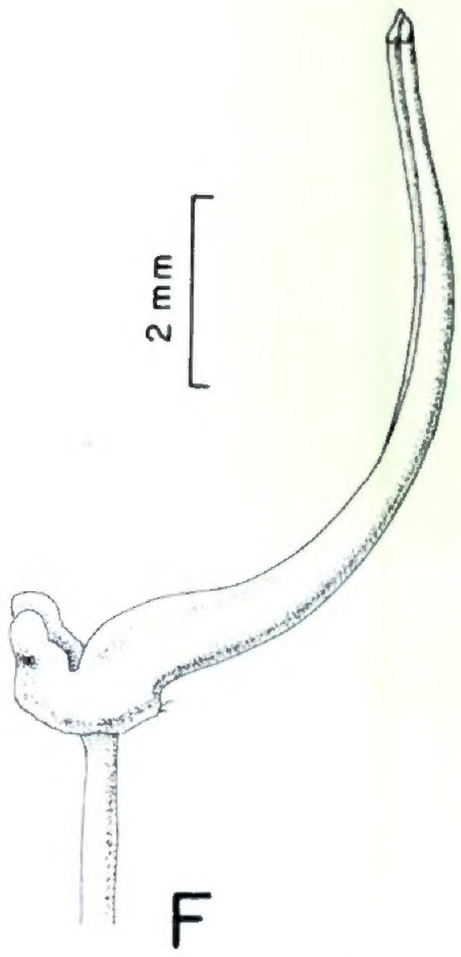
Trees to 11 m tall. Older cauline internodes terete and glabrous; the subquadrangular distal branchlets, vegetative buds, and inflorescences moderately to densely covered with a mixture of dark brown shaggy-dendritic and irregularly-shaped lepidote hairs. Leaves of a pair essentially equal in size; petioles 0.5–1.4 cm long; blades coriaceous, 4.3–8.5 cm long, 1.7–4.4 cm wide, elliptic to elliptic-ovate, apex gradually acuminate with a short acumen (2–3 mm), this obtuse to broadly rounded and curved downward, base obtuse, margin entire and revolute distally, 5-nerved abaxially, the outermost pair of primaries often inconspicuous and concealed by the revolute margins when dry, the transverse secondaries elevated like the primaries and spaced 2.5–4 mm apart at the widest portion of the blade, glabrous and sulcate above at maturity, covered with a mixture of dendritic and lepidote hairs on the elevated primaries below, otherwise moderately beset only with lepidote hairs. Inflorescence a terminal multiflowered panicle 3–5.5 cm long; bracteoles paired, early caducous, linear-oblong to narrowly obovate, 1.5–5 mm long, 0.5–2 mm wide, margin entire, glabrate above, moderately lepidote below. Pedicels 3–6 mm long, densely lepidote. Hypanthia (at anthesis) cylindric, 7–8 mm long to the torus, moderately to copiously lepidote. Calyx tube 1.5 mm long on flowering hypanthia; calyx lobes reportedly white, ovate but appearing deltoid abaxially because of the carinate clawlike tooth (ca. 1 mm high) at the incurved summit, 2.5 mm long (excluding tooth) and 3 mm wide basally between sinuses, the margins entire. Petals 5(–6), reportedly pale pink, 7–7.5 mm long, 5.5–6 mm wide, obovate-suborbicular, rounded apically, abruptly tapering to a basal claw 2–2.5 mm long, glabrous adaxially but puberulent distally on the abaxial surface, the margin retrorsely erose-ciliolate. Stamens 10(–12), strongly dimorphic with larger stamens inserted on the torus opposite the calyx lobes and smaller ones inserted opposite the petals; filaments somewhat declinate, complanate and glabrous; anthers yellow and 2-celled. Larger stamens: filaments 6.5–7 mm long; anthers geniculate at the filament insertion, 9.5–10 mm long and 0.5 mm wide, subulate, ventrally arcuate and channeled between the thecae, opening by 2 ven-











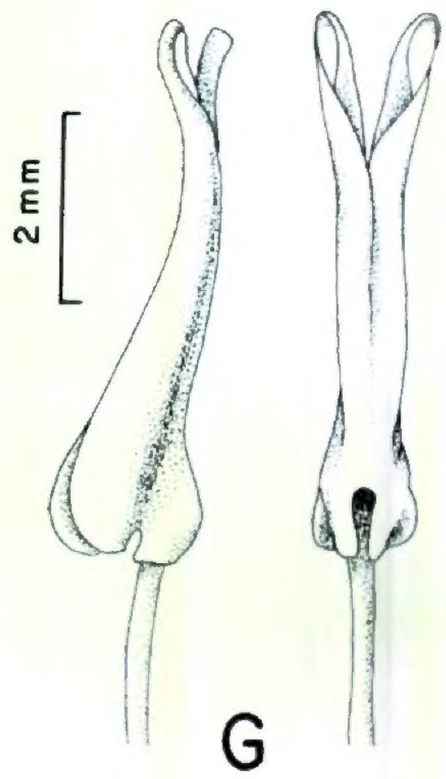


FIGURE 1. *Tessmannianthus carinatus.*—A. Habit.—B. Representative leaf.—C. Base of leaf blade (abaxial surface) with enlarged lepidote hairs.—D. Hypanthium (at anthesis); petals, stamens, and style removed.—E. Petals, abaxial surface (left), adaxial surface (right).—F. Larger stamens (lateral view).—G. Smaller stamens, lateral view (left), dorsal view (right). Drawn by Ellen del Valle from the holotype.

trally inclined confluent pores; connective thickened dorsally and prolonged at the minutely puberulent base into a ventrally upturned biauriculate appendage, with each lobe 1–1.5 mm long and 0.5 mm wide. Smaller stamens; filaments 5.5–6 mm long; anthers 6 mm long and 0.5 mm wide basally, linear-oblong, erect to somewhat incurved distally with the 2 thecae of each anther diverging from one another, each theca opening by a dorsally inclined pore; connective thickened dorsally and prolonged at the base just above the filament insertion into a deflexed, deeply bifid appendage 0.5

mm long having each lobe caudiform in dorsal and ventral view. Ovary (at anthesis) ca. ⅔ inferior, 3-celled, oblong, glabrous at the apex. Style 7.5–8 mm long, 0.5–1 mm wide, glabrous, somewhat declinate and slightly incurved distally; stigma round to subtruncate. Mature capsule and seeds not seen.

Distribution. Known only from the summit area of Cerro Jefe in central Panama at about 850 m, where the new species is evidently an uncommon member of the low cloud forest vegetation. It grows with but appears to be greatly outnumbered by the vegetatively similar Cerro Jefe race of *Conostegia montana* (Sw.) D. Don ex DC.

Tessmannianthus carinatus differs from other members of the genus in characters of the foliage, indument, and calyx lobes. The leaves of this species are leathery and sulcate, with a rounded terminal acumen that is turned downward. The indument on young branches, inflorescences, and the elevated primary nerves on lower leaf surfaces consists of a mixture of appressed lepidote hairs and spreading dendritic or pinoid hairs. The former hair type is found in all other members of the genus; the latter is unique to *T. carinatus*. The specific epithet draws attention to the distinctive calyx morphology. Each lobe is beset with a carinate abaxial keel that forms an apically incurved clawlike tooth (Fig. 1D).

Tessmannianthus carinatus appears to be without close relatives. Its leathery leaves are vaguely reminiscent of *T. heterostemon*, which differs markedly in having larger (9–20.5 × 6.4–13.5 cm) apically rounded obovate blades, shorter hypanthia (3–4 mm) with minute caducous exterior calyx teeth, and elliptic-oblong, papillate petals.

Tessmannianthus gordonii Almeda, sp. nov.
TYPE: Panama. Chiriquí: Fortuna Dam watershed, above Río Hornito, 08°45′N, 82°15′W, 1,250 m, 1 July 1987 (fl), *McPherson 11161* (holotype, CAS; isotypes, AAU, BM, COL, CR, DUKE, EAP, F, K, LE, MEXU, MO, NY, P, PMA, QCA, TEX, U, US, VEN, not seen). Figure 2.

Ramuli primum quadrangulati demum teretes sicut petioli foliorum subtus venae primariae inflorescentiaque squamis lepidotis demum caducis sparsiuscule induti. Petioli 0.6–1.3 cm longi; lamina 4.4–6.8 × 2.1–2.9 cm elliptica apice acuminato, basi acuta vel obtusa, 3–5-nervata vel 3–5-plinervata (pari tenui marginali neglecto) firme membranacea et integra. Panicula 2.5–3.5 cm longa multiflora; flores 5-meri, pedicellis (ad anthesim) 2–3.5 mm longis. Hypanthium (ad torum) 3(–3.5) mm longum; calycis tubus ca. 0.5 mm longus, lobis 1 × 2 mm ovatis, dentibus exterioribus crassis 0.5 mm eminentibus. Petala glabra 4–4.5 × 2–2.5 mm elliptico-oblonga ca. 0.5–1 mm unguiculata. Stamina dimorphica glabra; antherae ad basim in staminibus maioribus et staminibus minoribus distincte biappendiculatae. Ovarium triloculare; capsula ca. 5–6 mm longa; semina numerosa 2–2.5 mm longa anguste pyramidata.

Trees 9–16 m tall. Older cauline internodes terete and glabrous; the quadrangular distal branchlets, lower leaf surfaces, and inflorescences beset with a moderate covering of caducous lepidote hairs. Leaves of a pair essentially equal in size; petioles 0.6–1.3 cm long; blades firmly membranaceous, 4.4–6.8 cm long, 2.1–2.9 cm wide, elliptic, apex acuminate, base acute to obtuse, margin entire, 3–5-nerved or 3–5-plinerved abaxially with the innermost pair of primary nerves elevated and diverging from the median nerve in opposite fashion about 2–4 mm above the blade base, the outermost pair of primaries mostly depressed and inconspicuous, essentially glabrous above at maturity, sparingly to moderately beset with brown lepidote hairs below. Inflorescence a terminal multiflowered panicle 2.5–3.5 cm long with ultimate branchlets terminating in umbelliform clusters; bracteoles paired, sessile, persistent to tardily deciduous on the infructescence, ovate to oblong-ovate, rounded apically, 0.5–3 mm long, 0.5–2 mm wide, margin entire, glabrous on the concave upper surface, moderately to copiously lepidote to glabrate on the lower surface. Pedicels 2–3.5 mm long, sparingly lepidote to glabrate. Hypanthia (at anthesis) subcylindric to narrowly campanulate, 3 (–3.5) mm long to the torus, glabrous or sparingly lepidote toward the base but typically glabrous at maturity. Calyx tube ca. 0.5 mm long on fruiting hypanthia; calyx lobes broadly ovate but appearing bluntly deltoid because of the terminal tooth (to 0.5 mm long) on the glabrous abaxial surface, 1 mm long, 2 mm wide basally between sinuses, the margins entire and somewhat incurved apically. Petals 5, glabrous, reportedly pink-white, elliptic-oblong to narrowly obovate, rounded to shallowly and irregularly lobed apically, gradually tapering to a short (0.5–1 mm) basal claw, 4–4.5 mm long, 2–2.5 mm wide, retrorsely erose-ciliolate. Stamens 10, strongly dimorphic with larger stamens inserted on the torus opposite the calyx lobes and smaller ones inserted opposite the petals; filaments somewhat declinate, complanate and glabrous; anthers yellow, 2-celled. Larger stamens: filaments 5 mm long; anthers geniculate at the filament insertion, 4.5 mm long, 0.5 mm wide, linear-oblong, arcuate and channeled ventrally between the thecae, opening by 2 ventrally inclined confluent pores; connective thickened dorsally and prolonged at the

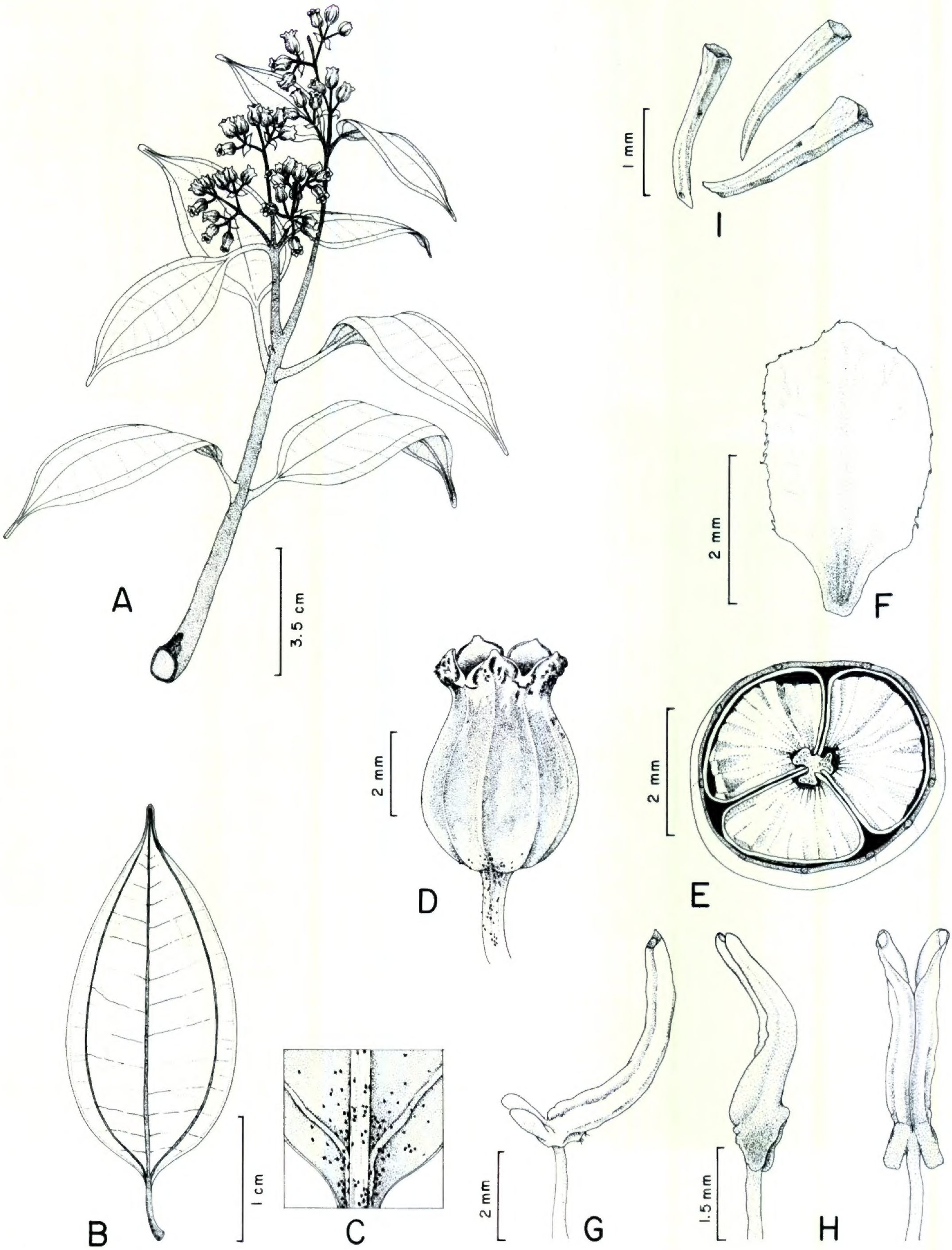


FIGURE 2. *Tessmannianthus gordonii.*—A. Habit. —B. Representative leaf (abaxial surface).—C. Base of leaf blade (abaxial surface) with enlarged lepidote hairs.—D. Hypanthium (in fruit).—E. Cross section of capsule and enveloping hypanthium.—F. Petal (abaxial surface).—G. Larger stamens (lateral view).—H. Smaller stamens, lateral view (left), dorsal view (right).—I. Seeds. Drawn by Ellen del Valle. (A–C, F–H from the holotype; D, E, I from *McPherson 9877.*)

minutely puberulent base into a ventrally upturned deeply bifid appendage, with each lobe 1 mm long and 0.5 mm wide. Smaller stamens: filaments 4–5 mm long; anthers 2.5–3 mm long, 0.5 mm wide basally, linear-oblong, erect to somewhat incurved distally where the 2 thecae diverge from one another, each theca opening by a dorsally inclined pore; connective thickened dorsally and prolonged

basally into a deflexed biauriculate skirtlike appendage (0.5–0.75 mm long), with each of its lobes tail-like in ventral and dorsal view and obdeltoid in lateral view. Ovary (at anthesis) ca. ½ inferior, 3-celled, narrowly elliptic, glabrous apically. Style 5–6 mm long, 0.5 mm wide, glabrous, declinate and somewhat incurved distally; stigma rounded to subtruncate. Fruit a many-seeded loculicidal capsule ca. 5–6 mm long and 4.5–5 mm diam. Seeds narrowly pyramidate, cuneate and angulate, 2–2.5 mm long, white or beige, glabrous but vaguely papillate on the angles.

Distribution. Known only from montane forests of the Fortuna Dam watershed above Río Hornito at 1,100–1,250 m in Chiriquí Province, Panama.

Additional specimen examined. PANAMA. CHIRIQUÍ: vicinity of Fortuna Dam along trail near Río Hornito, ca. 8°45′N, 82°15′W. Forest ca. 1,100 m, 8 Aug. 1986 (fr), *McPherson 9877* (CAS).

In the size, shape, and indument of its leaves, *T. gordonii* most closely resembles *T. cenepensis*. The latter differs in the following characters: anther sacs of the larger stamens are linear-oblong and conspicuously retuse or bifurcate distally for about 0.5 mm; anther sacs of the smaller stamens are bifurcate for the distal two-thirds of their length and have connectives that are obscurely lobed but not prolonged into biauriculate appendages; the ovary is puberulent; the petals are copiously furfuraceous-lepidote abaxially; and the hypanthia are markedly constricted below the torus into a tubular neck that shortens to a tight constriction on fruiting hypanthia. *Tessmannianthus cenepensis* also appears to differ in other modal tendencies. Its inflorescences are longer (5–8 cm) and more floriferous than those of *T. gordonii*, and its petals are broadly ovate and appear to lack a well-developed basal claw. The consistency of these latter differences will become apparent only when better flowering material is available for study.

This species is named for Gordon McPherson (1947–), collector of the type and all other known Panamanian specimens of this genus. His many fine collections of trees, shrubs, and epiphytes have added a number of new and interesting species to the flora of Panama.

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THE GENUS *ARGOSTEMMA* (RUBIACEAE—ARGOSTEMMATEAE) IN BORNEO[1]

Birgitta Bremer[2]

ABSTRACT

Argostemma is a large paleotropical genus of the tribe Argostemmateae. From Borneo 28 species are recognized. All are herbs growing in rainforests. Six species, *A. apiculatum*, *A. burttii*, *A. geesinkii*, *A. gaharuense*, *A. brookei*, and *A. calcicolum*, are new. There is one new name, *A. chaii*. *Argostemma* is the larger genus of the tribe; the other genus is *Neurocalyx*. The sister group to the Argostemmateae is the mainly Central American tribe Hamelieae. These two tribes form a monophyletic group within the subfamily Rubioideae. About two-thirds of the *Argostemma* species are endemic to Borneo. The species belong to at least three different monophyletic groups, each having its sister group outside Borneo. Nomenclature, descriptions, illustrations, maps, and a key for all species are provided.

Argostemma Wall. in Roxb. is a large, complex genus with about 220 described species. The revision of the genus will be published in parts dealing with different geographical areas. About 51 taxa have been described from Borneo. There is no treatment covering the whole island. In this study I have recognized 28 species, of which six are new. Most of the 28 species are endemic to Borneo, although six of them were described from specimens collected outside of Borneo. The remaining 22 are typified on Borneo specimens.

Only synonyms typified by specimens from Borneo are listed under the species.

During the 1950s, the late Dr. Bakhuizen van den Brink, Jr. studied the genus for the Flora Malesiana project. He annotated many herbarium labels about typifications. I have studied his lectotypifications, and in most cases I do agree with him, and have accepted the lectotypifications which are published in this paper.

No infraspecific taxa are recognized in this study. Most species are stenomorphous, and a few species are polymorphous. Among the latter, *A. elatostemma* occurs as two differing populations on Borneo, but since its whole variation outside Borneo is not yet known, they are not recognized as separate taxa. The substantial variation in *A. borragineum* is not correlated with geographical distribution and does not reveal distinct evolutionary lines. *Argostemma hameliifolium* and *A. moultonii* form a complex without discrete infraspecific units. The distinction between the two species is more or less preliminary. *Argostemma densifolium* is dimorphic, but as the variation seems small, I have treated the two morphs as one taxon.

MATERIALS AND METHODS

All cited specimens including types have been studied, unless otherwise stated. I have seen material from the following herbaria: A, AAU, B, BM, BO, BR, E, G, GH, HBG, K, KLU, L, MO, NY, P, S, SAR, SING, U, UC, and US.

I have studied *Argostemma parvifolium*, *A. elatostemma*, *A. ophirense*, *A. rupestre*, *A. hameliifolium*, *A. moultonii*, *A. gracile*, *A. havilandii*, *A. calcicolum*, *A. psychotrioides*, and *A. bryophilum* in the field. Material of most of these species was fixed in the field and later embedded and sectioned for anatomical studies of leaves, an-

[1] I am grateful to Mr. Paul Chai and his staff at the Forest Department at Kuching for assistance during my fieldwork, to the late Dr. Bakhuizen van den Brink, Jr. for much information about the genus, to Dr. John Dwyer for checking my Latin diagnoses, as well as to Mrs. Gunilla Hägglund, Miss Kerstin Kustås, and Miss Mari Källersjö for technical assistance. I am also indebted to the directors and curators of the herbaria listed in the Materials & Methods and to the reviewers for many useful comments. I thank Dr. Peter Raven, Director of the Missouri Botanical Garden, where I finished this study. Financial support from the Swedish Institute, the Royal Academy of Sciences, Stockholm, the Swedish Natural Science Research Council, and the University of Stockholm is gratefully acknowledged.

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thers, and ovaries. For endothecial structure, whole anthers of all species were mounted in Hoyer's solution for study.

The species are arranged roughly in phylogenetic order. Species 1–12 (the *A. parvifolium* group) belong to one evolutionary group, species 13–26 (the *A. psychotrioides* group) to a second group, species 28 (*A. neurocalyx*) to a third group, and species 27 (*A. bryophilum*) assumes an uncertain position within the genus.

The drawings are my own. In the figures (4–31), all details of plants indicated by the same letter (B–I) are drawn at the same magnification and illustrate the same plant part. Hence, if a particular part is not illustrated, the corresponding letter is not used in the figure. The branch, indicated by letter A, is drawn twice as large in Figures 7–15, 17, 19–22, 30, and 31 as in Figures 4–6, 16, 18, and 23–29.

Systematic Position and Interrelationships within *Argostemma*

Argostemma is the largest genus of the Argostemmateae (Verdcourt, 1958; B. Bremer, 1987; Argostemmatideae fide Darwin, 1975, sphalm., pers. comm.). The other genus of the tribe is *Neurocalyx* (B. Bremer, 1979), a small genus endemic to Sri Lanka and southern India. The sister group to the Argostemmateae is the mainly Central American tribe Hamelieae (B. Bremer, 1987). These two tribes form a monophyletic group within the subfamily Rubioideae.

In Borneo there are 28 species of *Argostemma*. About two-thirds of these are endemic. The Bornean species belong to at least three different monophyletic groups, each having its sister group outside Borneo.

The *A. parvifolium* group is represented by species 1–12, characterized by "radial" endothecium (see morphological notes), anisophyllous leaves, rotate corollas, a narrowly ovoidal anther cone, thin and smooth apical appendages, and a glabrous style with a hardly widened to slightly capitate stigma. Three species from this group (*A. parvifolium*, *A. elatostemma*, and *A. ophirense*) also occur in the Malay Peninsula and on other Sunda Islands.

The *A. psychotrioides* group, species 13–26, is characterized by a sturdy connective, umbelliform inflorescences, in most species a corolla cleft to less than half its length, and usually a style much longer than the stamens. Most species also have a "polarized" endothecium (one species cannot be classified as "radial" or "polarized"), and most species have an endothecium with distinct cell margins (see morphological notes). *Argostemma hameliifolium*, *A. moultonii*, *A. psychotrioides*, and *A. borragineum* also occur on other Sunda Islands but not in the Malay Peninsula.

The remaining species, *A. bryophilum* (27) and *A. neurocalyx* (28), are more isolated. *Argostemma neurocalyx* belongs to a totally different group within *Argostemma*. It is characterized by an apical leaf rosette and free stamens, of which the anthers open by pores instead of slits. The group to which it belongs has a very wide distribution from West Africa to the Philippines. The systematic position of *A. bryophilum* is not yet clear. It does not fit in any of the groups mentioned above and is part of a complex of taxa common in the Philippines and New Guinea.

Morphological Notes

Raphides. Raphides are found in most parts of the plants and can be seen easily in corollas or in young glabrous stems.

Colleters. On living material the colleters can be seen easily, but on old dry specimens they are hardly visible. They are of the standard rubiaceous type (Lersten, 1975), with elongated axial cells surrounded by a palisade epidermal layer. The colleters are found singly or a few together between the calyx lobes. At each node they surround the stem in a ring and occur on the adaxial side of the petiole and at stipule bases. In species with few colleters in each ring, the colleters are generally round in outline, whereas in species with a dense ring of several hundred colleters they are narrow, often reduced, and almost without a palisade epidermis (Lersten, 1974). The stipules often end in apical colleters. In *Argostemma chaii*, with fringed stipules, each of the processes making up the fringe ends in a distinct colleter.

Hairs. In Borneo, only *A. apiculatum* is glabrous. The other species are more or less entirely or partially pubescent. There are no substantial differences between hairs on vegetative organs and those on flowers. Normal hairs are monoseriate and completely septate, with thin to very thick walls, and they generally do not collapse when dry. They may occur all over the leaf surfaces or only on (or rarely only between) the veins. If there is indumentum on the inside of the corolla or on the style, the hairs are shorter, mostly one- or few-celled and thinner (Verdcourt, 1958). Another hair type occurs on, e.g., *A. rupestre* (Fig. 13I) and *A. gee-*

sinkii (Fig. 14I). On the upper leaf surfaces of these species there are three or five rows of stiff, pluricellular hairs. One row occurs along the midrib and the others along the margins, making them appear more or less serrulate.

Leaf anatomy. I have studied in detail cross sections of field-fixed material of *A. bryophilum*, *A. elatostemma*, *A. havilandii*, *A. moultonii*, *A. ophirense*, *A. psychotrioides*, and *A. rupestre*. Cross sections of young leaves of the species are generally very similar. With the exception of *A. bryophilum*, cross sections of these species can be described as follows: upper epidermis of one layer of large, rectangular cells with rather thin walls and lacking plastids; palisade chlorenchyma of one or a few layers of small carrot-shaped cells filled with plastids; spongy parenchyma of a few to many layers of small to medium-sized cells almost without plastids; lower epidermis of one layer of large, rounded cells with thin walls and without plastids; stomata quite exposed. This type of leaf also occurs in *Neurocalyx* (B. Bremer, unpubl.). *Argostemma bryophilum*, aberrant in many other ways, differs from the others in leaf cross section. Its epidermal layers are thinner with smaller cells, and the chlorenchyma consists of large rounded cells with few plastids.

Species whose lower leaf surface appears white (e.g., *A. rupestre* and *A. gracile*) have more intercellular spaces in the spongy parenchyma than other species.

Endothecium. The endothecium of *Argostemma* (Fig. 1) was studied with light microscope on whole mounts of anthers. The endothecium varies between groups of *Argostemma* species. In *A. bryophilum* and *A. neurocalyx*, in many ways aberrant species, only narrow longitudinal bands of cells close to the stomium have wall thickenings, while in all other species from Borneo, wall thickenings occur in all cells of the endothecial layer. In the following, the terms endothecium, endothecial layer, and endothecial type will only be used for those cells with wall thickenings.

The endothecial cells are generally elongated longitudinally or horizontally compared with the line of dehiscence and with the anther-length axis, or rarely they are isodiametric. In *Argostemma* the wall thickenings are U-shaped ribs arranged transversely in relation to the longest axis of the cell and with their openings toward the epidermal layer. The ribs end in knobs.

Dormer (1962), Nordenstam (1978), Noel (1983), and French (1985) have shown the systematic significance of endothecial structures. This study shows that different endothecium types occur in *Argostemma* and that these types are restricted to different systematic units within the genus. Dormer (1962) and Noel (1983) presented systems for classification of endothecial structures. Dormer (1962) classified endothecial cells in the Compositae as "polarized" or "radial." In a polarized endothecium the thickenings are concentrated mainly at the upper and lower ends of the cells, and when ribs occur they are parallel to the line of dehiscence. In a radial endothecium the cells are ribbed all around; on elongated cells the bars are arranged transversely, parallel to the line of dehiscence. I have found Dormer's system somewhat difficult to use with Rubiaceae because the endothecial cells are different, often elongated horizontally, i.e., transversely to the anther-length axis. In Compositae (Nordenstam, 1978; Dormer, 1962; K. Bremer, pers. comm.), when the cells are elongated, the elongation is parallel to the anther-length axis.

Noel (1983) presented a more general system which embraces over 500 taxa from different families. He distinguished several endothecial characters, such as size and shape of the cells, organization of the thickenings, whether a basal plate and/or ribs occur, and the shape and number of these. In general, the endothecial cells of *Argostemma* can be characterized following Noel's scheme (1983: 837): cells medium-sized, 27–60 μm on the longest side, isodiametric, rectangular or fusiform; wall thickenings localized; base plate absent; ribs U-shaped; 5–ca. 15 ribs per cell (in several species the cell margins become indistinct, and it is difficult to see where the cell ends); spacing from close to wide; branching absent; tips knobbed.

There are four types of endothecial cells in *Argostemma*. The first two are "polarized." In the first type, in *A. bryophilum*, *A. hameliifolium* (Fig. 1A), *A. moultonii*, and *A. neurocalyx*, the cell margins become indistinct, and the endothecial layer can be described as consisting of long, horizontal, rather narrow bands with many close distinct transverse ribs and knobs. This type also occurs in the sister genus *Neurocalyx*. I have examined the endothecia of *Hamelia patens*, *Hoffmannia vesciculifera*, and *Xerococcus congestus*, belonging to Hameliieae, the sister tribe to Argostemmateae (B. Bremer, 1987), and they are of the same type.

In the second type (e.g., *A. enerve*, *A. gracile*, *A. havilandii*, and *A. psychotrioides* (Fig. 1B)), the cells are horizontally elongated and fusiform but with distinct cell margins. The ribs are not as close together, and the knobs are larger than in the first type.

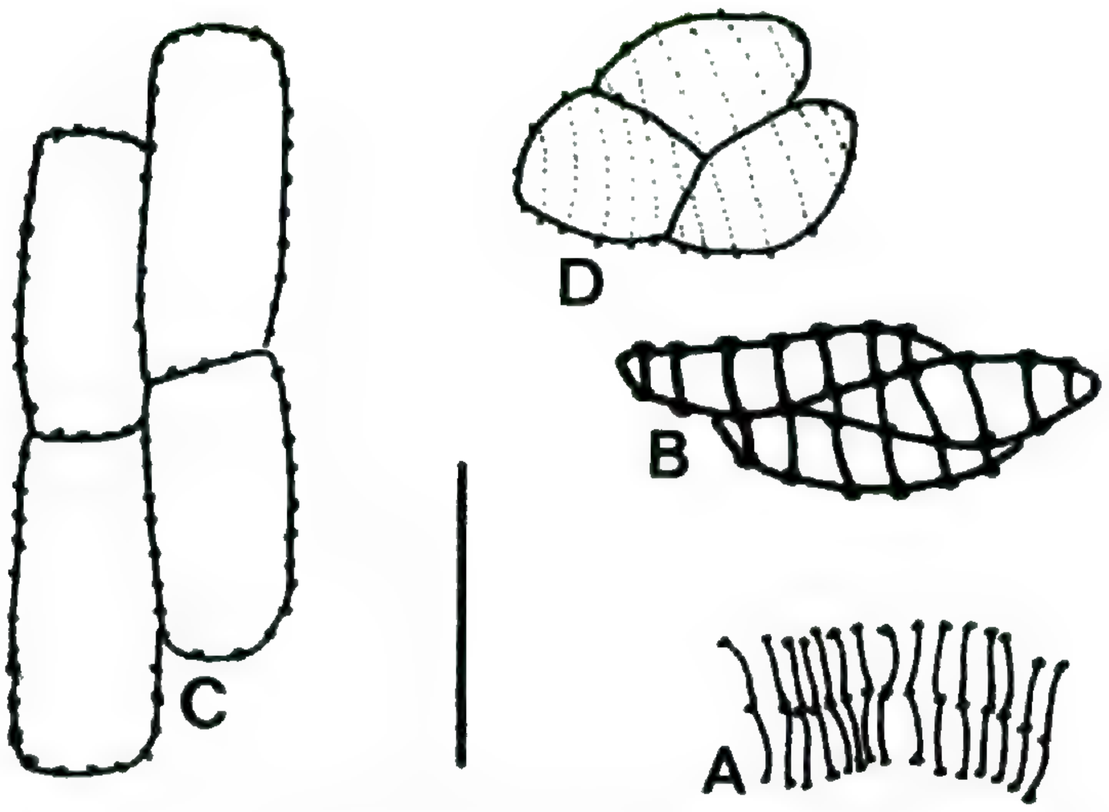


FIGURE 1. Endothecial cell thickenings. Scale bar = 50 μm—A. *Argostemma hameliifolium*.—B. *A. psychotrioides*.—C. *A. parvifolium*.—D. *A. borragineum*.

The third type could be classified as "radial." This type occurs in many species, e.g., *A. ophirense*, *A. parvifolium* (Fig. 1C), and *A. rupestre*. The cells are generally rectangular, with the longitudinal axis parallel to the dehiscence line. The cells are larger than in the "polarized" group. The transverse ribs are indistinct to hardly visible, and the knobs are smaller and look like a string of pearls surrounding the cell margins.

The fourth group consists solely of *A. borragineum* (Fig. 1D), whose endothecium is unique at least among the Borneo species of *Argostemma*. The cells are generally isodiametric and large. The ribs are indistinct, generally arranged parallel to the dehiscence line, and the knobs are indistinct. Since the ribs are not transversely arranged in relation to the anther-length axis, this type cannot be described as "radial," and since the knobs surround the cells on all margins, it cannot be described as "polarized."

Fruit. After anthesis the pedicels and peduncles become erect. These parts and the fruit, crowned with the calyx lobes, become fleshy and succulent. The fruit opens by an apical operculum. Such fleshy capsules are not uncommon in the tropics (Ehrendorfer, 1983: 829). Bakhuizen f. (1975) said about fruits of Rubiaceae:

> I am convinced that true capsules are not found in Rubiaceae. The rubiaceous "capsules" distinctly possess a (very) thin, often leathery endocarp. For that reason I propose to distinguish two main types of fruits in Rubiaceae: pyreniferous and non-pyreniferous. The pyreniferous fruits may be subdivided into pachypericarpous (having a thick, fleshy pericarp, known as "drupe") and leptopericarpous (having a (very) thin, dry, often leathery pericarp, so-called "capsule"). Non-pyreniferous fruits are conventionally termed "berry."

The fruit of *Argostemma* does not fit into this system. Although Bakhuizen f. was an expert on this genus, he had never seen it in the field (pers. comm.), and on dry material he had probably misinterpreted the fruit type.

When the fruit is open the fibrous endocarp separates from the remaining pericarp and splits into threads, which are visible in the opening. The septum, with the attached placentas, is also fibrous and will split. Among the resulting threads the numerous seeds will be exposed. Perhaps the threads prevent sudden dispersal. It is not uncommon to find specimens with many seeds germinated within the capsules. This kind of "vivipary" or germination in situ is described earlier from *Ophiorrhiza tomentosa* (Tan & Rao, 1981).

Placentation. Placentation is axile with the placentas (Fig. 2) attached at the top of the septum. The placentas are stalked, pendulous, fleshy, and in front view broadly ovoidal to kidney-shaped.

Seeds. *Argostemma* has numerous, small (ca. 0.5 mm), angular to ovoidal seeds (Fig. 3). The testa seems to be unique to this genus. The surface is mostly reticulate with a mamilla or a ring in each cell.

DISTRIBUTION

The maps (1–28) of *Argostemma* show that most localities are from northwestern Borneo. This is not because *Argostemma* is more common there, but indicates that this part, Sarawak, is botanically most well known. The same pattern can be seen in *Memecylon* (K. Bremer, 1983) and other genera. The few localities in Kalimantan result from comparatively few botanical expeditions, and large areas of former rainforest have been deforested.

Taxonomically, *Argostemma* in Borneo belongs to at least three different species groups which are more or less sympatric, and many species within the same group are sympatric. The distributions of different species of *Argostemma* are influenced by altitude, a fact that is hardly evident on the maps. *Argostemma elatostemma*, *A. densifolium*, *A. gaharuense*, *A. chaii*, *A. havilandii*, *A. calcicolum*, *A. trichosanthes*, *A. psychotrioides*, and *A. variegatum* grow only at low altitude; and *A. anisophyllum*, *A. dulitense*, *A. apiculatum*, *A. burttii*, *A. geesinkii*, *A. gracile*, *A. brachyantherum*, and *A. brookei* grow only at altitudes over 1,000 m. Some species occur at both low and high altitudes: *A. parvifolium*, *A. subfalcifolium*, *A. ophirense*, *A. rupestre*, *A. hameliifolium*, *A. moultonii*, and *A. borragineum*.

Most of the lowland species and those growing

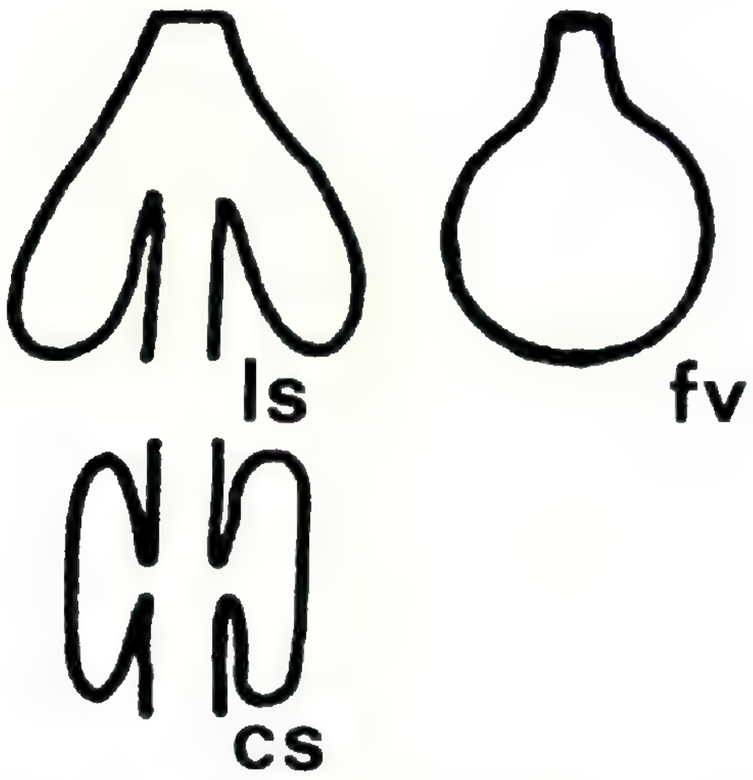


FIGURE 2. Placenta in ripe fruit (diagrammatic). ls, longitudinal section; fv, front view; cs, cross section.

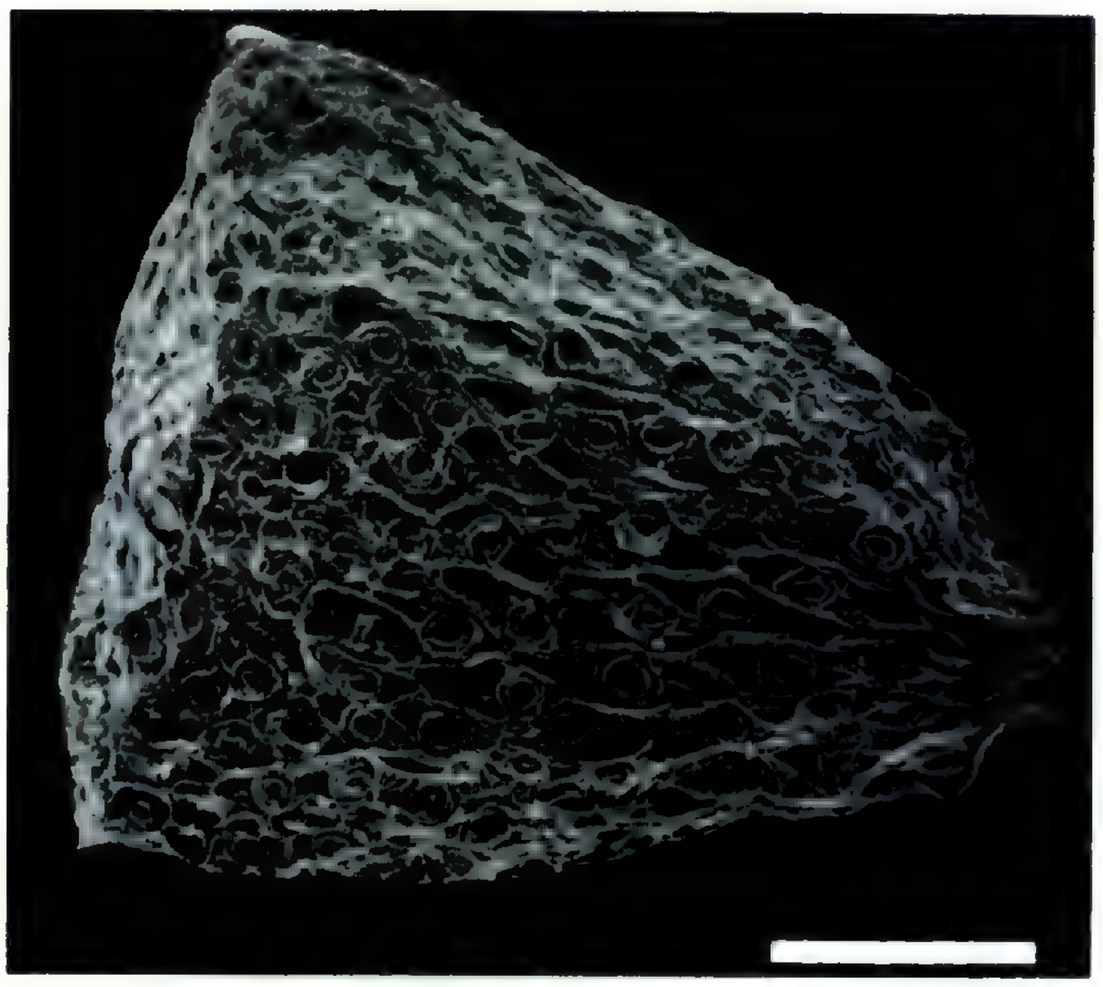


FIGURE 3. Seed of *A. borragineum* in SEM surface view. From *Bremer 1668* (S). Scale bar = 100 μm.

from low to high altitude are widespread, and many of them are sympatric. Of the eight species known only from a single locality each, four are from high altitude, the altitudes of three are unknown, and only one is from low altitude (ca. 700 m).

TAXONOMIC TREATMENT

Argostemma Wall. in Roxb., Flora Indica 2: 324, 1824. *Pomangium* Reinwardt, Syll. Pl. Rat. 2: 10. 1825. *Argostemmella* Ridley, J. Bot. 65: 41. 1927. TYPE: *Argostemma sarmentosum* Wall. (Pfeiffer, Nomenclator Botanicus, 1873).

Erect, suberect, or creeping herbs, isophyllous or anisophyllous, glabrous to densely pubescent, often succulent. Stem usually unbranched or slightly branched, often succulent; internodes very short to 85 mm long. Leaves opposite or verticillate, when anisophyllous unequal, scattered along the stems, or decussate, or distichous, or rosulate on a short stem, or apically rosulate on a well-developed stem, herbaceous, or coriaceous, or membranaceous; stipules interpetiolar, persistent or deciduous, small to large, usually entire, rarely slightly cleft or fringed, with colleters near the base on the adaxial side or rarely at the apex, if fringed then with a colleter at each point; midrib distinct, the primary veins distinct or obscure, the veinlets generally not visible. Anisophyllous leaves with the small (nanophyllous) leaf persistent or deciduous, similar in shape to the stipules or to the larger leaf, often cordiform, with or without a short petiole. Inflorescences terminal, subterminal or rarely axillary, solitary or a few together, 1–160-flowered, cymose, corymbiform to umbelliform, glabrous or pubescent; peduncles up to 10 cm long or rarely absent; bracts often persistent and small; pedicels in fruiting stage succulent. Flowers (4–)5(–6)-merous, actinomorphic or rarely zygomorphic, perfect. Calyx with a very short tube; lobes shorter or rarely as long as the corolla lobes, erect or spreading to reflexed, in fruiting stage succulent, glabrous or pubescent. Corolla with valvate aestivation, white, sometimes with green nectar guides at the base, rotate, or subcampanulate but with recurved lobes, or campanulate, 3–12 mm long, with the tube more than ⅔ as long as the lobes, externally glabrous or pubescent, internally glabrous or pubescent with the pubescence often only on the lobes; lobes erect-spreading to recurved or reflexed. Stamens 4 or 5(6), equal in number to the corolla lobes, inserted near the base of the corolla, introrse, coherent into an anther cone or free; if coherent then fused along the whole anther or partially so; thecae with two sacs (loculi); anthers bright yellow to cream-colored, erect or slightly upcurved; filaments free, short or long, mostly equal, erect or rarely curved, smooth, glabrous; sacs opening by vertical slits, rarely with pores; apical appendages ca. ½ as long as the anther or absent, thin to coriaceous, smooth to papillose; connectives distinct to indistinct from the thecae, smooth to papillose. Ovary 2-celled; style filiform, glabrous to pubescent, shortly to long-exserted, with a capitate, clavate, or scarcely widened stigma, shallowly to rarely distinctly bifid. Fruit a succulent capsule with a fibrous endocarp, opening by an apical operculum, smooth or rarely with emergences, furrows, or ribs (at least on dry specimens), glabrous to densely pubescent. Seeds brown, numerous, minute, angular or ovoid, the testa generally reticulate with a central mamilla or ring in each cavity.

KEY TO THE SPECIES OF *ARGOSTEMMA* IN BORNEO

1a. Leaves more or less condensed into an apical rosette. Stamens free at least after anthesis 2
2a. Leaves membranaceous. Corolla campanulate, not deeply cleft. Stamens opening by apical pores ..... 28. *A. neurocalyx*
2b. Leaves herbaceous to coriaceous. Corolla rotate, cleft to near the base. Stamens opening by longitudinal slits ..... 17. *A. chaii*
1b. Leaves scattered along the stem, not condensed into an apical rosette. Stamens connate or free 3
3a. Leaves anisophyllous 4
(See also the insufficiently known 16. *A. flavescens* not included in the key.)
4a. Corolla cleft to near the base, starlike; lobes spreading, erect-spreading, or rarely reflexed, never recurved. Stamens as high as the style with stigma only slightly exserted 5
5a. Flowers slightly zygomorphic. Calyx lobes almost as long as the corolla lobes. Filaments unequal, curved ..... 1. *A. parvifolium*
5b. Flowers actinomorphic. Calyx lobes much shorter than the corolla lobes. Filaments equal, straight 6
6a. Plant creeping. The larger of the anisophyllous leaf pair basally very unequal-sided. Peduncles and the outside of the corolla pubescent. Anther cone black when pressed and dried ..... 2. *A. elatostemma*
6b. Plant erect or creeping. The larger of the anisophyllous leaf pair unequal- or equal-sided. Peduncles and the outside of the corolla generally glabrous. Anther cone not black when pressed and dried 7
7a. Larger leaf of the anisophyllous pair generally subfalcate; nanophyllous leaves lanceolate. Fruits with longitudinal furrows ..... 3. *A. subfalcifolium*
7b. Larger leaf of the anisophyllous pair not subfalcate; nanophyllous leaves cordiform, ovate or lanceolate. Fruits without furrows but rarely with 5 ribs 8
8a. The larger of the anisophyllous leaf pair basally unequal-sided or oblique; nanophyllous leaves cordiform 9
9a. Stems and leaf veins pubescent. Leaves herbaceous or coriaceous. Corolla up to ca. 6 mm long 10
10a. Plant a rosette or creeping with generally short internodes and obovate to oblanceolate leaves ..... 4. *A. densifolium*
10b. Plant erect with obvious internodes and lanceolate to linear leaves ..... 5. *A. ophirense*
9b. Stems and leaves glabrous or glabrate. Leaves herbaceous to membranaceous. Corolla 8–9 mm long ..... 6. *A. anisophyllum*
8b. The larger of the anisophyllous leaf pair basally equal-sided; nanophyllous leaves ovate, elliptic, or lanceolate 11
11a. Leaves without stiff pluricellular hairs 12
12a. Leaves pubescent. Corolla ca. 4 mm long, lobes reflexed. Fruit with 5 ribs ..... 12. *A. gaharuense*
12b. Leaves glabrous. Corolla more than 9 mm long, lobes not reflexed. Fruit without ribs 13
13a. Stems pubescent. Leaves coriaceous with pale lower surfaces. Apical appendage ca. ⅓ of the anther length ..... 7. *A. dulitense*
13b. Stems and whole plant glabrous. Leaves herbaceous to membranaceous, both sides of the same color. Apical appendage ca. ¼ of the anther length ..... 8. *A. apiculatum*
11b. Leaves with stiff pluricellular hairs in 3 or 5 rows 14
14a. Corolla ca. 9 mm long or more; lobes ovate, spreading. Apical appendage less than ¼ of the anther length ..... 9. *A. burttii*
14b. Corolla ca. 7 mm long or less; lobes ovate or lanceolate, erect-spreading. Apical appendage ca. ⅓ of the anther length 15
15a. Corolla lobes lanceolate, not pink in press. Stipules ovate to lanceolate ..... 10. *A. rupestre*
15b. Corolla lobes ovate, often pink in press. Stipules ovate to cordiform ..... 11. *A. geesinkii*
4b. Corolla generally cleft ½ its length or less; lobes recurved, erect, or spreading. Stamens shorter than the much-exserted stigma 16
16a. Corolla cleft to less than ⅓ its length; lobes erect or spreading 17
17a. Leaves distichous. Flowers solitary, almost sessile. Stigma disc-shaped and distinctly bifid ..... 18. *A. gracile*
17b. Leaves not distichous. Flowers in up to 12-flowered inflorescences, rarely solitary, with peduncles. Stigma capitate and indistinctly bifid ..... 19. *A. brachyantherum*
16b. Corolla cleft to at least ½ its length; lobes recurved 18
18a. Corolla cleft to near the base. Stamens free at anthesis. Stigma slightly capitate ..... 20. *A. brookei*
18b. Corolla cleft to ca. ½ its length. Stamens connate at anthesis. Stigma clavate 19

19a. Calyx lobes 2–6 mm long, distinctly reflexed. Style generally glabrous 20
20a. Plant erect. Leaves basally acute to cuneate or attenuate and equal-sided ..... 25. *A. psychotrioides*
20b. Plant creeping. Leaves basally rounded to obtuse and unequal-sided ..... 26. *A. variegatum*
19b. Calyx lobes up to 1 mm long, erect. Style generally pubescent 21
21a. Stems green, smooth. Nanophyllous leaves persistent, cordiform ..... 24. *A. humifusum*
21b. Stems in lower part generally pale brown to gray with elevated corky to papery longitudinal ridges. Nanophyllous leaves deciduous, lanceolate to linear ..... 21. *A. havilandii*

3b. Leaves isophyllous 22
22a. Corolla cleft to near the base, starlike; lobes spreading or reflexed 23
23a. Leaves membranaceous. Stipules persistent, broadly ovate to cordiform. Inflorescences 1–2-flowered. Apical anther appendages almost wanting ..... 27. *A. bryophilum*
23b. Leaves herbaceous. Stipules deciduous. Inflorescences 3–40-flowered. Apical anther appendages form open cylinders (Figs. 16, 17) 24
24a. Plant 10–100 cm, erect. Stamens with short filaments and short apical appendages ..... 13. *A. hameliifolium*
24b. Plant 2–40 cm, more or less creeping. Stamens with long filaments and long apical appendages ..... 14. *A. moultonii*
22b. Corolla cleft to ca. ½ its length; lobes recurved 25
25a. Stems generally pale brown to gray with elevated corky to papery longitudinal ridges, without scars. Anther cone with connate apical appendages. Stigma clavate. Fruit smooth 26
26a. Plant wholly covered with a dense indumentum of stiff long hairs ..... 23. *A. trichosanthes*
26b. Plant slightly pubescent with soft hairs ..... 22. *A. calcicolum*
25b. Stems generally black with wavy scars, without longitudinal ridges. Anther cone with free apical appendages. Stigma capitate. Fruit with emergences ..... 15. *A. borragineum*

1. Argostemma parvifolium Benn., Plantae Javanicae Rariores. 1: 96. 1838. TYPE: Java(?), Sumatra: *Horsfield s.n.* (holotype, BM). Figure 4.

Erect, anisophyllous, densely pubescent herb. Stem 15–50 cm long, usually unbranched, densely pubescent; internodes 6–15 mm. Leaves opposite, very unequal; stipules persistent, 4–7 mm long, ovate to cordiform, acute to acuminate at apex; larger leaves of the anisophyllous pairs with pubescent petioles 3–6 mm long, the lamina 4–13 × 1.4–3 cm, generally oblanceolate or obovate to elliptic, basally acute and oblique, marginally serrulate, apically acuminate, herbaceous, pubescent on both surfaces; midrib and primary veins (9–18 pairs) distinct. Nanophyllous leaves persistent, 5–10(–32) mm long, cordiform to ovate. Inflorescences solitary or a few together, 1–9-flowered, corymbiform, pubescent; peduncle 0.9–3.2 cm long, bracts to 1 cm long, broadly ovate to lanceolate; lateral branches, if present, to 1.5 cm long; pedicels 0.7–1.4 cm long. Flowers 5-merous, slightly zygomorphic; calyx lobes 4–6 mm long, triangular to ovate, acuminate, pubescent; corolla 5–6 mm long, cleft to near the base, externally pubescent, internally glabrous; lobes triangular, spreading. Stamens 6–10 mm long, coherent; anther cells and apical appendages connate except for the most apical part; anther cone narrowly ovoid, slightly upcurved; filaments short, unequal, curved; sacs opening completely and longitudinally; apical appendage ca. ⅓ the anther length, thin and smooth; connective distinct, smooth. Style 6–10 mm long, glabrous with a slightly capitate stigma, shortly exserted. Fruit without furrows or ribs.

There is a question mark after Java on the label of the type specimen, and on the label there is also written "Sumatra," as is indicated in the protologue. *Argostemma parvifolium* grows on sandstone, sandy banks, and cliffs near streams, from 350 to 1,450 m. The species is based on non-Borneo material. The habit of the Borneo population is similar to the type of *A. parvifolium* var. *involucratum* (Hemsl.) Bakh. f. I have not studied the complete variation of *A. parvifolium* outside Borneo, and so for now I avoid infraspecific taxa. Except for the inner floral parts, the whole plant is densely covered by long soft hairs. As in all *Argostemma* species, the flowers are slightly pendulous at anthesis, and in this species the flowers are slightly zygomorphic. The rotate corolla has at its center distinct green nectar guides on the upper half. The anther cone is bent upwards and the stamens, in the upper half of the flower, have curved filaments. It is the only Borneo species with these characters.

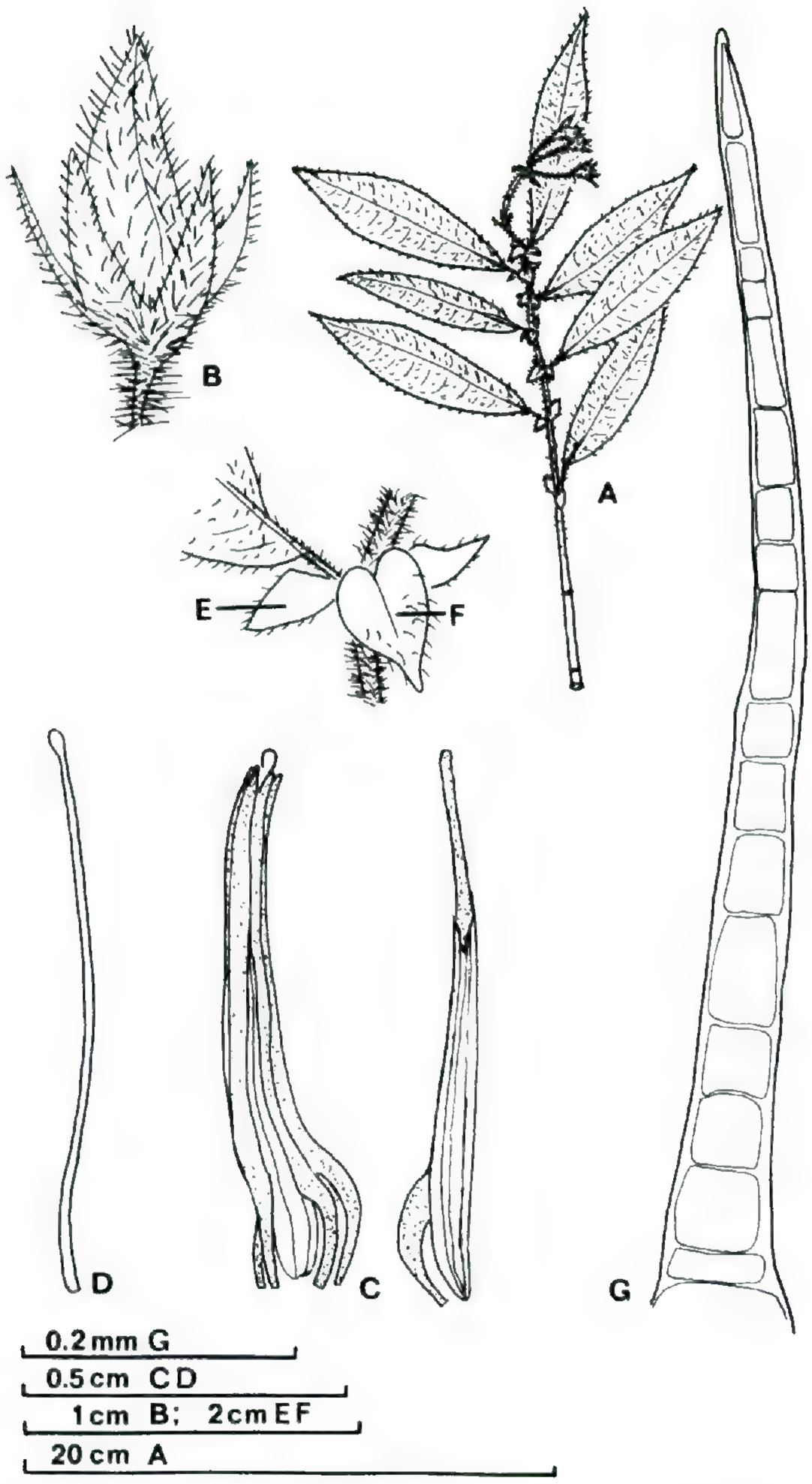


FIGURE 4. *Argostemma parvifolium.*—A. Branch.—B. Flower bud.—C. Anthers.—D. Style.—E. Stipule.—F. Nanophyllous leaf.—G. Hair from outer surface of the corolla. A, C–F from *Burtt 11521* (E); B, G from *Winkler 767* (L).

Additional specimens examined. BORNEO. SARAWAK: 1st Div., Gunong Berumput, 3,500 ft., 1962, *Burtt & Woods 2816* (E, SAR); 1st Div., Sabal, 350 m, 1979, *Bremer 1652* (S, SAR); 4th Div., Mt. Lambir, 1962, *Burtt & Woods 2366* (E, SAR); 1979, *Burtt 11521* (E, S); 1,200–1,500 ft., 1978, *Burtt 11640* (E, S); 1,450 m, 1976, *Ilias & Yeo S38349* (L, SAR); 7th Div., Hose Mts., 800 m, 1975, *Chai et al. S37338* (K, L, MO, SAR). KALIMANTAN: W Prov., Bidang Menabei, 700 m, 1924, *Winkler 767* (L).

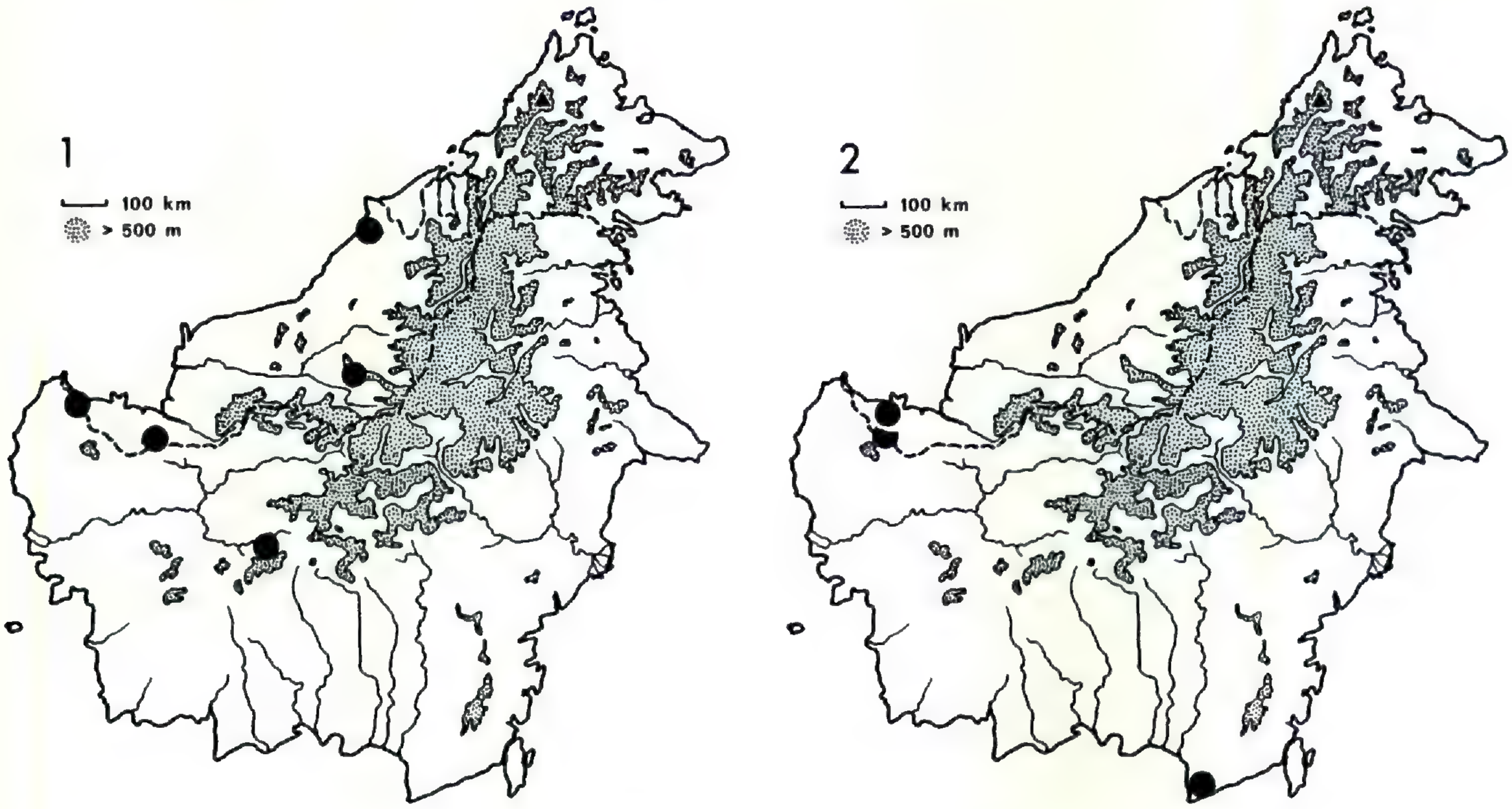
2. Argostemma elatostemma Hook. f., The Flora of British India 3(7): 45. 1880. TYPE: Penang, *Griffith s.n.* (lectotype, K; Bakh. f. in herb., confirmed here). Figure 5.

A. motleyi Ridley, J. Bot. 65: 39. 1927. TYPE: Borneo: Bangarmassing, 1857–1858, *Motley 1174* (holotype, K).

Creeping, anisophyllous herb. Stem 2–36 cm long, slightly branched or unbranched, pubescent; internodes 5–25 mm. Leaves opposite, very unequal; stipules persistent, 4–10 mm long, ovate to broadly ovate or cordiform, acuminate to acute at apex; larger leaves of anisophyllous pairs with pubescent petioles 4–7 mm long; lamina 2–9.5 × 1.3–3.5 cm, obovate to ovate and slightly subfalcate, basally subcordate to auriculate with the lobes unequal, marginally entire, apically acute, herbaceous, glabrous above and with a few hairs on the veins below; midrib and primary veins (5–11 pairs) distinct. Nanophyllous leaves persistent, 4–12 mm long, cordiform. Inflorescences solitary, 1–20-flowered, densely corymbiform or umbelliform, pubescent; peduncle 0.8–4 cm long; bracts to 0.7 cm long, ovate or lanceolate; lateral branches, if present, to 2.5 cm long; pedicels 0.4–1 cm long. Flowers 5-merous; calyx lobes 1–2 mm long, ovate to triangular, acute, pubescent; corolla 5–6 mm long, cleft to near the base, externally pubescent, internally glabrous; lobes ovate to lanceolate, spreading. Stamens 5–6 mm long, coherent; anther cells and apical appendages connate; anther cone ovoid, straight; filaments short, equal, straight; sacs opening completely longitudinally; apical appendage ca. ⅓ the anther length, thin and smooth; connective indistinctly passing over to the thecae, smooth. Style 5–7 mm long, glabrous with a slightly capitate stigma, shortly exserted. Fruit without furrows or ribs.

Hooker based *A. elatostemma* on two collections, by *Lobb* and *Griffith*. Both are suitable for lectotypification. Bakhuizen f. (in herb.) selected the *Griffith* specimen in K, and I follow his choice.

Argostemma elatostemma grows in wet shady forests, from 100 to 750 m. It occurs in the first division of Sarawak and on the southern tip of Kalimantan. The collections from these two areas are different. The Sarawak specimens are alike and similar to the type collection from the Malay Peninsula, while the Kalimantan specimen, described as *A. motleyi*, agrees well with the type of *A. elatostemma* var. *obovata* King (1904). In this study I have not dealt with any infraspecific taxa because I have not yet studied the complete variation outside Borneo. The specimen from Kalimantan is smaller with shorter leaves, and there is only one flower in the collection. *Argostemma elatostemma* is characterized by its creeping habit, rooting at the nodes, silvery mottled leaves, and unequal leaf bases. The stems, petioles, veins of the lower leaf surfaces, and the inflorescences are densely pubescent. The flowers are rotate with a long pale anther cone which blackens in the press.



MAPS 1, 2, Distributions in Borneo.—1. *Argostemma parvifolium*—2. *A. elatostemma*.

Additional specimens examined. BORNEO. SARAWAK: 1st Div., Mt. Matang 2,300 ft., 1979, *Bremer 1722* (S, SAR); 500 ft., 1954, *Brooke 9465* (L); 1962, *Burtt & Woods 1959* (E); 1,500 ft., 1929, *Clemens 20912* (NY); 2,500–3,000 ft., *Mjöberg s.n.* (US); 1893, *Ridley 12303* (BM, K, SING); 1st Div., Bau, S of Bukit Krian, 100 m, 1964, *Anderson et al. S20288* (L); Gunong Tra-an, 300 ft., 1975, *Burtt 8175* (E); 1893, *Ridley 11753* (BM, K, SING).

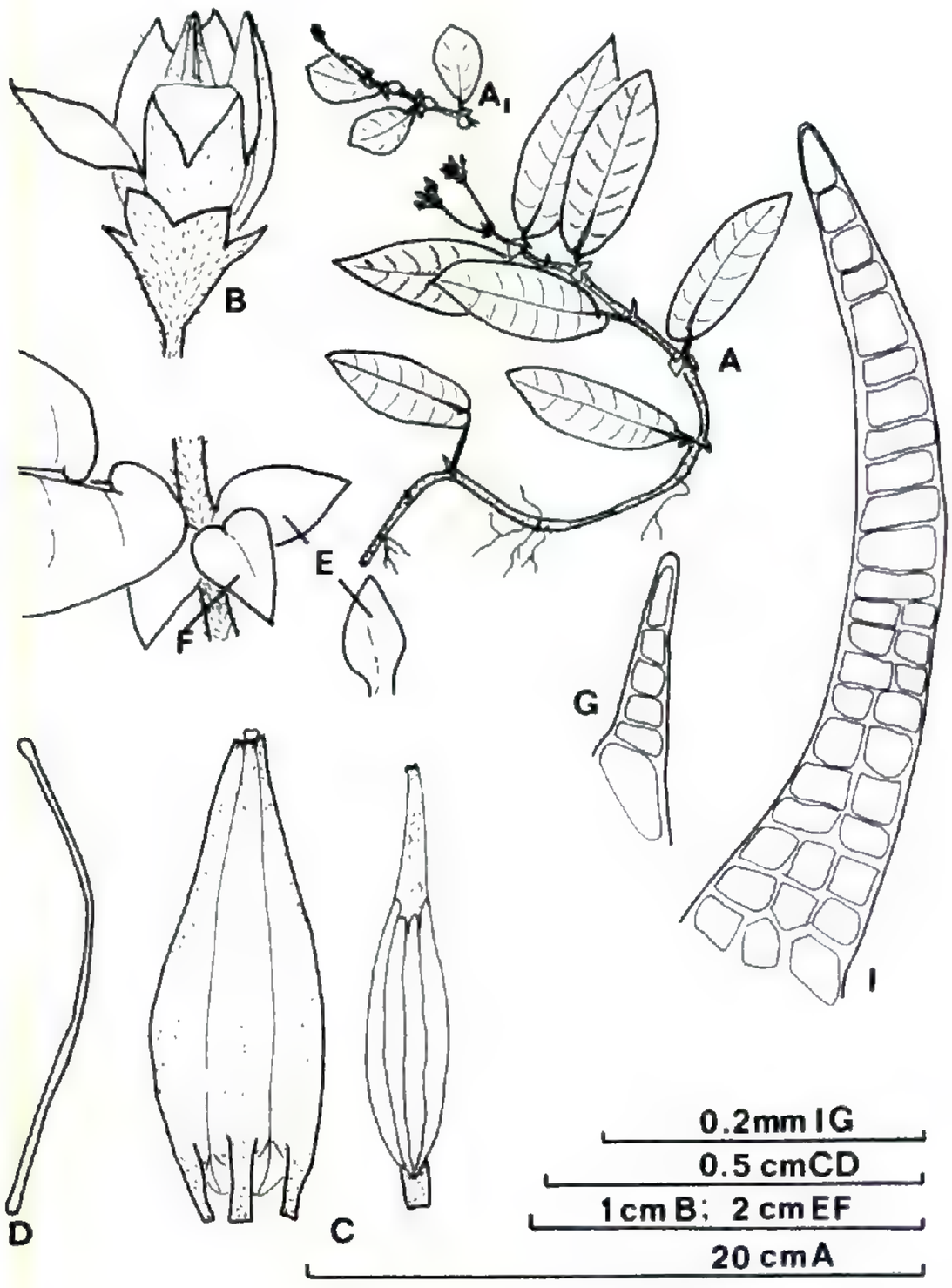
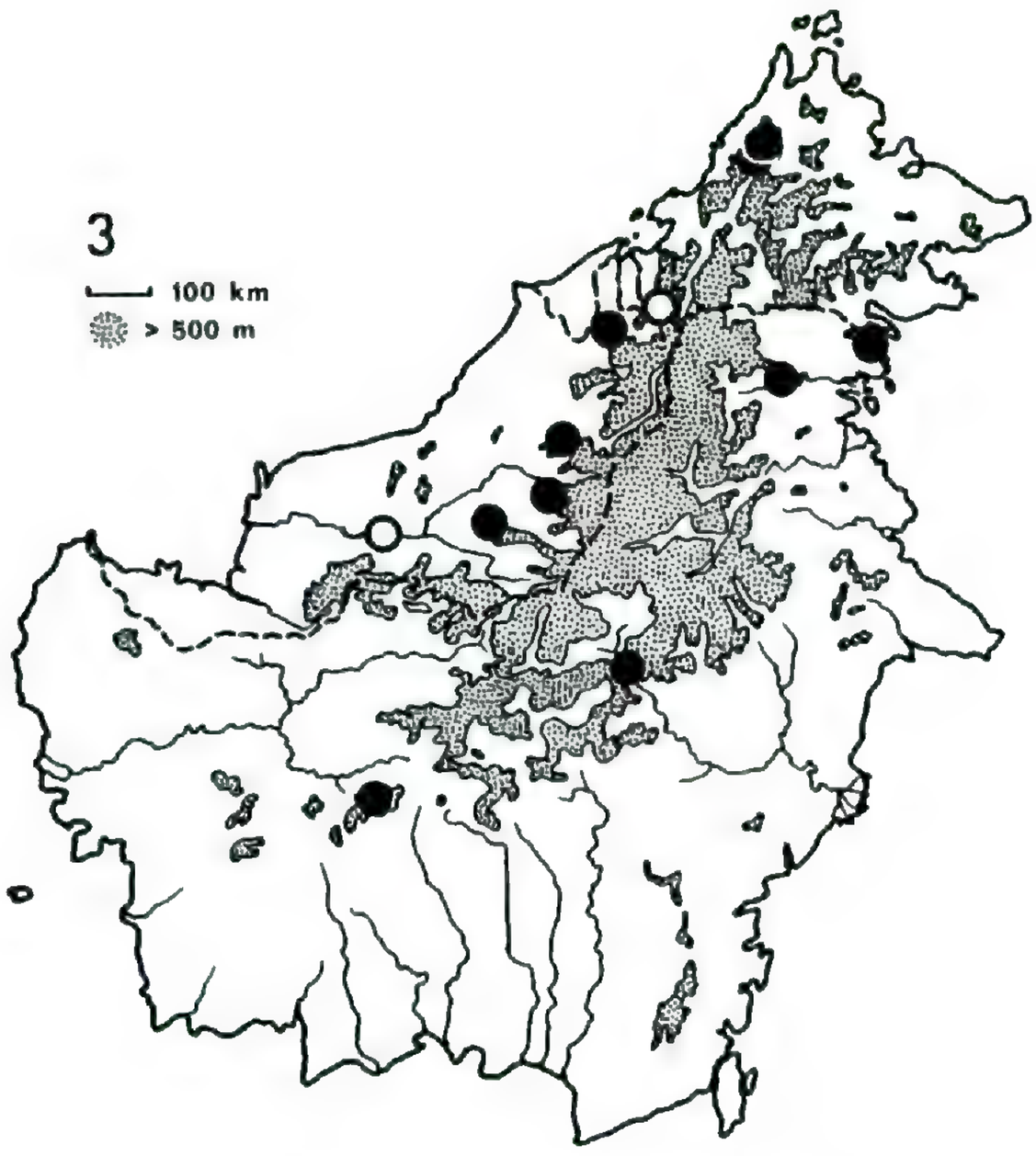
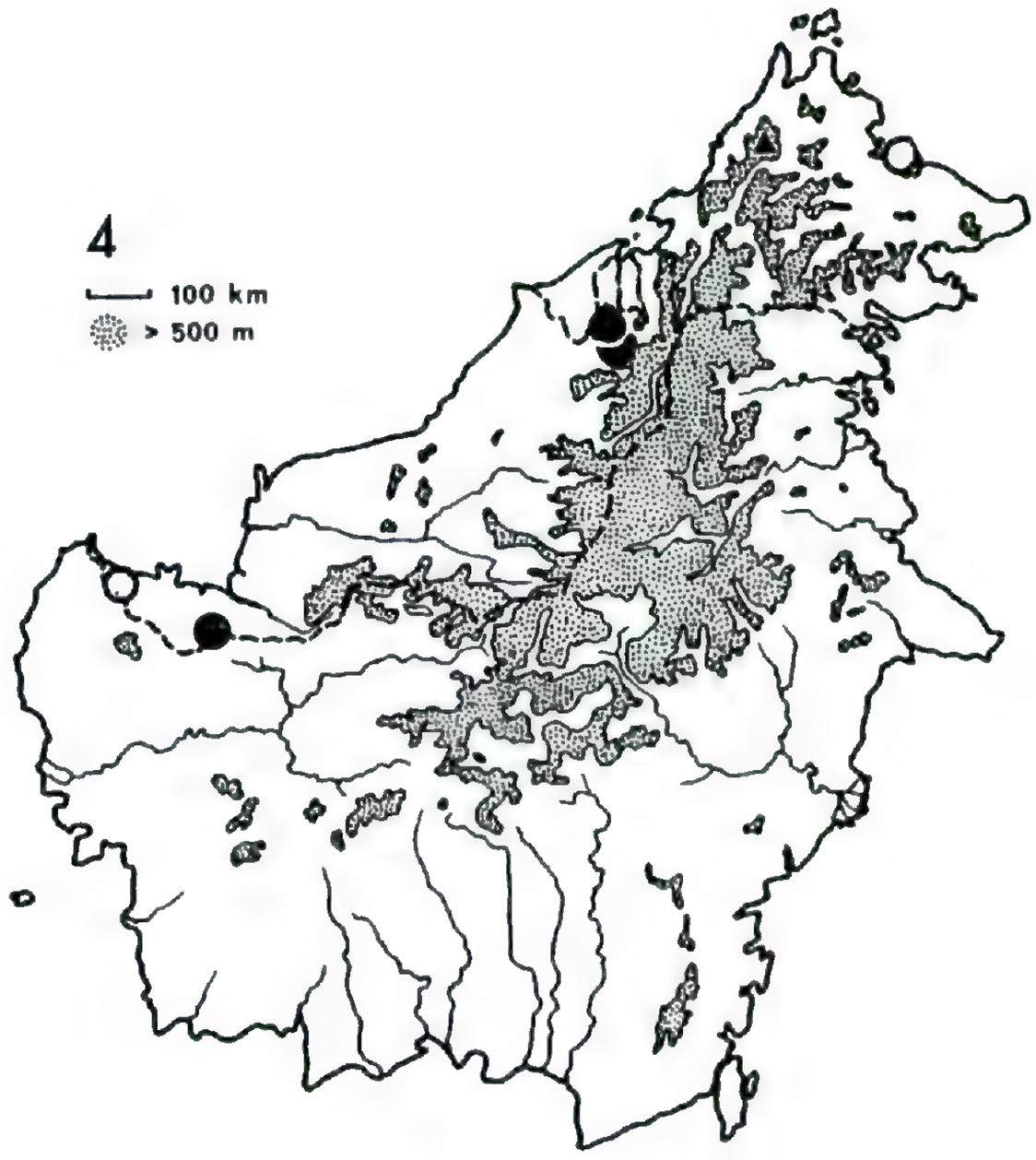


FIGURE 5. *Argostemma elatostemma.*—A. Habit.—B. Flower.—C. Anthers.—D. Style.—E. Stipules.—F. Nanophyllous leaf.—G. Hair from outer surface of the corolla.—I. Stiff, pluricellular leaf hair. A–I from *Bremer 1722* (S); A_1 from *Motley 1174* (K).

3. Argostemma subfalcifolium Bakh. f., Blumea 7: 332. 1953. TYPE: Borneo. Sarawak: Mt. Dulit, Dulit trail, ca. 100 m, 1932, *Richards 2090A* (holotype, K). Figure 6.

Erect, anisophyllous herb. Stem 15–35 cm long, unbranched, glabrous or sparsely pubescent; internodes 7–23(–45) mm long. Leaves opposite, very unequal; stipules deciduous or persistent, 5–12 mm long, ovate to lanceolate or broadly ovate, acute at apex; larger leaves of the anisophyllous pairs with glabrous or sparsely pubescent petioles 2–12 mm long; lamina 7–22 × 1.5–5 cm, generally subfalcate to lanceolate or ovate to obovate, basally acute and oblique, marginally entire or rarely serrulate, apically acuminate or rarely acute, herbaceous, generally glabrous on both surfaces or finely pubescent on the veins below; midrib and primary veins (6–15 pairs) distinct, rarely obscure. Nanophyllous leaves deciduous or persistent, 7–12 mm long, lanceolate. Inflorescences solitary or a few together, to 45-flowered, laxly corymbiform; peduncle 1.5–6 cm long, glabrous; bracts to 0.7 cm long, ovate to lanceolate; lateral branches 1–3.3 cm long, glabrous or pubescent; pedicels 0.5–1.2 cm long, pubescent. Flowers 5-merous; calyx lobes 2–4 mm long, ovate to triangular to lanceo-





MAPS 3, 4. Distributions in Borneo.—3. *Argostemma subfalcifolium*.—4. *A. densifolium*.

late, acute to acuminate, ± glabrous; corolla 5–6.5 mm long, cleft to near the base, glabrate on both sides; lobes ovate to lanceolate, spreading. Stamens 5–7 mm long, coherent; anther cells and apical appendages connate except for the most apical part; anther cone ovoid, straight; filaments short, equal, straight; sacs opening completely longitudinally; apical appendage ca. ⅓ the anther length, thin and smooth; connective indistinctly passing over to the thecae, smooth. Style 5–7.5 mm long, glabrous with a slightly capitate stigma, shortly exserted. Fruit with distinct longitudinal furrows.

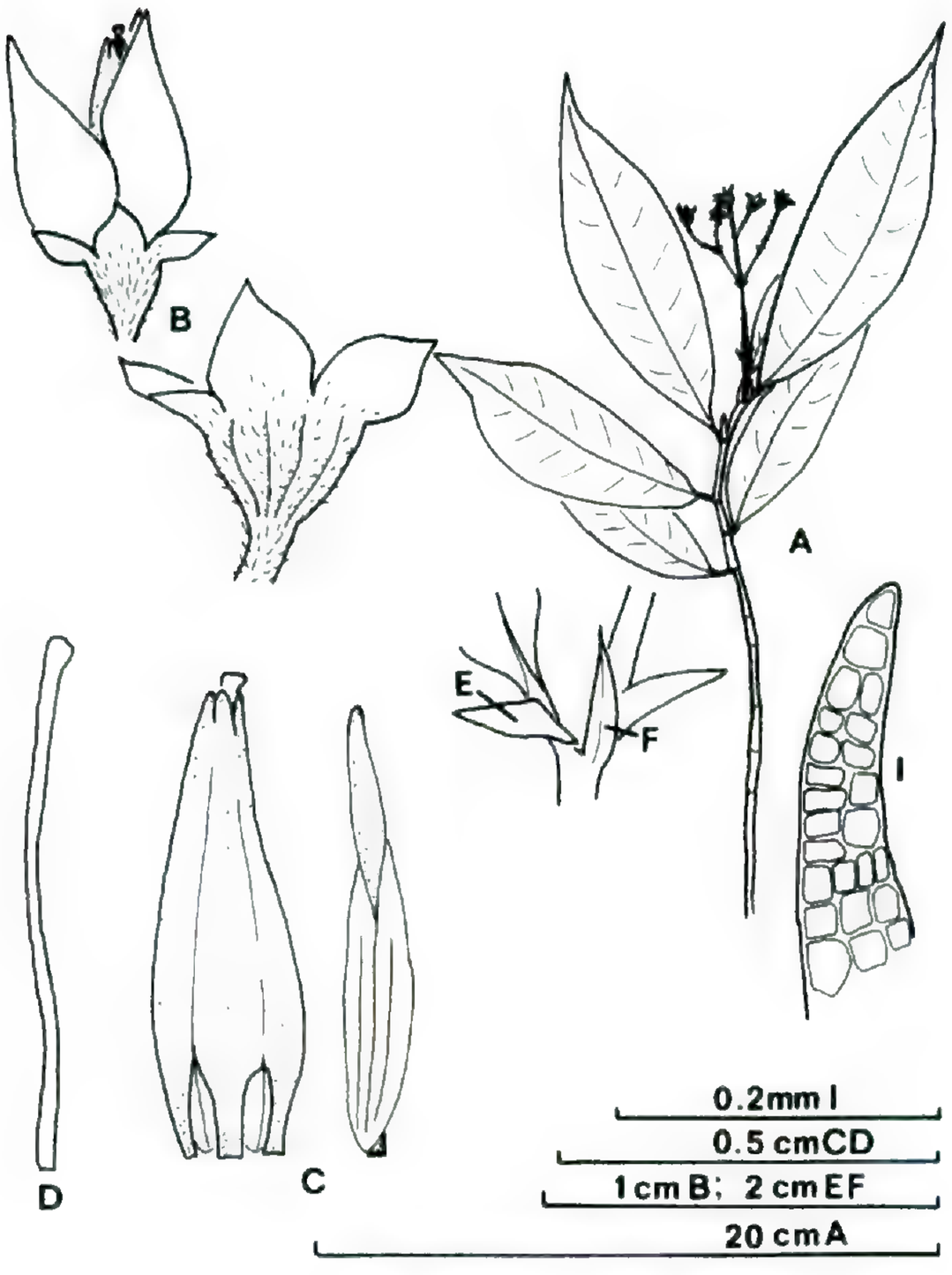


FIGURE 6. *Argostemma subfalcifolium*.—A. Flowering branch.—B. Flower and fruit.—C. Anthers.—D. Style.—E. Stipule.—F. Nanophyllous leaf.—I. Stiff, pluricellular leaf hair. A, B (fruit) from *Clemens 30650* (NY); B (flower)–I from *Burtt 8228* (E).

Argostemma subfalcifolium grows in damp shady places in the lowland rainforest at altitudes from 100 to 1,500 m. It tends to have subfalcate leaves. The species is characterized by rather long calyx lobes and by furrowed fruits. The stems are glabrate and sometimes slightly pubescent. The peduncles and lateral branches of the inflorescence are mostly glabrous, whereas the pedicels, ovary, and lower part of the calyx lobes are pubescent. The flowers are rotate, and the buds are distinctly angular in cross section. The staminal cone is high. From the outside the thecae are completely shed by the connectives but can be seen as immersed sacs between the filaments.

There are a few aberrant specimens. *Anderson 4090*, from Bako in Sarawak, consists of very small plants. They were collected on fallen tree trunks and have a peculiar habit, but no other details contradict inclusion in this species. *Meijer 2286*, from Kalimantan, has nearly cordiform nanophyllous leaves, but otherwise fits. *Brooke 9194*, from Sarawak, has very narrow leaves with obscure primary veins.

Additional specimens examined. BORNEO. SABAH: W Coast Res., Kinabulu, Penibukan, 4,000 ft., 1933, *Clemens 30650* (BM, BO, GH, K, L, NY, UC); Penibukan, 4,000 ft., 1933, *Clemens 31963* (BM, GH, L, NY, UC); Gurulau ridge, 30–40 m, 1965, *Kanis & Kuripin 53966* (K, L). SARAWAK: 4th Div., Gunong Mulu, 100 ft., 1975, *Burtt 8228* (E); 130 m, *Hansen 20* (K); 5th Div., one day from Maputi, 2,000 ft., 1955, *Brooke 10183* (BM, L); 5th Div., Ulu Sungei Melinau, Paku, 400 ft., 1961, *Anderson 4090* (L); 7th Div., Hose Mts., Ulu Tamalad, 900 m, 1964, *Ashton S17606* (K, L); 7th Div., ridge E of Sungei Tellini, 2,800 ft., 1987, *Burtt 11419* (E). KALIMANTAN: W Prov., Bukit Mehipit, 500 m, 1924, *Winkler 660* (HBG); W Prov., Bidang Menabai, 700 m, 1924, *Winkler 791* (HBG, NY); E Prov., W Kutei, near Kemoel, 1,600 m, 1925, *Endert 4327* (BO, L); E Prov., Camp Mailinau, 1982, *Axelius 314* (S); Nanukan, N of Tarakan, low alt., 1953, *Meijer 2286* (K, L).

4. Argostemma densifolium Ridley, J. Bot. 65: 39. 1927. TYPE: Borneo. Puak (near Lundu?), 1894, *Ridley 12448* (holotype, K; isotype, SING). Figure 7.

Argostemma densifolium var. *latifolium* Ridley, J. Bot. 65: 40. 1927. TYPE: British North Borneo: Bongaya, 1897, *Ridley s.n.* (holotype, SING).

Rosette or creeping, anisophyllous herb. Stem 5–16 cm long, slightly branched or unbranched, pubescent; internodes very short to 15 mm. Leaves opposite, very unequal; stipules persistent, 4–6 mm long, ovate to cordiform, obtuse to acuminate at apex; larger leaves of the anisophyllous pairs with pubescent petioles to 5 mm long; lamina 4–14 × 1–4.5 cm, obovate to oblanceolate, basally acute to subcordate and oblique or with the lobes unequal, marginally entire or serrulate, apically obtuse or acute, herbaceous, glabrous above and pubescent on the veins below; midrib and primary veins (10–17 pairs) distinct. Nanophyllous leaves persistent, 4–10 mm long, cordiform. Inflorescences solitary or a few together, 3–20-flowered, laxly to densely corymbiform; peduncle 1.5–7 cm long, pubescent or rarely glabrous; bracts to 0.2 cm long, ovate or lanceolate; lateral branches, if present, to 3 cm long, glabrous or pubescent; pedicels to 2 cm long, pubescent or rarely glabrous. Flowers 5-merous; calyx lobes ca. 1 mm long, stiff, narrowly triangular, acute, pubescent; corolla ca. 5 mm long, cleft to near the base, glabrous on both surfaces, the lobes lanceolate, spreading. Stamens ca. 5 mm long, coherent; anther cells and apical appendages connate; anther cone ovoid, straight; filaments short; sacs opening completely longitudinally(?); apical appendage thin and smooth; connective indistinctly passing over to the thecae, smooth. Style ca. 6 mm long, glabrous with a slightly capitate stigma, shortly exserted. Fruit without furrows or ribs.

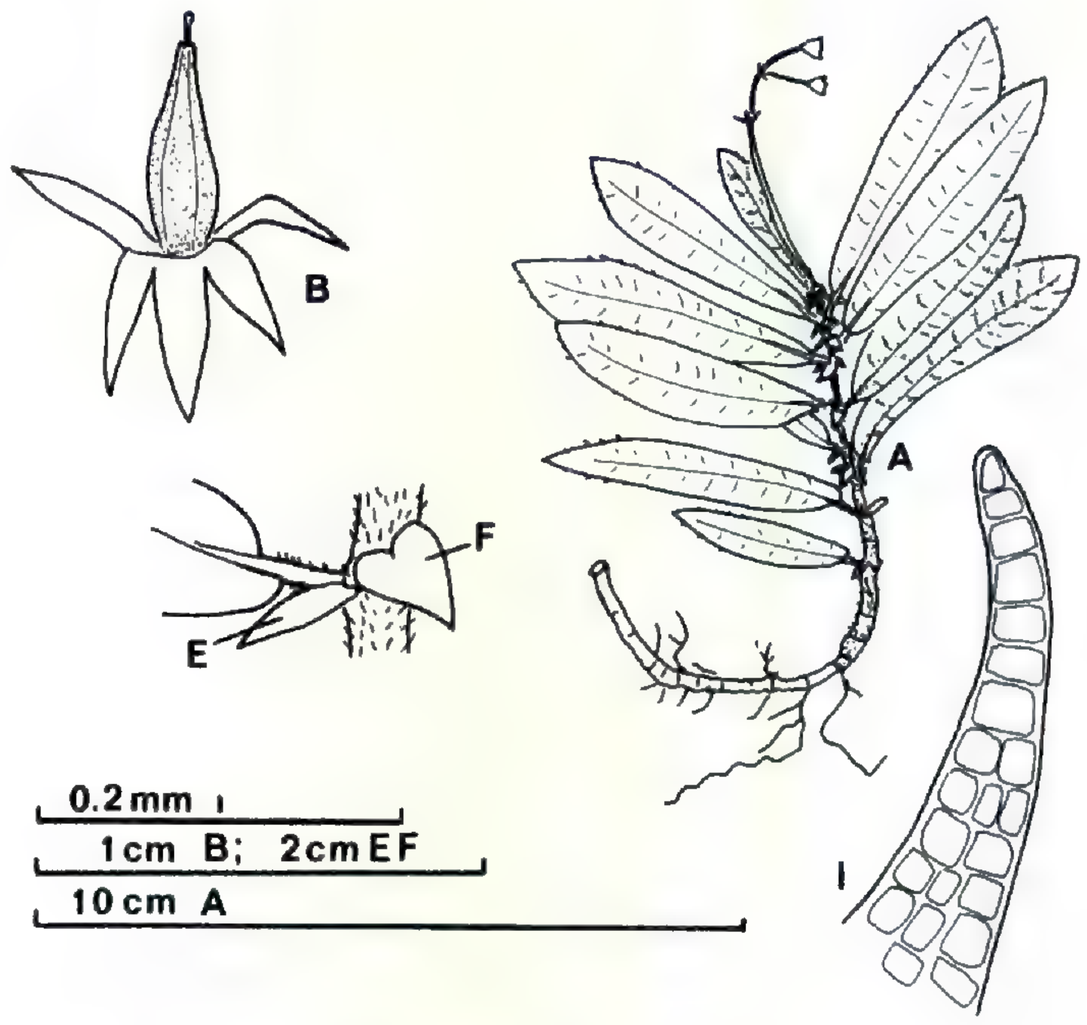


FIGURE 7. *Argostemma densifolium.*—A. Habit.—B. Flower.—E. Stipule.—F. Nanophyllous leaf.—I. Stiff, pluricellular leaf hair. A, E–I from *Sylvester Tong S34346* (K); B from *Nielsen 538* (K).

There are only a few collections of this species, and they are in bad condition. The description of the flowers was prepared from undissected flowers, and so some information is lacking. The scanty information on its habitat indicates that it grows on steep sandstone slopes and on gentle slopes on litter. It was collected at low altitude in southwestern and northeastern parts of Sarawak and in Sabah. I have not managed to find the locality "Bongaya," but according to Steenis-Kruseman (1950), Ridley visited the Kudat, Sandakan, and Lubak Bay in 1897, so it must be somewhere in this area. Ridley (1927) described two varieties of this species. I agree with him that the two populations are different. The southwestern population (Fig. 7A), including the type of *A. densifolium*, has narrow leaves and glabrous inflorescences, while the northeastern population, including the type of var. *latifolium*, has denser foliage with larger, broader leaves and pubescent inflorescences. In this study, however, I have chosen not to deal with infraspecific taxa. On herbarium labels, Bakhuizen f. has treated these taxa as synonyms of *A. ophirense*. *Argostemma ophirense* and its allies are complex, but *A. ophirense* and *A. densifolium* from Borneo are two distinct taxa, in my opinion. *Argostemma densifolium* has a different leaf shape, denser foliage, and long peduncles.

Additional specimens examined. BORNEO. SARAWAK: 1st Div., Sabal, 1974, *Sylvester Tong S34346* (K, L, MO); 4th Div., Melinau gorge pathway, 1962, *Burtt & Woods 2214* (E); 7th Div., Gunong Mulu, Melinau gorge, 100 m, 1978, *Nielsen 538* (AAU, K); 200 m, 1978, *Nielsen 445* (AAU).

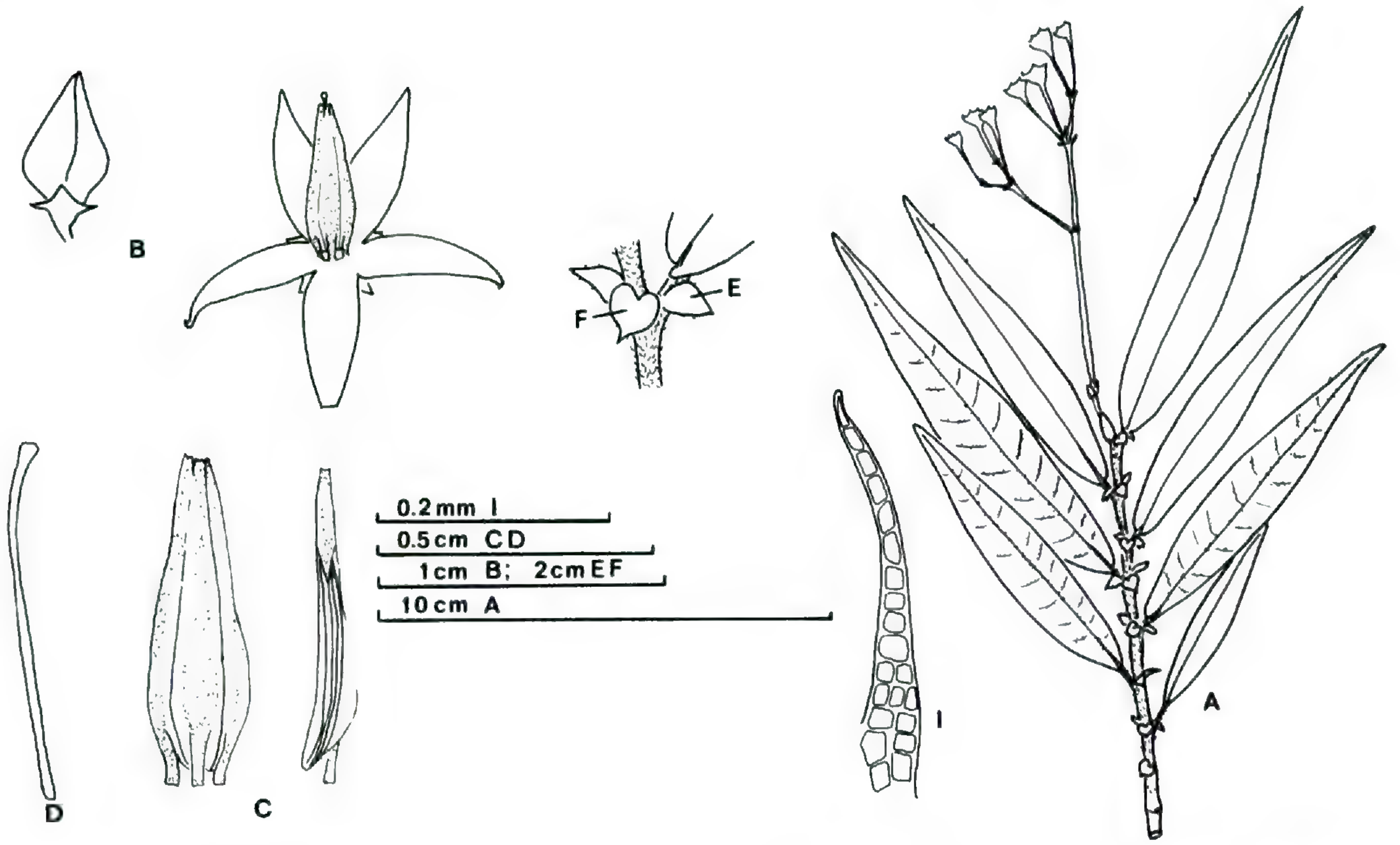


FIGURE 8. *Argostemma ophirense*. — A. Flowering branch. — B. Flowers. — C. Anthers. — D. Style. — E. Stipule. — F. Nanophyllous leaf. — I. Stiff, pluricellular leaf hair. A, E, F from *Bremer 1688* (S); B–D, I from *Burtt & Woods 2701* (E).

5. Argostemma ophirense Maingay ex Hook. f., The Flora of British India 3(7): 45. 1880. TYPE: Malacca. Mt. Ophir, 1867–1868, *Maingay 2578* (holotype, K). Figure 8.

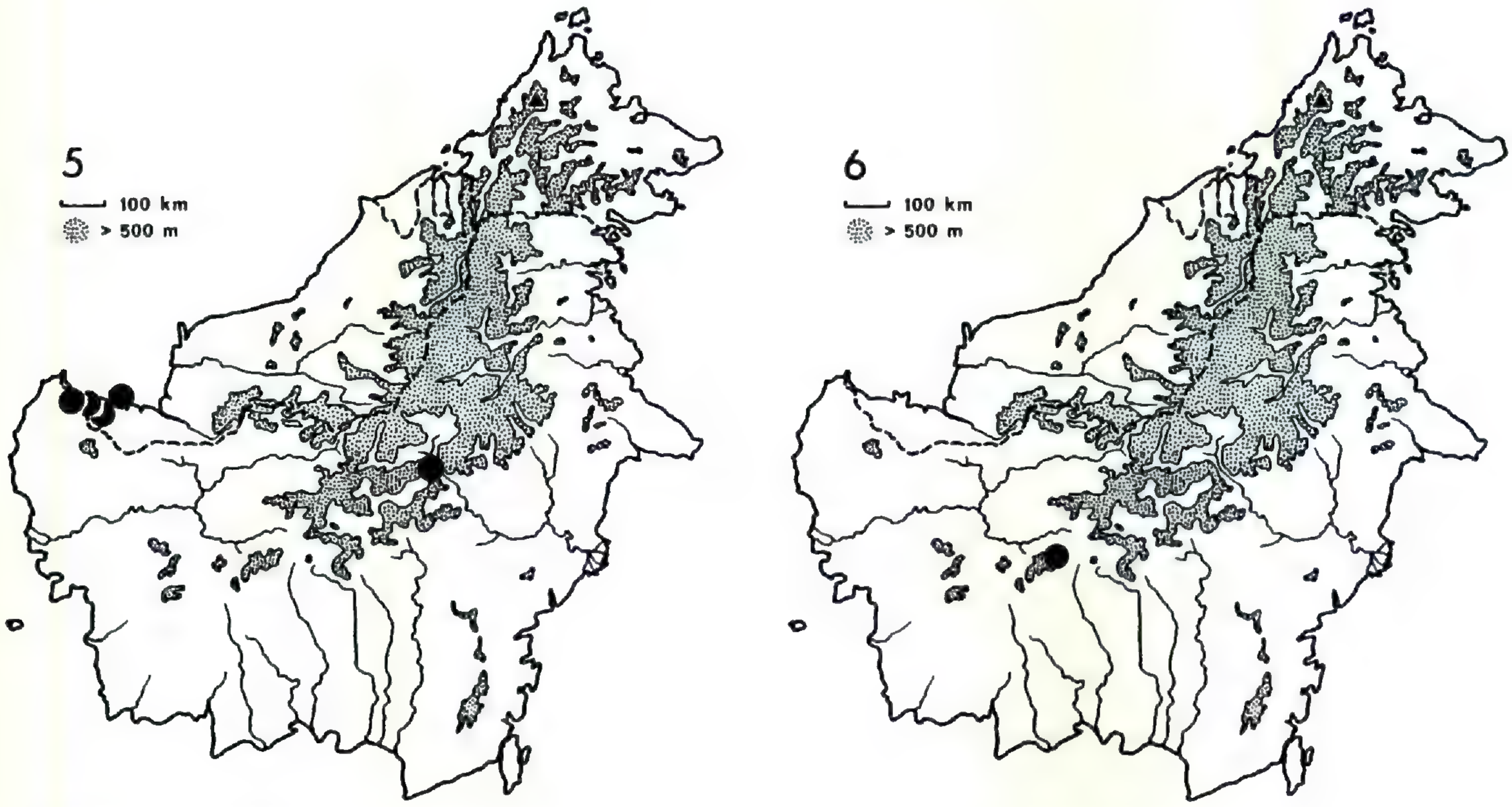
A. salicifolium Ridley, J. Straits Branch Roy. Asiat. Soc. 61: 14. 1912. TYPE: Mt. Matang, *Ridley 11751* (holotype, SING; isotypes, BM, K).

Erect, anisophyllous herb. Stem 7–30 cm long, slightly branched or unbranched, pubescent; internodes 3–15 mm. Leaves opposite, very unequal; stipules persistent, 3–5 mm long, ovate to lanceolate or oblanceolate, acute to obtuse; larger leaves of the anisophyllous pairs with pubescent petioles, to 5 mm long; lamina 5–16 × 0.4–3 cm, lanceolate to linear, basally cuneate or acute to subcordate and oblique or with the lobes unequal, marginally entire, apically acuminate to narrowly acuminate, herbaceous to coriaceous, with a few stiff pluricellular hairs on the upper surface, pubescent on the veins below; midrib and primary veins (10–20 pairs) distinct, at least below. Nanophyllous leaves persistent, 3–5 mm long, cordiform. Inflorescences solitary or a few together, 7–18-flowered, laxly corymbiform, glabrous; peduncle 1–3 cm long; bracts to 0.5 cm long, ovate to linear; lateral branches 1–2 cm long; pedicels 0.4–0.7 cm long. Flowers 5-merous; calyx lobes ca. 1 mm long, stiff, narrowly triangular, acute, glabrous; corolla 4–5 mm long, cleft to near the base, glabrous on both surfaces; lobes ovate, acute, spreading. Stamens 4–6 mm long, coherent; anther cells and apical appendages connate except for the most apical part; anther cone ovoid, straight; filaments short, equal, straight; sacs opening completely longitudinally; apical appendage ca. ⅓ the anther length, thin and smooth; connective indistinctly passing over to the thecae, smooth. Style 4–7.5 mm long, glabrous, with a slightly capitate stigma, shortly exserted. Fruit without furrows or ribs.

When Ridley (1912) described *A. salicifolium* he stated that the specimens are preserved in the Singapore Gardens Herbarium. Bakhuizen f. indicated, on the herbarium label, the K specimen as the type (= holotype). The SING specimen must be treated as the holotype and the K specimen as an isotype, as Ridley (1912) said that the specimens are preserved in SING.

Argostemma ophirense grows on ground or on rocks in forest from 50 to 1,300 m; most collections are from under 1,000 m.

There is little morphological variation in this species except for variation in leaf width and distinctness of foliar veins. It is characterized by indumentum on the stems, petioles, and veins beneath. The leaves are generally lanceolate with oblique bases. The cordiform nanophyllous leaves



MAPS 5, 6. Distributions in Borneo.—5. *Argostemma ophirense.*—6. *A. anisophyllum.*

and stipules are persistent. The inflorescences are lax cymes. The type specimens of *A. salicifolium*, probably collected from near the summit of Mt. Matang, have very narrow leaves with indistinct primary veins on the upper side. The specimens from Kalimantan have more obovate leaves.

Additional specimens examined. BORNEO. SARAWAK: 1st Div., Berumput, 1954, *Brooke 8670* (L); 3,000 ft., 1962, *Burtt & Woods 2762* (E, SAR); 1st Div., Mt. Poi (= Pueh), 1929, *Clemens field no. 6958* (NY); 1929, *Clemens field no. 7083* (NY); 3,000 ft., 1955, *Purseglove & Shah 4811* (K, L, SING); 1st Div., Sungei Lundu, 1962, *Burtt & Woods 2701* (E, SAR); 1st Div., Lundu, 1929, *Clemens s.n.* (NY); 1st Div., Bako, at Serai path, 1979, *Bremer 1688* (S, SAR); Telok Delima, 200 ft., 1956, *Purseglove 4987* (K, L, SAR, SING, NY); 1st Div., Mt. Matang, 1,200 ft., 1954, *Brooke 9517* (BM, L); 1,000 ft., 1955, *Brooke 9743* (L); 2,000 ft., 1962,

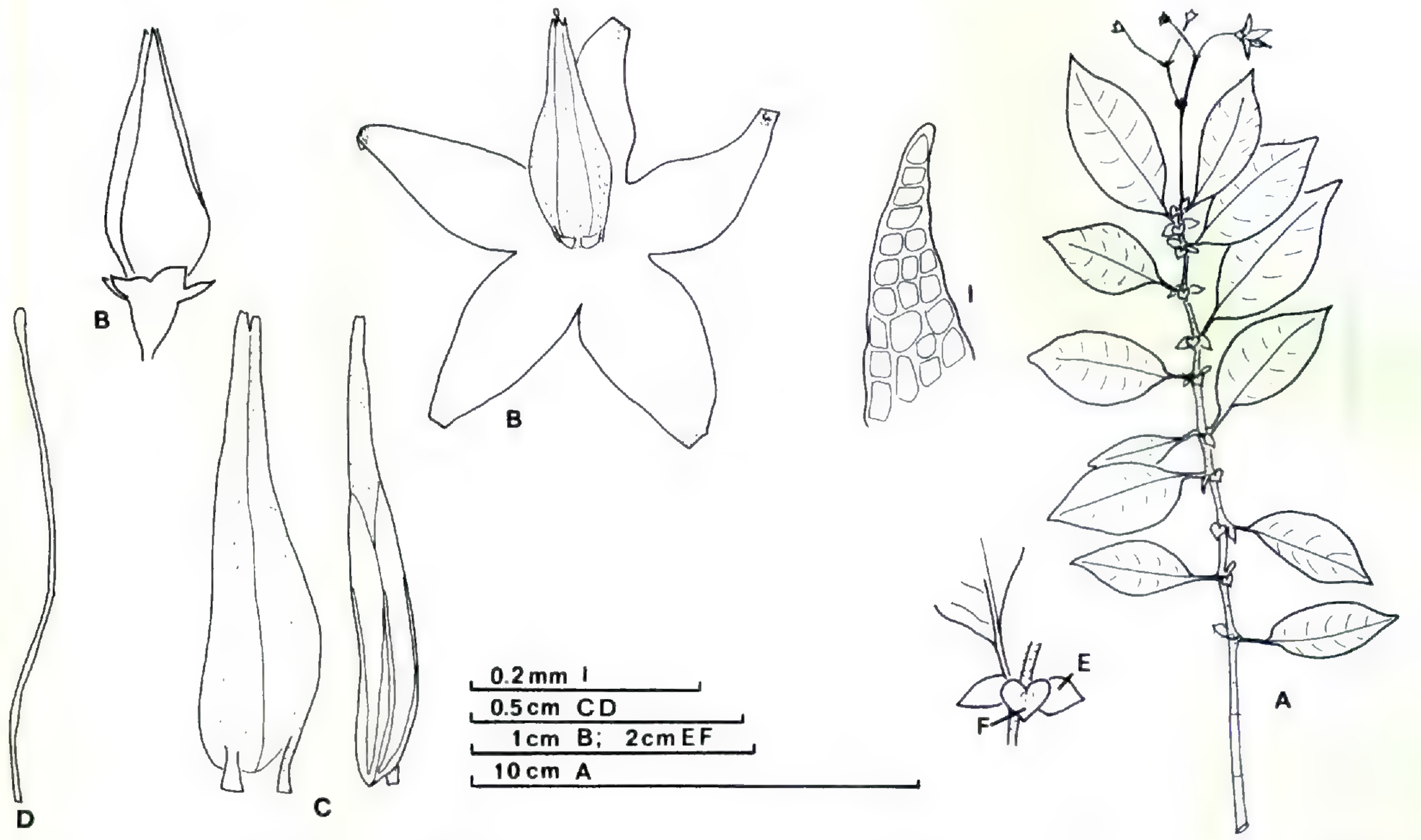


FIGURE 9. *Argostemma anisophyllum.*—A. Flowering branch.—B. Flower.—C. Anthers.—D. Style.—E. Stipule.—F. Nanophyllous leaf.—I. Stiff, pluricellular leaf hair. From *Winkler 897* (HBG).

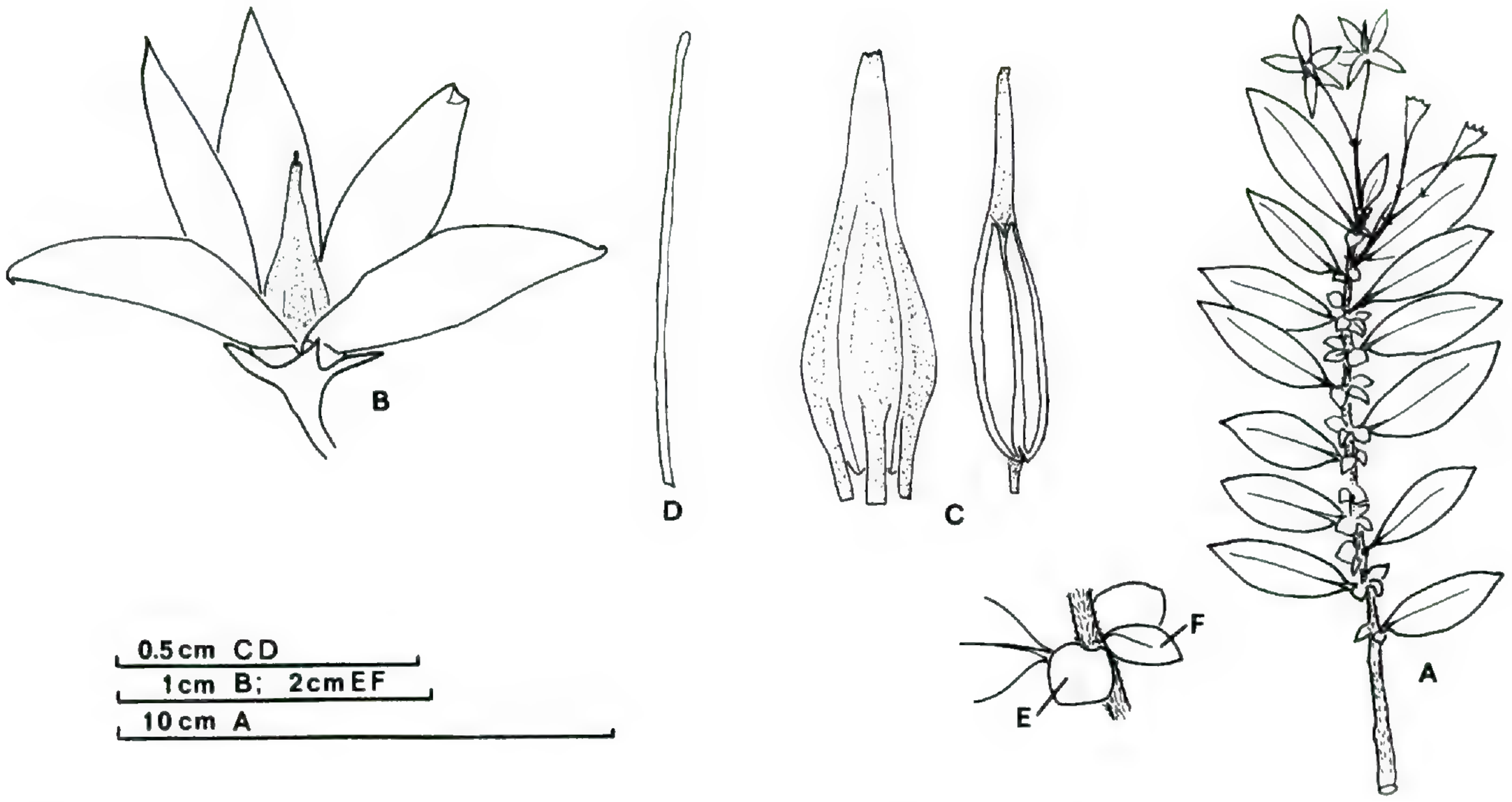


FIGURE 10. *Argostemma dulitense.*—A. Flowering branch.—B. Flower.—C. Anthers.—D. Style.—E. Stipule.—F. Nanophyllous leaf. A from *Richards 1711* (K); B–F from *Richards 2101* (K).

Burtt & Woods 2512 (E, SAR); 2,500 ft., 1962, *Burtt & Woods 2518* (E, SAR); 1,500 ft., 1929, *Clemens 20910* (K, NY, SAR); 1,500 ft., 1929, *Clemens 20911* (BO, K, NY); 2,000–3,000 ft., 1890, *Hullett s.n.* (SING); 1927–1928, *native collector s.n.* (NY); 1,000 ft., 1924, *Mjöberg 205* (NY, SING, UC); 1924, *Mjöberg 206* (NY, UC); 2,500–3,000 ft., *Mjöberg s.n.* (UC); 1890?, *Ridley 11751* (BM, K, SING). KALIMANTAN: E Prov., Gunong Beratus (Peak of Balikpapan), 800–900 m, 1952, *Kostermans 7437* (BO, L); 750 m, 1952, *Meijer 687* (BO, L).

6. Argostemma anisophyllum Merr., Mitt. Inst. Allg. Bot. Hamburg 7: 278. 1937. TYPE: West Borneo. Bukit Raja, 1,250 m, 1924, *Winkler 897* (holotype, HBG; isotype, NY). Figure 9.

Erect, anisophyllous herb. Stem 10–30 cm long, slightly branched or unbranched, glabrous or glabrate; internodes 5–25 mm. Leaves opposite, very unequal; stipules persistent, 4–5 mm long, broadly ovate to lanceolate, acute at apex; larger leaves of the anisophyllous pairs with glabrous petioles 3–7 mm long; lamina 2–6.2 × 1.2–2.2 cm long, obovate to oblanceolate, basally acute to attenuate and oblique, marginally entire, apically acuminate, herbaceous to membranaceous, with a few stiff pluricellular hairs on the upper surface, glabrous below; midrib and primary veins (6–10 pairs) distinct. Nanophyllous leaves persistent, 2–4 mm long, cordiform. Inflorescences solitary, 1–5-flowered, laxly corymbiform, glabrous; peduncle 2–2.8 cm long; lateral branches 1–1.5 cm long; bracts ca. 0.1 cm long, lanceolate or triangular; pedicels 1–2.2 cm long. Flowers 5-merous; calyx lobes ca. 1 mm long, stiff, narrowly triangular, acute, glabrous; corolla 8–9 mm long, cleft to near the base, glabrous on both surfaces; lobes ovate to broadly ovate, spreading. Stamens 9–11 mm long, coherent; anther cells and apical appendages connate except for the most apical part; anther cone narrowly ovoid or ovoid, straight; filaments short, equal, straight; sacs opening completely longitudinally; apical appendage ca. ⅓ the anther length, thin and smooth; connective indistinctly passing over to the thecae, smooth. Style 10–12 mm long, glabrous, with a slightly capitate stigma, exserted. Fruit without furrows or ribs.

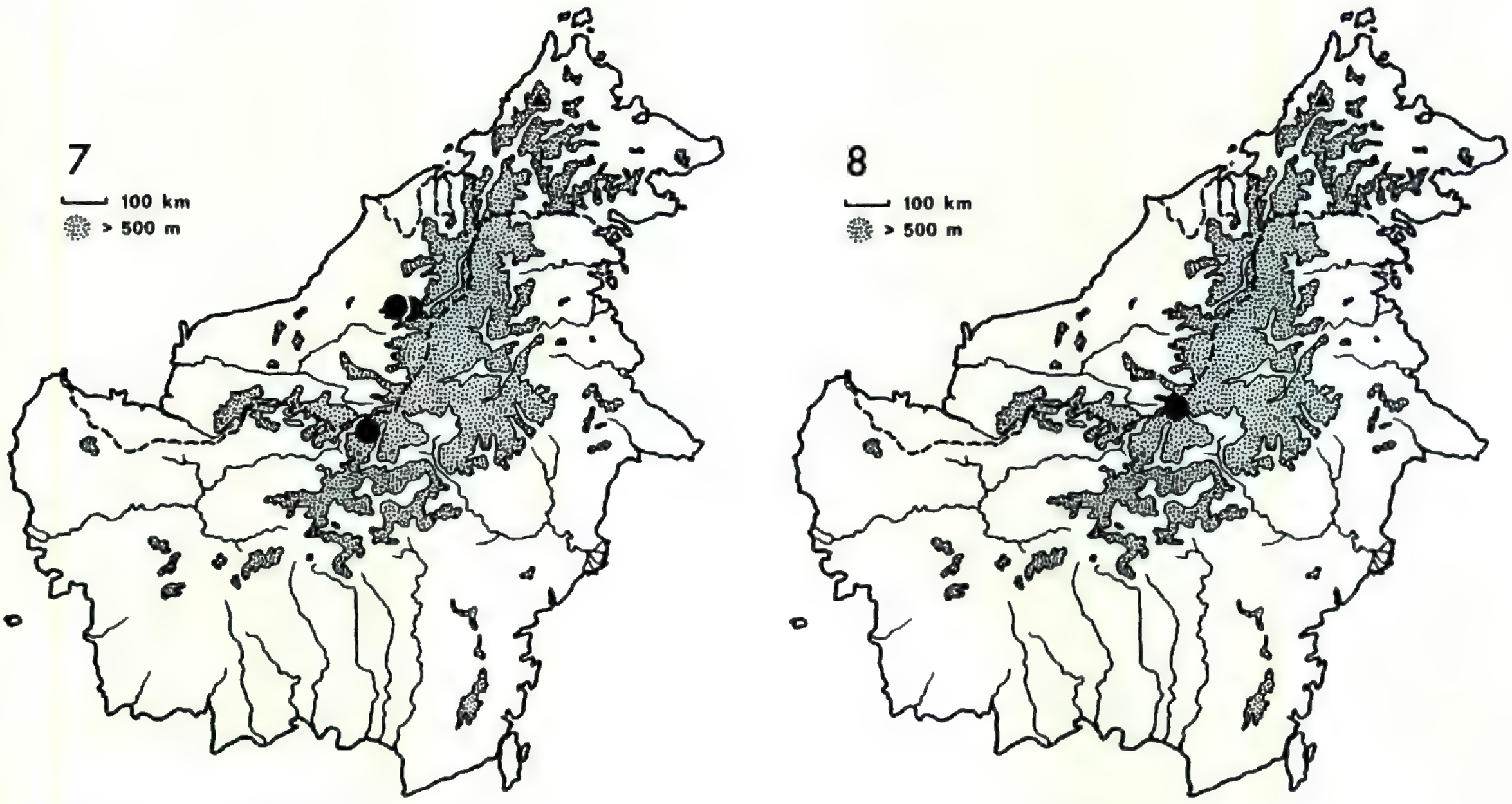
Argostemma anisophyllum grows from 1,250 to 1,400 m at Bukit Raja.

It has been treated as a synonym of *A. ophirense* by Bakhuizen f. on herbarium labels. *Argostemma anisophyllum* has fewer hairs on the stems, much smaller and thinner leaves, longer peduncles and pedicels, and much larger flowers.

Additional specimen examined. BORNEO. KALIMANTAN: Bukit Raja, 1,400 m, 1924, *Winkler 950* (HBG).

7. Argostemma dulitense Merr., Sarawak Mus. J. 3: 554. 1928. TYPE: Borneo. Sarawak: Mt. Dulit, 1,200–1,500 m, 1923, *Mjöberg 8* (holotype, UC). Figure 10.

Erect anisophyllous herb. Stem 10–40 cm long, slightly branched or unbranched, densely pubescent; internodes to 8 mm. Leaves opposite, very unequal; stipules persistent, 2–4 mm long, broadly ovate, acute at apex; larger leaves of the aniso-



MAPS 7, 8. Distributions in Borneo.—7. *Argostemma dulitense.*—8. *A. apiculatum.*

phyllous pairs with glabrous petioles ca. 3 mm long; lamina 2–6 × 0.4–1.5 cm, lanceolate or narrowly elliptic to obovate, basally cuneate to attenuate and with the lobes equal, marginally entire, apically acute to acuminate, coriaceous, glabrous on both surfaces; midrib distinct, primary veins generally obscure. Nanophyllous leaves persistent, ca. 5 mm long, ovate. Inflorescences solitary or a few together, 1–3-flowered, glabrous; peduncle 1–2.5 cm long; bracts to 0.3 cm long, ovate to triangular or lanceolate; pedicels 1–2.7 cm long. Flowers 5-merous; calyx lobes ca. 2 mm long, stiff, narrowly triangular, glabrous. Corolla 9–12 mm long, cleft to near the base, glabrous on both surfaces; lobes ovate to lanceolate, spreading. Stamens ca. 7 mm long, coherent; anther cells and apical appendages connate except for the most apical part; anther cone ovoid or narrowly so, straight; filaments short, equal, straight; sacs opening completely longitudinally; apical appendage ca. ⅓ the anther length, thin and smooth; connective indistinctly passing over to the thecae, smooth. Style ca. 8 mm long, glabrous with a scarcely widened stigma, shortly exserted. Fruit without furrows or ribs.

Argostemma dulitense grows in shady places on tree trunks or on rocks near waterfalls in moss and heath forests.

It is characterized by its glossy dark green upper leaf surfaces, pale lower leaf surfaces and very firm leaf texture. The stems are covered by appressed hairs; otherwise it is glabrous. The corolla is large and rotate with green spots at the base, and the anther cone is high. The specimens from Kalimantan have distinct primary veins, while the Sarawak specimens have obscure veins.

Additional specimens examined. BORNEO. SARAWAK: 4th Div., Dulit Ridge 1,250 m, 1932, *Richards 1711* (K); 1,000 m, 1932, *Richards 2101* (K, L); 4th Div., Gunong Dulit, at Long Atun, 1,300 m, 1965, *Asah ak Luang S22752* (K, L); 1,200–1,500 m, 4th Div., Ulu Tinjar, 2,600 ft., 1974, *Sylvester Tong S34847* (K, L). KALIMANTAN: E Prov., Boekit Batue Ajah, 1896–1897, *Jaheri in exp. Nieuwenhuis 1636* (BO, L).

8. Argostemma apiculatum B. Bremer, sp. nov. TYPE: Borneo. Sarawak: 7th Div., summit of Bukit Tibang, 5,000 ft., 1969, *Anderson & Ilias Paie S28657* (holotype, K; isotypes, E, L). Figure 11.

Herba erecta, glabra, inflorescentiis floribus paucis. Folia opposita, illis parium inaequalissimis. Inflorescentia corymbosa, floribus grandibus. Lobi calycis rigidi, anguste triangulares, acuti. Lobi corollae apiculati. Antherae et appendices apicales connatae praeter partem apicalissimam. Appendix apicalis ¼ anthera brevior, tenuis, laevis. Connectivum indistinctum. Stylus glaber stigmate vix dilatato.

Argostemma burttii simile sed planta glabra, lobis corollae apiculatis differt.

Erect, anisophyllous, glabrous herb. Stem 2–30 cm, unbranched; internodes 6–16 mm. Leaves opposite, very unequal; stipules persistent, 5–7 mm long, ovate to cordiform, acute at apex; larger leaves of the anisophyllous pairs with petioles 3–5 mm long, the lamina 3–8.5 × 0.8–1.9 cm, narrowly elliptic, basally cuneate to attenuate with

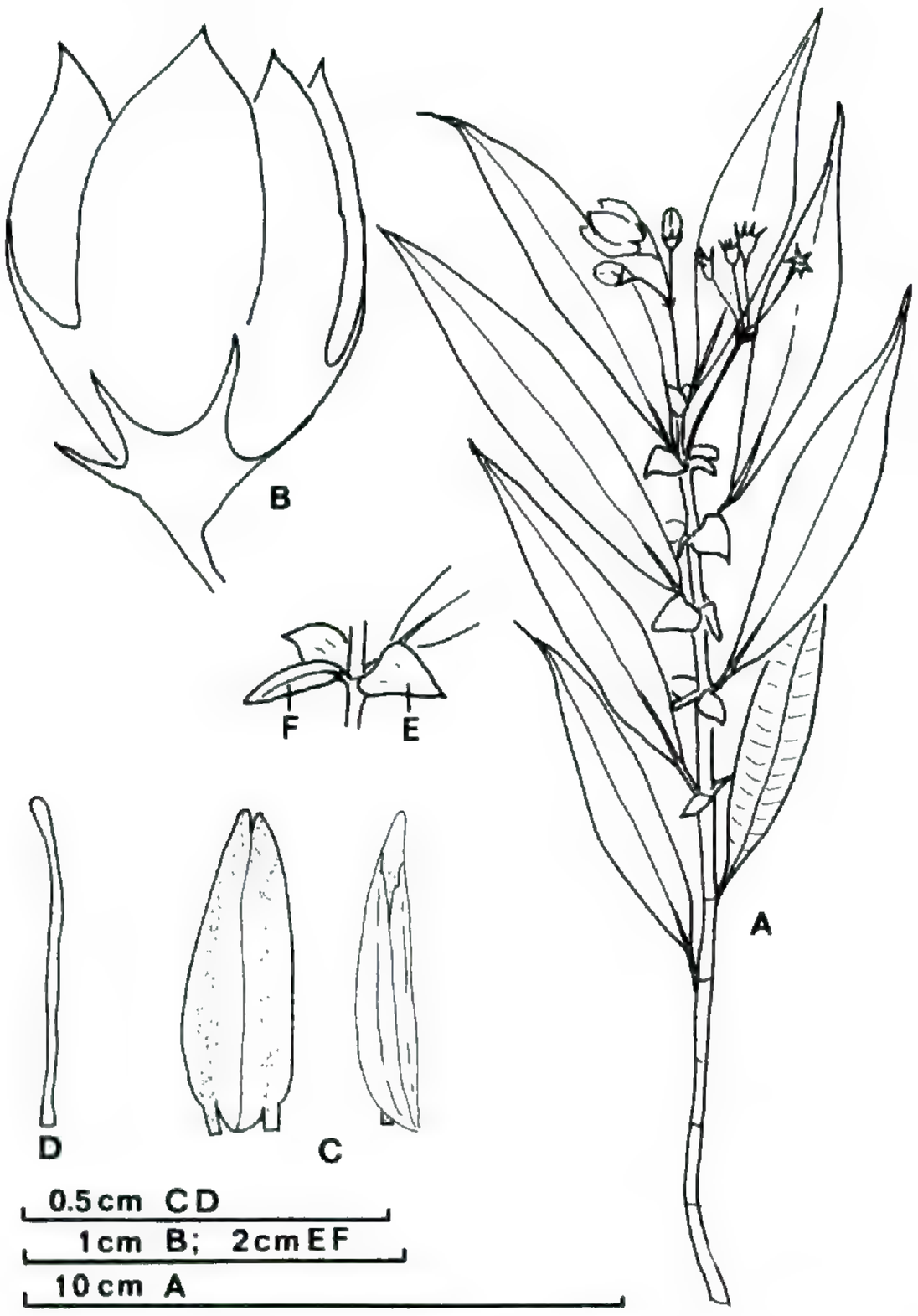


FIGURE 11. *Argostemma apiculatum.*—A. Flowering branch.—B. Flower.—C. Anthers.—D. Style.—E. Stipule.—F. Nanophyllous leaf. From *Anderson & Ilias Paie S28657* (K).

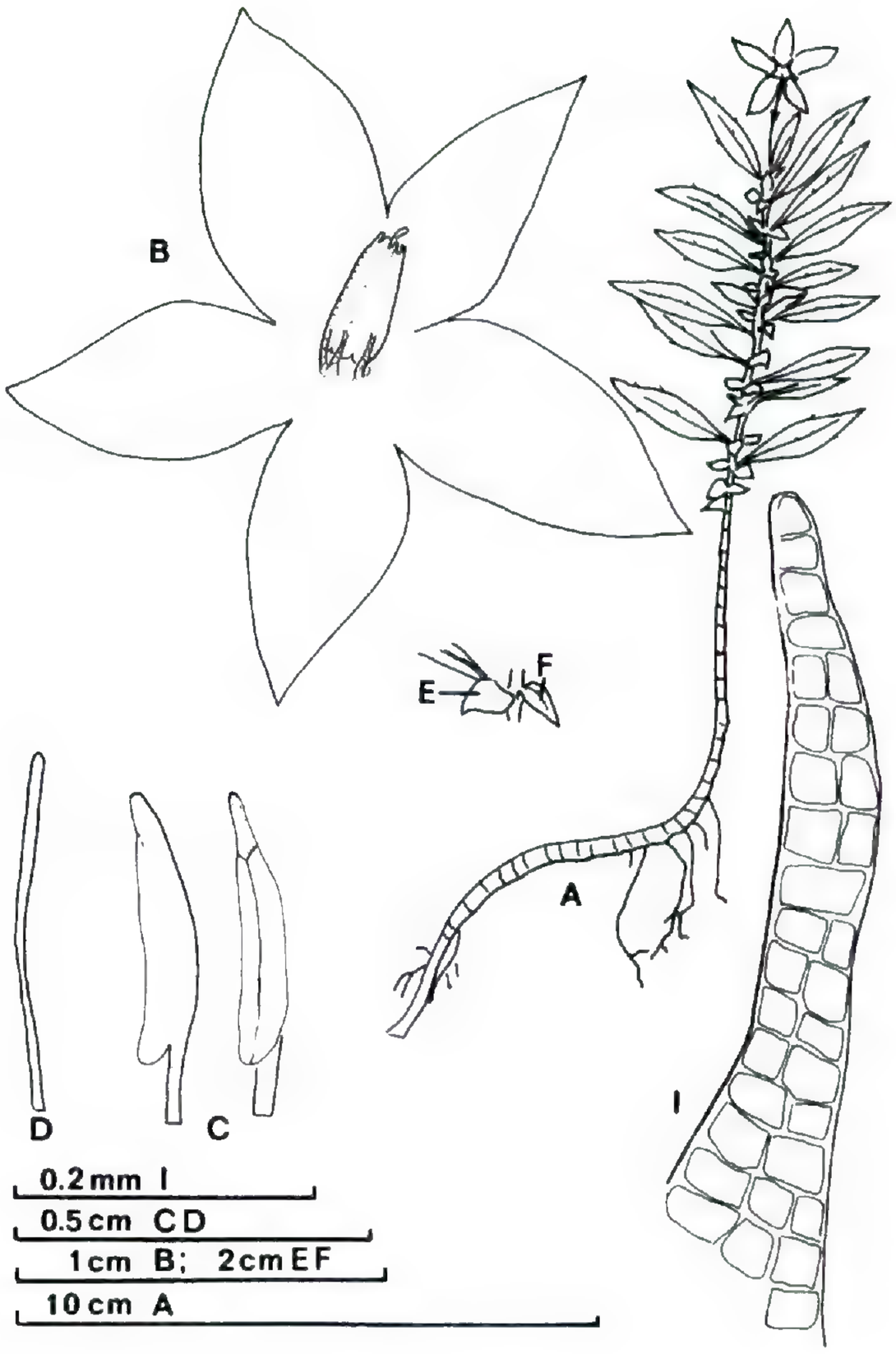


FIGURE 12. *Argostemma burttii.*—A. Habit.—B. Flower.—C. Anthers.—D. Style.—E. Stipule.—F. Nanophyllous leaf.—I. Stiff, pluricellular leaf hair. From *Burtt & Martin 4986* (E).

the lobes equal, marginally entire, apically acuminate, herbaceous to membranaceous; midrib distinct, the primary veins (10–16 pairs) obscure. Nanophyllous leaves persistent, 5–6 mm long, elliptic to lanceolate. Inflorescences 1–4-flowered, laxly corymbiform, solitary or a few together; peduncle 1.5–2 cm; bracts to 0.5 cm long, lanceolate; pedicels to 0.8 mm. Flowers 5-merous; calyx lobes ca. 3 mm long, stiff, narrowly triangular, acute, glabrous; corolla 10–12 mm long, cleft to near the base; lobes ovate to broadly so, pointed, spreading. Stamens 4.5–5 mm long, coherent; anther cells and apical appendages connate except for the most apical part; anther cone ovoid, straight; filaments short, equal, straight; sacs opening completely longitudinally; apical appendage less than ¼ the anther length, thin and smooth; connective indistinctly passing over the thecae, smooth. Style ca. 5 mm long, glabrous, with a scarcely widened stigma, shortly exserted. Fruit without furrows or ribs.

Argostemma apiculatum was collected once at Bukit Tibang, on igneous soil at 1,600 m in mossy forest.

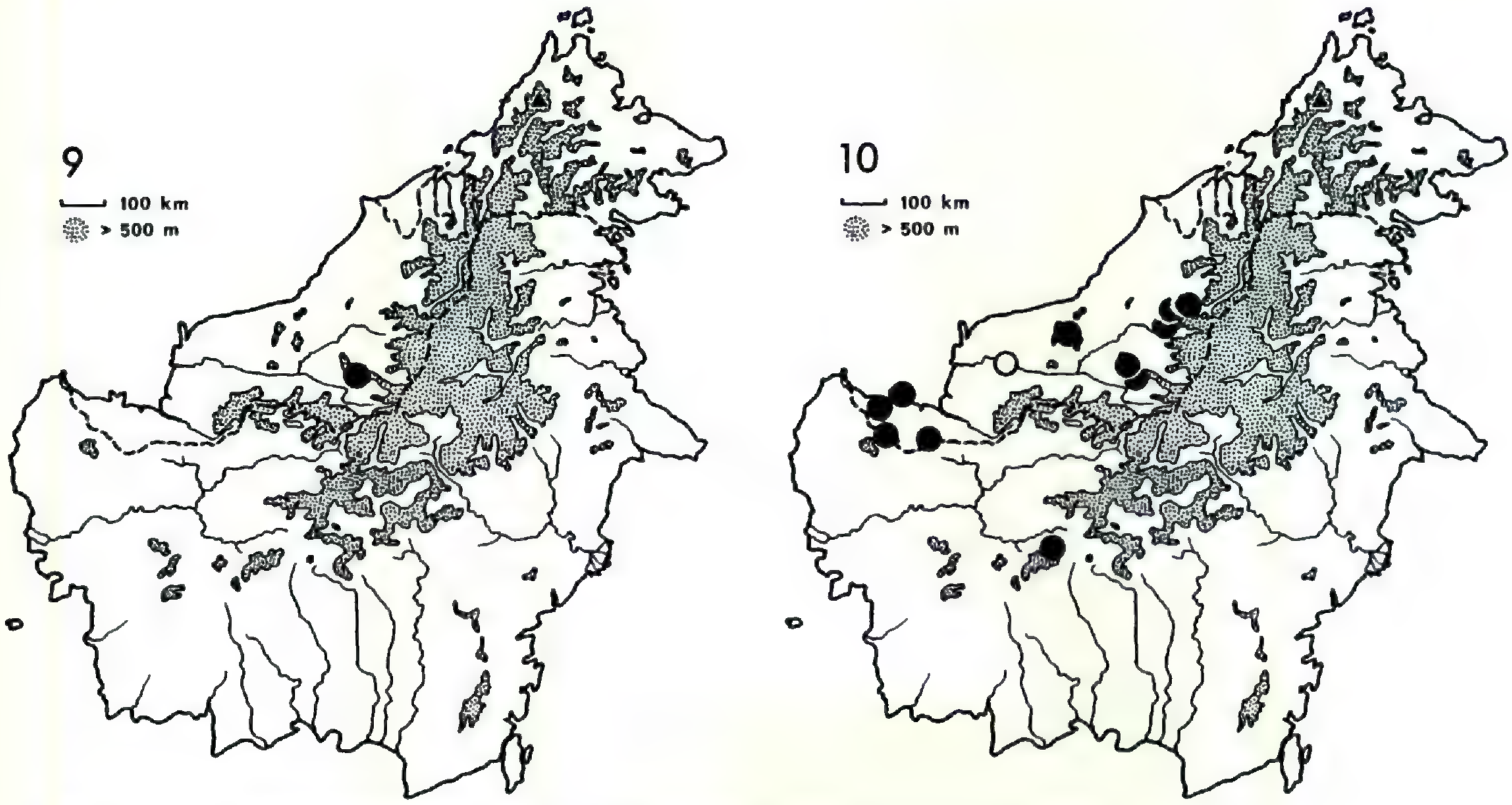
It is a glabrous plant with large, broad, pointed corolla lobes. The apical appendages of the anthers are short. It is similar to *A. burttii* because of its large corollas and the short apical appendages. *Argostemma apiculatum* differs from that species by its apiculate corolla lobes and erect glabrous habit.

9. Argostemma burttii B. Bremer, sp. nov.
TYPE: Borneo. Sarawak: SE of Hose Mts., above Ulu Melinau Falls, ca. 4,000 ft., 1967, *Burtt & Martin 4986* (holotype, E). Figure 12.

Herba repens vel suberecta, inflorescentiis floribus solitariis paucisve. Folia opposita, illis parium inaequalissimis, serrulata. Inflorescentia monochasialis, floribus grandibus. Lobi calycis rigidi, anguste triangulares, acuti. Antherae et appendices apicales connatae praeter partem apicalissimam. Appendix apicalis ¼ anthera brevior, tenuis, laevis. Connectivum indistinctum. Stylus glaber stigmate vix dilatato.

Argostemma apiculatum simile sed foliis serrulatis, lobis corollae non apiculatis differt.

Creeping or suberect, anisophyllous herb. Stem to 20 cm, slightly branched or unbranched, glabrous; internodes 2–4 mm. Leaves opposite, very



MAPS 9, 10. Distributions in Borneo.—9. *Argostemma burtii*.—10. *A. rupestre*.

unequal; stipules 2–4 mm long, broadly ovate to cordiform, acute at apex. Larger leaves of the anisophyllous pairs with glabrous petioles 1–3 mm long; lamina 1–3.5 × 0.4–0.9 cm, narrowly elliptic, basally cuneate to attenuate with the lobes equal, marginally serrulate, apically acuminate, herbaceous to membranaceous, glabrous on both surfaces but with 3 or 5 rows of stiff pluricellular hairs on the upper surface; midrib distinct, the primary veins obscure. Nanophyllous leaves persistent, to 4 mm long, ovate to lanceolate. Inflorescences 1–2-flowered, monochasial, solitary or a few together; peduncle 1–2 cm, glabrous; bracts to 0.2 cm long, lanceolate to linear; pedicels 0.7–1.5 cm, glabrous. Flowers 5-merous; calyx lobes ca. 1.5 mm long, stiff, triangular to narrowly triangular, acute, glabrous; corolla 9–12 mm long, cleft to near the base, glabrous on both surfaces; lobes ovate, spreading. Stamens 4–5 mm long, coherent; anther cells and apical appendages connate except for the most apical part; anther cone ovoid, straight; filaments short, equal, straight; sacs opening completely longitudinally; apical appendage less than ¼ the anther length, thin and smooth; connective indistinctly passing over to the thecae, smooth. Style ca. 5 mm long, glabrous, with a scarcely widened stigma, shortly exserted. Fruit without furrows or ribs.

Argostemma burttii was found growing at bases of trees among mosses at ca. 1,300 m. It is a local endemic species from the Hose Mountains. Mr. B. L. Burtt has collected it at three different places. It is a beautiful little plant with very large flowers. The corolla is open and flat with green spots at the center, and the anther cone is cream-colored. The border between the filaments and the thecae is indistinct, as in, for example, *A. apiculatum*, *A. rupestre*, and *A. geesinkii*. With the last two it also shares the character of three or five rows of stiff, pluricellular hairs on the upper leaf surface. *Argostemma burtii* is most similar to *A. apiculatum*, both having large corollas and short apical appendages, but *A. burtii* differs by having serrulate leaves and creeping or suberect habit.

Additional specimens examined. BORNEO. SARAWAK: 7th Div., S Hose Mts., W of Bukit Sanpandai, 1980, *Burtt 12750* (E); E of Bukit Sanpandai, 4,500 ft., 1980, *Burtt 12817* (E).

10. Argostemma rupestre Ridley, J. Bot. 65: 41. 1927. TYPE: Borneo. On the hill near Matang, *Haviland 1031* (holotype, K; isotypes, SAR, SING). Figure 13.

Creeping or suberect, anisophyllous herb. Stem 3–14 cm, generally unbranched, glabrous or with a few hairs; internodes very short to 7 mm. Leaves opposite, very unequal; stipules persistent, 2–7 mm long, ovate to lanceolate, acute at apex; larger leaves of the anisophyllous pairs with glabrous petioles to 5 mm long; lamina 1.3–5.5 × 0.2–1.8 cm, narrowly elliptic to lanceolate or oblanceolate, rarely elliptic or linear; basally cuneate to attenuate with the lobes equal; marginally serrulate, apically acuminate; herbaceous to membranaceous, gla-

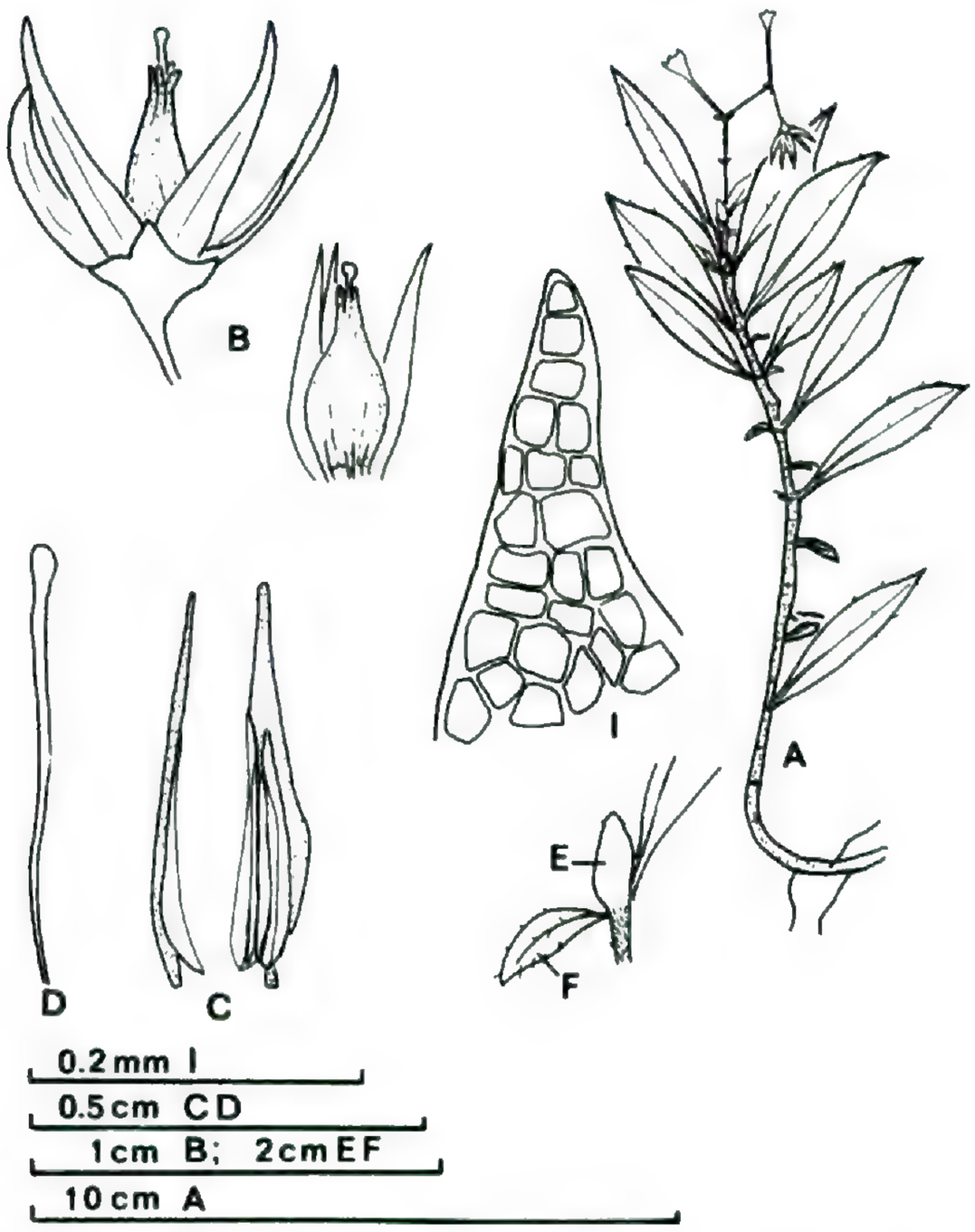


FIGURE 13. *Argostemma rupestre.*—A. Habit.—B. Flower.—C. Anthers.—D. Style.—E. Stipule.—F. Nanophyllous leaf.—I. Stiff, pluricellular leaf hair. From *Bremer 1665* (S).

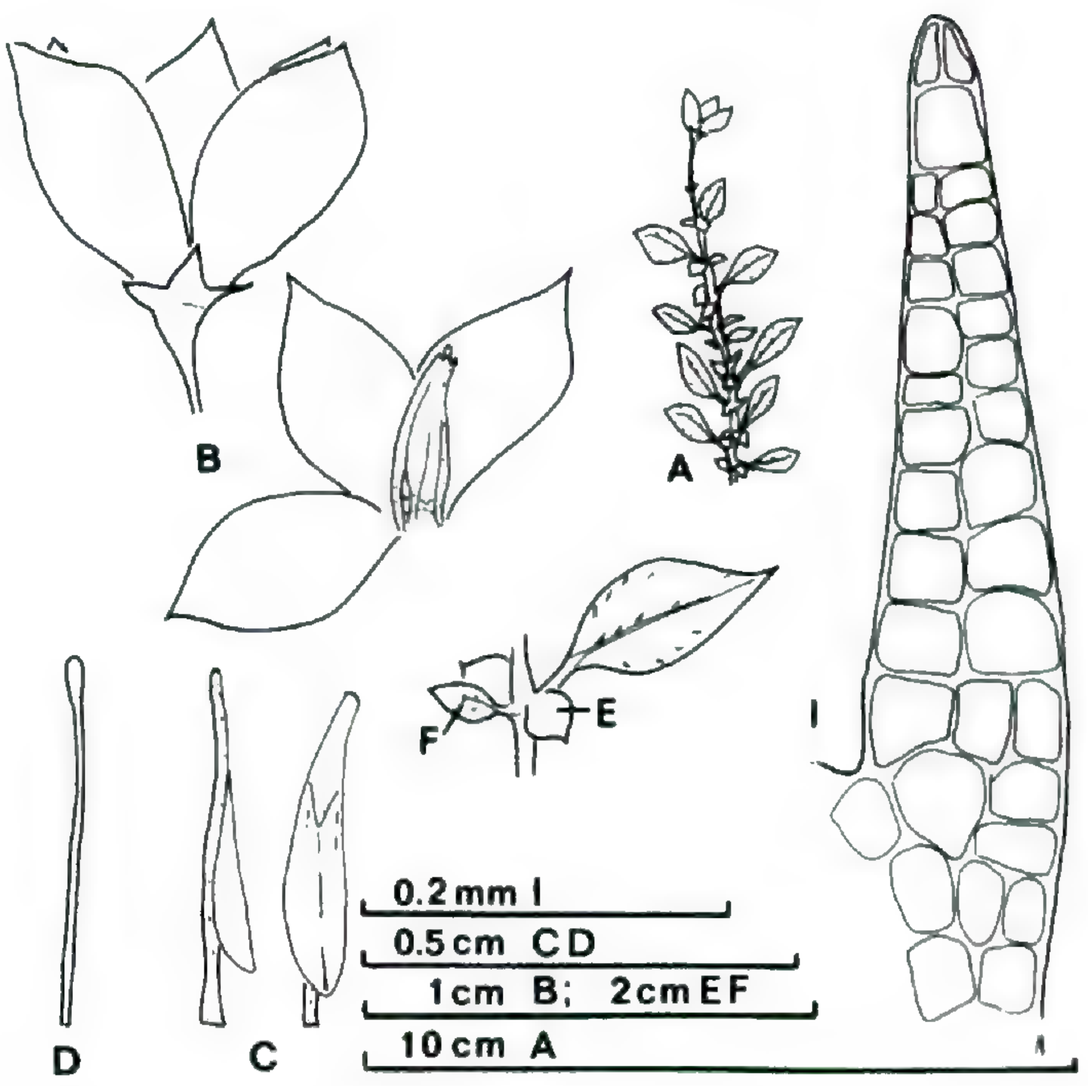


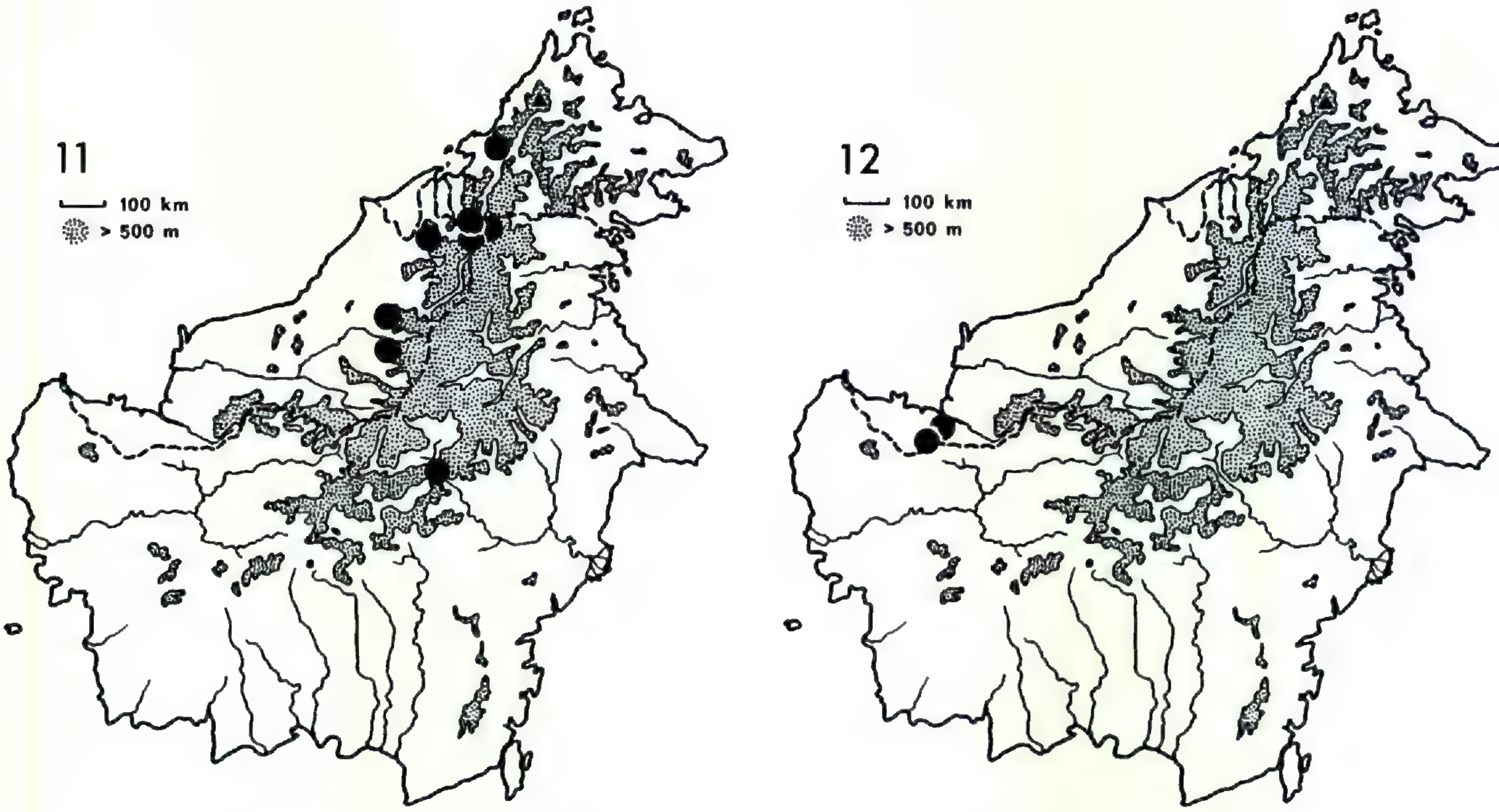
FIGURE 14. *Argostemma geesinkii.*—A. Flowering branch.—B. Flower.—C. Anthers.—D. Style.—E. Stipule.—F. Nanophyllous leaf.—I. Stiff, pluricellular leaf hair. From *Geesink 9272* (L).

brous on both surfaces except for 3 or 5 rows of stiff pluricellular hairs above; midrib distinct, the primary veins obscure. Nanophyllous leaves persistent, 2–10 mm long, ovate to elliptic or lanceolate. Inflorescences 1–3(–5)-flowered, laxly corymbiform, solitary or a few together; peduncle 1–3 cm, glabrous or pubescent; bracts 0.1–0.3 cm long, lanceolate; pedicels 0.5–1.5 cm, glabrous or pubescent. Flowers 5-merous; calyx lobes ca. 1 mm long, stiff, triangular to narrowly triangular, acute, glabrous; corolla 4–7 mm long, cleft to near the base; lobes lanceolate, acute to acuminate, erect-spreading. Stamens 5–7 mm long, coherent; anther cells and apical appendages connate except for the most apical part; anther cone ovoid, straight; filaments short, equal, straight; sacs opening completely longitudinally; apical appendage ca. ⅓ the anther length, thin and smooth; connective indistinctly passing over to the thecae, smooth. Style 6–8 mm long, glabrous, with a slightly capitate stigma, shortly exserted. Fruit without furrows or ribs.

Argostemma rupestre is a small herb growing on wet sandstone boulders or other wet places in or near streams or waterfalls, chiefly among mosses. It occurs from low altitudes up to ca. 1,500 m in mossy forests.

This anisophyllous herb has glabrous leaves except for three or five rows of stiff pluricellular hairs on the midrib and along the margins. The marginal hairs make the leaves serrulate. The lower surface of the leaves is pale. The stipules and nanophyllous leaves are similar in shape. The corolla is cleft to near the base into narrow and erect-spreading lobes. The anther cone is high with a pale yellow color near the base and whitish at the apex. The inflorescences are lax cymes with one to five flowers. The peduncles and pedicels are narrow and generally glabrous. The specimens from Bako are all pubescent on the peduncles, pedicels, and ovaries and have somewhat broader corolla lobes. There are two collections from different areas (*Brooke 9131* and *Richards 2455*) with very narrow leaves; both were collected in or near streams and may be ecotypes. *Clemens 21737* came from an uncertain locality: on the herbarium label is written "Gat, Upper Rajang River," while on the attached field label both "Gat" and "Mt. Matang" are written. This plant has pubescent pedicels, as does the Bako population.

Additional specimens examined. BORNEO. SARAWAK: 1st Div., N slopes of Mt. Penrissen, 1,000–1,100 m, 1958, *Jacobs 5065* (B, G, K, L, SAR, UC); 1st Div., Bako, on slopes just N of the office, 1979, *Bremer 1675* (S, SAR); at Serai path S of the office, 1979, *Bremer 1687* (S, SAR); Telok Asam, 100 m, 1956, *Purseglove 5095* (K, L, NY, SAR, SING); Telok Asam, 100 m, 1957, *Purseglove 5534* (K, L, SAR, SING); 1st Div., Sabal, 350 m, 1979, *Bremer 1665* (S, SAR); 3rd Div., Teneong, 1954, *Brooke 9131* (BM, L); 4th Div., Ulu Mersing, Ulu Anap, 100 m, 1963, *Ashton S17691* (K, L, SAR); 4th Div., Mt. Dulit, 300 m, 1932, *Richards*



MAPS 11, 12. Distributions in Borneo.—11. *Argostemma geesinkii.*—12. *A. gaharuense.*

2455 (K, L); 4th Div., Ulu Sungei Chipidi, Ulu Tinjar, 2,300 ft., 1974, *Chai S34797* (K, L, MO, SAR); 7th Div., Sungei Melinau, 450 ft., 1980, *Burtt 12667* (E); 7th Div., Hose Mts., Bukit Salong, 1982, *Burtt 12734* (E); Bukit Sanpandai, 4,500 ft., 1980, *Burtt 12796* (E); without loc., *Clemens 21737* (NY). KALIMANTAN: W Prov., Bukit Raja, 1,400 m, *Winkler 951* (HBG).

11. Argostemma geesinkii B. Bremer, sp. nov. TYPE: Borneo. Kalimantan Timur, between Papadi and Pamilau, 1,400 m, 1981, *Geesink 9272* (holotype, L). Figure 14.

Herba pusilla, repens, inflorescentiis floribus solitariis aut duobus. Folia opposita, illis parium inaequalissimis, serratula vel integra. Inflorescentia monochasialis, floribus mediocribus. Lobi calycis, rigidi, anguste triangulares, acuti. Lobi corollae erecto-patentes, in exsiccatis subrosei. Antherae et appendices apicales connatae praeter partem apicalissimam. Appendix apicalis ⅓ longitudinem antherae aequans, tenuis, laevis. Connectivum indistinctum. Stylus glaber stigmate leviter capitato.

Argostemma rupestre simile sed planta pusilla, lobis corollae latis erecto-patentibus differt.

Small, creeping, anisophyllous herb. Stem 2–20 cm, slightly branched or unbranched, glabrous; internodes very short to 5 mm. Leaves opposite, very unequal; stipules 2–4 mm long, ovate to cordiform, acute to obtuse at apex; larger leaves of the anisophyllous pairs with glabrous petioles 1–2 mm long; lamina 2.5–7 × 0.6–1.5 cm, elliptic to obovate, basally cuneate to attenuate with the lobes equal, marginally serrulate or entire, apically acute to shortly acuminate or rarely obtuse, membranaceous, glabrous on both surfaces but with 3 or 5 rows of stiff pluricellular hairs on the upper surface; midrib distinct, the primary veins generally obscure. Nanophyllous leaves persistent, 2–5 mm long, ovate to elliptic, acute. Inflorescences 1–2-flowered, monochasial, solitary or a few together; peduncle 0.2–1 cm, glabrous; bracts ca. 1 mm long, lanceolate to triangular; pedicels 0.5–1 cm, glabrous. Flowers 5-merous; calyx lobes ca. 1 mm long, stiff, narrowly triangular, acute, glabrous; corolla 5–7 mm long, cleft to near the base, glabrous on both surfaces; lobes ovate to broadly ovate, acute, erect-spreading. Stamens 4–5 mm long, coherent; anther cells and apical appendages connate except for the most apical part; anther cone ovoid, straight; filaments short, equal, straight; sacs opening completely longitudinally; apical appendage ca. ⅓ the anther length, thin and smooth; connective indistinctly passing over to the thecae, smooth. Style 4–5 mm long, glabrous, with a slightly capitate stigma, shortly exserted. Fruit without furrows or ribs.

Argostemma geesinkii grows on tree trunks and on boulders among mosses, from 950 to 1,500 m. A few collections are from sandstone.

Argostemma geesinkii is a very small creeping species with small anisophyllous leaves and cordiform stipules. It is glabrous except for the stiff pluricellular hairs in three or five rows on the upper leaf surfaces. The flowers are generally solitary on thin pedicels. The corolla lobes are broad and often become pinkish in the press. All specimens except *Endert 3916* are very similar. This aberrant spec-

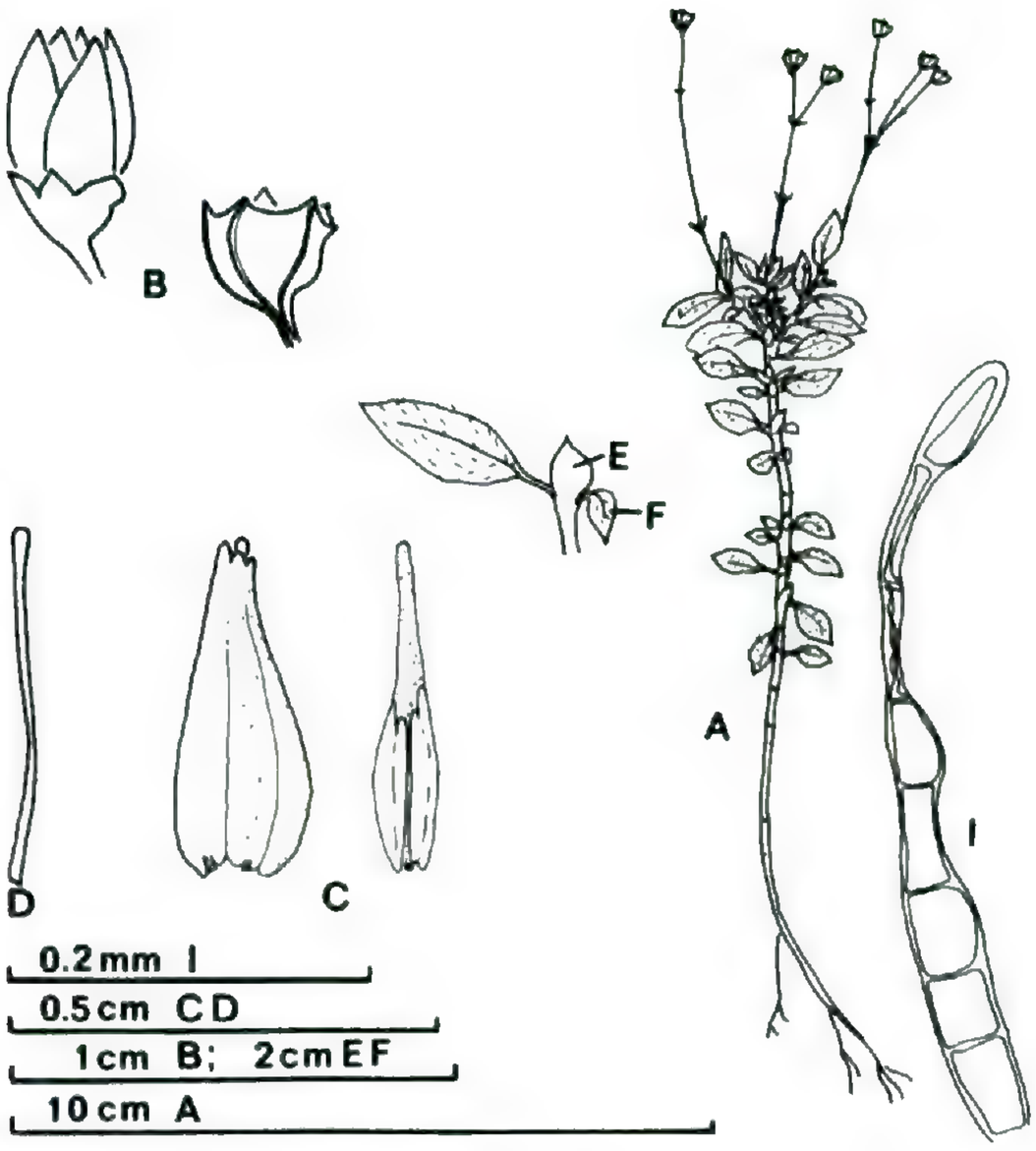


FIGURE 15. *Argostemma gaharuense*.—A. Habit.—B. Flower and fruit.—C. Anthers.—D. Style.—E. Stipule.—F. Nanophyllous leaf.—I. Hair from upper surface of leaf. From *Burtt 2655* (E).

imen lacks stiff hairs and has thicker leaves and prominent primary veins, but there are no floral differences between it and the other collections of *A. geesinkii*. There is another specimen from the same area (*Endert 3800*) that does not deviate from the others. Perhaps *Endert 3916* is a different taxon.

Additional specimens examined. BORNEO. SABAH: Kimanis road, Keningau, 4,400 ft., 1979, *Collenette 4179* (E). SARAWAK: 4th Div., Gunong Mulu, 4,000 ft., 1962, *Burtt & Woods 2185* (E); 5th Div., Bakelalan, 4,000 ft., 1955, *Brooke 10411* (L); 5th Div., Kalabit Highlands, Apa Balu Buli, 1,700 m, 1970, *Nooteboom & Chai 2198* (L); 7th Div., ridge NW of Sungei Tellini, 2,900 ft., 1978, *Burtt 11443* (E); 7th Div., Bukit Lamut, Ulu Amau, 950 m, 1964, *Ashton S21265* (L). KALIMANTAN: E Prov., between Long Bawan and Panado, 1,800 m, 1981, *Geesink 9113* (L); E Prov., W Kutei, near Kemoel, 1,200 m, 1925, *Endert 3800* (L); 1,500 m, 1925, *Endert 3916* (A, K, L, SING).

12. Argostemma gaharuense B. Bremer, sp. nov. TYPE: Borneo. Sarawak: 1st Div., Bukit Gaharu, 2,000 ft., 1962, *Burtt 2655* (holotype, E). Figure 15.

Herba pusilla, ramosa, inflorescentiis floribus solitariis vel paucis. Folia opposita, illis parium inaequalissimis, pubescentia. Inflorescentia corymbosa, floribus pusillis. Lobi calycis triangulares, acuti. Lobi corallae reflexi. Antherae et appendices apicales connatae praeter partem apicalissimam. Appendix apicalis ½ longitudinem antherae aequans, tenuis, laevis. Connectivum indistinctum. Stylus glaber, stigmate vix dilatato.

Argostemma rupestre simile sed planta pubescens, ramosa, lobis corollae reflexis, fructu costato differt.

Small, creeping(?) herb. Stem to 20 cm, branched, glabrous; internodes very short to 4 mm. Leaves opposite, very unequal; stipules 2–3 mm long, ovate to cordiform, acute at apex; larger leaves of the anisophyllous pairs with glabrous petioles 1–2 mm long; lamina 0.4–0.6 × 0.2–0.4 mm, elliptic to narrowly so, basally cuneate to attenuate with the lobes equal, marginally entire, apically acute, coriaceous, pubescent above and glabrous below; midrib distinct but without primary veins. Nanophyllous leaves persistent, 2–3 mm long, ovate to elliptic, acute. Inflorescences 1–6-flowered, laxly corymbiform, many together; peduncle 1.4–2.8 cm, glabrous; bracts ca. 1 mm long, lanceolate; pedicels 0.5–1.4 cm, glabrous. Flowers 5-merous; calyx lobes ca. 1 mm long, triangular, acute, glabrous; corolla ca. 4 mm long, cleft to near the base, glabrous on both surfaces; lobes ovate, acute, reflexed. Stamens 3.5–4 mm long, coherent; anther cells and apical appendages connate except for the most apical part; anther cone ovoidal, straight; filaments very short, equal, straight; sacs opening completely longitudinally; apical appendage ca. ½ the anther length, thin and smooth; connective indistinctly passing over to the thecae, smooth. Style ca. 4.5 mm long, glabrous, with a scarcely widened stigma, shortly exserted. Fruit with 5 distinct ribs corresponding to the middle vascular strands of the calyx lobes.

Argostemma gaharuense was collected by Burtt at 660 m at Bukit Gaharu. Its habit is not given on the herbarium label.

On the label of the type specimen is written: "Leaves dark green above, white below. Corolla white, lobes strongly reflexed. Base of anther cone green, tips white." It is a small, easily recognized plant. The leaves are dark and pubescent on the upper surfaces, and below they are white and glabrous. The stems are distinctly branched distally with many apical inflorescences, each with one to six flowers in lax cymes. The vascular strand to each calyx lobe becomes a distinct rib, making the fruit five-ribbed. The habit is similar to that of *A. rupestre*, *A. geesinkii*, and *A. burttii*, but *A. gaharuense* differs from these by having monoseriate leaf hairs, branched stems, and reflexed corolla lobes. The leaf and stipule shapes are the same as those of *A. geesinkii*. The specimen from Gunong Apeng has narrower leaves than the type, and there is only one inflorescence with two flowers. However, it has reflexed corolla lobes and the same kind of indumentum.

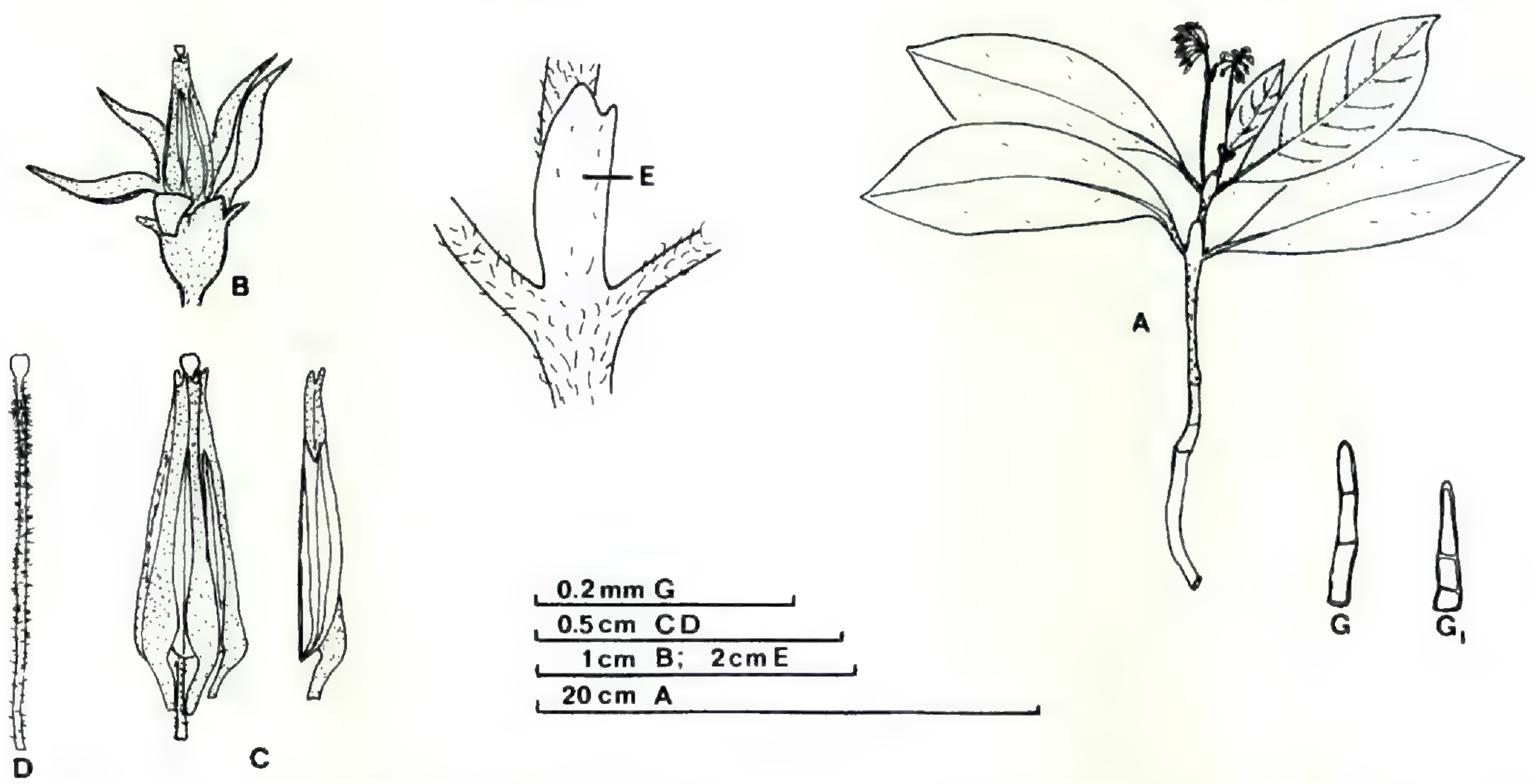


FIGURE 16. *Argostemma hameliifolium*.—A. Flowering branch.—B. Flower.—C. Anthers.—D. Style.—E. Stipule.—G. Hair from outer surface of the corolla.—G_1. Hair from inner surface of the corolla. A, E from *Bremer 1752* (S); B–D, G from *Richards 1799* (L).

Additional specimen examined. BORNEO. SARAWAK: 2nd Div., Gunong Apeng, 3,000 ft., 1961, *Collenette s.n.* (K).

13. Argostemma hameliifolium Wernham in Gibbs, J. Linn. Soc. Bot. 42: 89. 1914. TYPE: British North Borneo. Kinabalu: before Lobang rock, 5,000 ft., 1910, *Gibbs 4101* (holotype, K; isotype, BM). Figure 16.

A. hullettii Ridley, J. Bot. 65: 35. 1927. TYPE: Borneo. Sarawak: Matang, 2,000 ft., 1884, *Hullett 329* (lectotype, SING; Bakh. f. in herb., confirmed here).

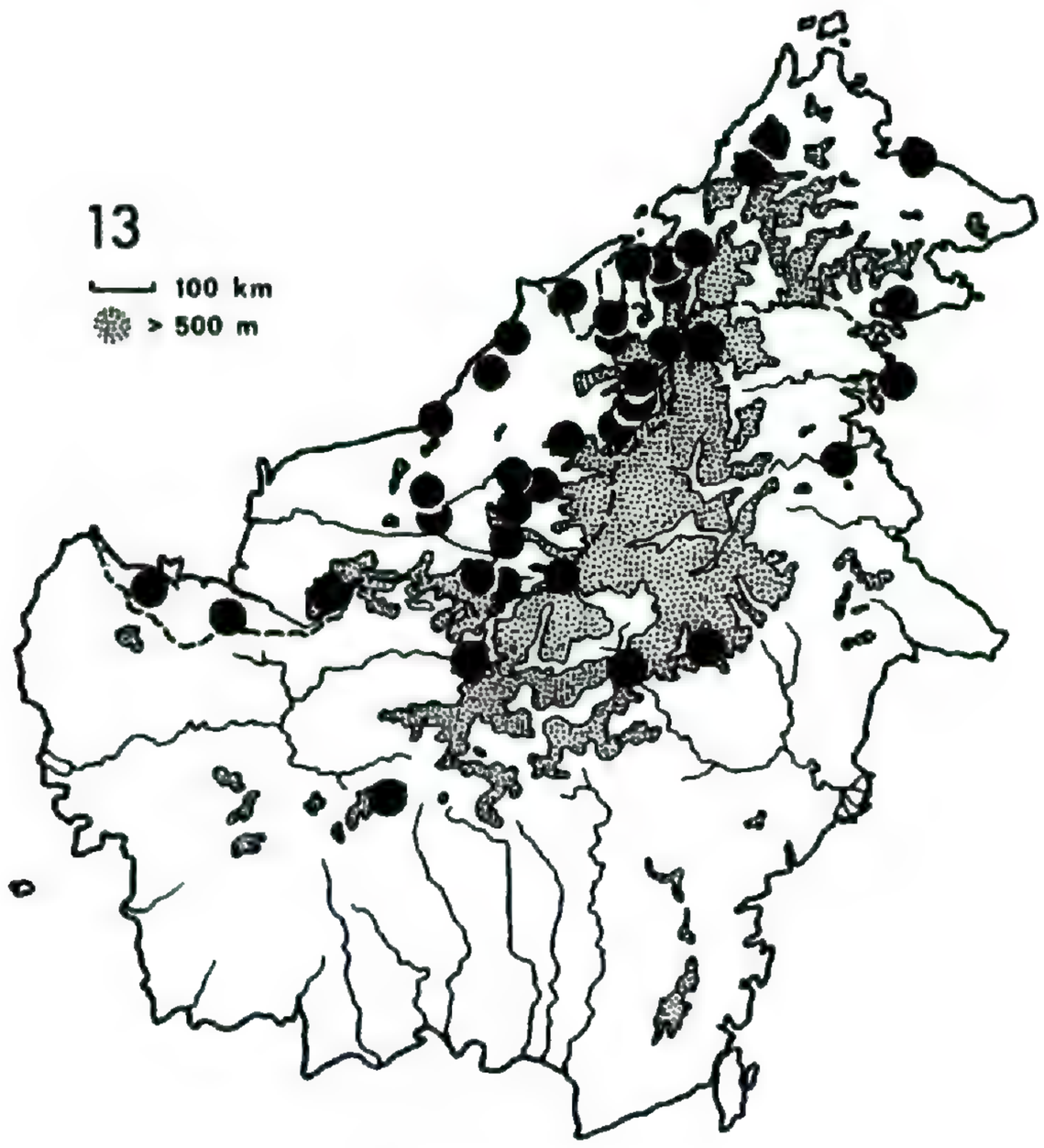
A. isophyllum Merr., Mitt. Inst. Allg. Bot. Hamburg 7: 279. 1937. TYPE: West Borneo: Bukit Raja, 1,400 m, 1924, *Winkler 949* (holotype, HBG; isotype, NY).

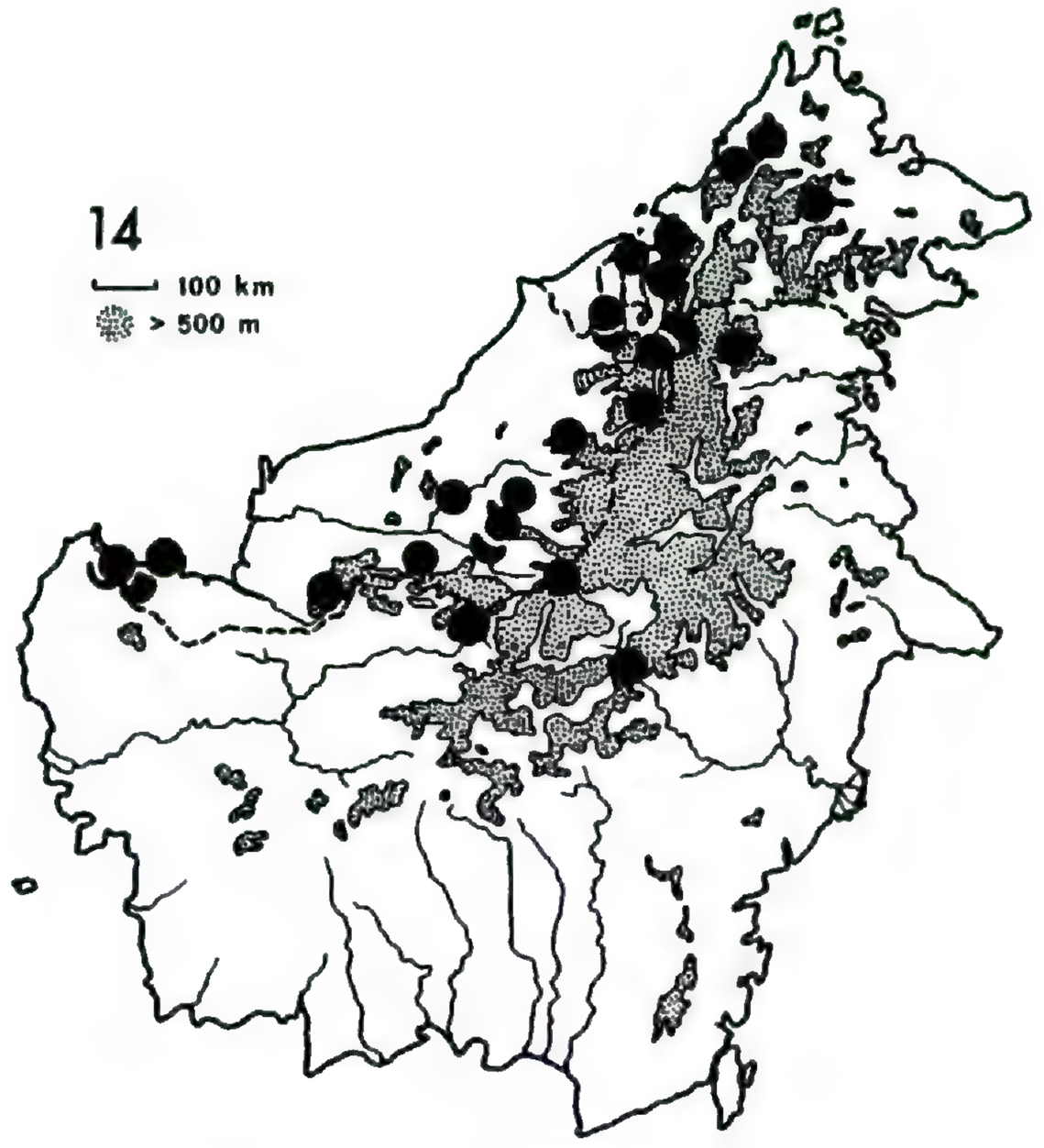
Large, erect, isophyllous herb. Stem 10–100 cm, unbranched, glabrous to pubescent, rarely with corky or papery bark; internodes 10–85 mm. Leaves opposite, equal; stipules deciduous, 5–27 mm long, oblong to lanceolate to ligulate, entire or slightly bifid, acute to acuminate or obtuse at apex; petiole 4–30 mm long, glabrous to pubescent; lamina 5–19 × 1–8.7 cm, oblanceolate or obovate to lanceolate or ovate, basally attenuate to acute or cuneate with the lobes equal, marginally entire, apically acuminate to acute or rarely obtuse, herbaceous, glabrous to finely pubescent above, glabrous to pubescent below; midrib and primary veins (6–12 pairs) distinct. Inflorescences 3–40-flowered, umbelliform and rarely with 2 or 3 scorpioid branches, generally solitary; peduncle 2–7.5 cm, almost glabrous; bracts to 5(–10) mm long, lanceolate to linear; lateral branches, if present, to 3.5 cm long, almost glabrous; pedicels 6–12 mm long, finely pubescent. Flowers 5-merous; calyx lobes 1–1.5 mm long, triangular to ovate, acute, finely pubescent; corolla 4–7 mm long, cleft to near the base, externally glabrous or pubescent, internally glabrous to pubescent; lobes lanceolate, spreading to reflexed. Stamens 3–6 mm long, coherent; anther cells and apical appendages connate except for the free and incurved most apical parts, each of these formed into an open cylinder; anther cone ovoid, straight; filaments generally short, equal, straight or bent; sacs opening completely longitudinally; apical appendage ca. ¼–⅓ the anther length, thin and smooth; connective distinct, generally smooth. Style 4.5–7.5 mm long, pubescent or rarely glabrous, with a capitate stigma, shortly exserted. Fruit without furrows or ribs.

Ridley based *A. hullettii* on three collections, by *Haviland* and by *Hullett*. All are suitable for lectotypification. Bakhuizen f. (in herb.) selected the single *Hullett* specimen in SING, and I follow his choice. The elevation mentioned in the protologue is indicated only on that specimen.

Argostemma hameliifolium is common and is widely collected. It grows from low altitude to 2,000 m. Most collections are from sandstone; a few are from limestone. It grows on boulders or sand in wet places near streams or waterfalls.

Argostemma hameliifolium is part of a big, poorly understood complex, which includes *A. moultonii* (see discussion under that species). Ap-





MAPS 13, 14. Distributions in Borneo.—13. *Argostemma hameliifolium.*—14. *A. moultonii.*

proximately 100 specimens have been referred to *A. hameliifolium*, all large plants with large, equal, opposite leaves and more or less erect stems. The leaves vary in shape and size and in distinctness of nervation. In a few cases the leaves are very broad and obtuse; these are similar in appearance to *A. borragineum*. The stipules, of which only the upper first to third pairs are persistent, are large, ovate to ligulate, and entire or slightly cleft. The flower buds are narrowly ovate in outline. The anther cone is high with short, free apical appendages and generally short filaments. The margins are longer than the central part and incurved so that each apical appendage forms an open cylinder. The style is generally hairy with a distinct capitate and slightly bifid, slightly exserted stigma. In this treatment I maintain *A. hameliifolium* separate from *A. moultonii*. There are many distinguishing characters, though not always constant, and many specimens are impossible to determine with certainty. *Argostemma hameliifolium* is more erect and has larger vegetative organs. Its anthers have short apical appendages and shorter filaments.

Additional specimens examined. BORNEO. BRUNEI: Kuala Belalong, Temburong, 200 ft., 1957, *Ashton 42* (K); Belatai District, Labi area, 1969, *van Niel 4580* (L). SABAH: W Coast Res., Kinabalu, E shoulder, 6,500 ft., 1961, *Chew et al. 1041* (K, L, SING); Ulu Liwagu and Ulu Mesilau, 1961, *Chew et al. 2875* (BO, K, L, SING); Dallas, 3,000 ft., 1931, *Clemens 26033* (BM, BO, G, GH, K, L, NY, UC); Tenompok, 4,500 ft., 1931, *Clemens 26990* (BM, BO, G, GH, L, NY, UC); Tenompok, 5,000 ft., 1932, *Clemens 29538* (BM, BO, G, K, L, NY); Marai Parai, 5,000 ft., 1933, *Clemens 32578* (A, BM, BO, L, NY, UC); Penibukan, 4,000 ft., 1933, *Clemens 35137* (BM); Penibukan, 4,000–5,000 ft., 1933, *Clemens s.n.* (BM); Kiau, 1915, *Clemens 10059* (UC); 1958, *Collenette 116* (BM); 1,650 m, 1966, *Ding Hou 220* (L); 1937, *Grieswold 29* (GH); western route, 1,780 m, 1963, *Fuchs 21031* (L); Penibukan, 1,200 m, *Nooteboom & Aban 1552* (L); Penibukan, 1,400 m, *Nooteboom & Aban 1593* (L); W Coast Res., Kandusan, 4,500 ft., 1957, *Cox 957* (L); 4,000 ft., 1966, *Sidek Kiah 2* (L); Sandakan Res., Bettotan near Sandakan, 1927, *Kloss SFN19154* (K, L, NY, SING, UC); Sandakan Res., Sandakan, 1977, *Anderson 4284* (MO, UC); Tawau Res., Tawau Hill, 1978, *Fedilis & Sumbing SAN88281* (K, L); Interior Res., Tenom District, along Sungei Bekuku, 1979, *Madani 90812* (L). SARAWAK: 1st Div., Mt. Matang, 1888, *Haviland s.n.* (SING); 1,000 ft., 1924, *Mjöberg s.n.* (UC); the boundary between 1st and 2nd Div., Gunong Bari, 1975, *Martin & Ismawi S36861* (L, SAR); 2nd Div., Bukit Lanjak, 4,300 ft., 1974, *Chai S33836* (L, SAR); 4th Div., Mt. Lambir, 250 m, 1979, *Bremer 1752* (S, SAR); 1962, *Burtt & Woods 2372* (E); Sungei Lapoh, 1978, *Burtt 11565* (E, S); 4th Div., Gunong Subis, 1972, *Anderson S31672* (L); 4th Div., Bintulu, 1963, *Ashton S18063* (K, SAR); 4th Div., Bukit Mersing, Tau Range, 3,000 ft., 1956, *Purseglove 5256* (A, K, L, NY, SAR, SING); 4th Div., Sungei Tau, 300 ft., 1956, *Purseglove 5129* (K, L, NY); 4th Div., Mt. Dulit, under 300 m, 1932, *native collector 1256* (K); Dulit ridge, 1932, *native collector 1428* (L); under 300 m, 1932, *Richards 1052* (K); 1,100 m, 1932, *Richards 1799* (A, BO, L); Dulit trail, 100 m, *Richards 7090* (K); 4th Div., Gunong Api, 3,000 ft., *Chai S30081* (K, L); 4th Div., Gunong Mulu, 4,000 ft., *Burtt & Woods 2182* (E, SAR); N of Sungei Lansat, 1978, *Nielsen 204* (K); 800–1,000 m, *Nielsen 494* (AAU); 4th Div., Upper Baram River, *van Niel 3558* (L); 4th Div., Kalabit Highlands, Bario, 1,000 m, 1970, *Nooteboom & Chai 1704* (L); Batu Lawi, 1,250 m, 1970, *Nooteboom & Chai 2307* (B, L, SAR, US); 5th Div., Maputi, 1955, *Brooke 10123* (L); 5th Div., Lawas, 1955, *Brooke 10283* (BM, L); 5th

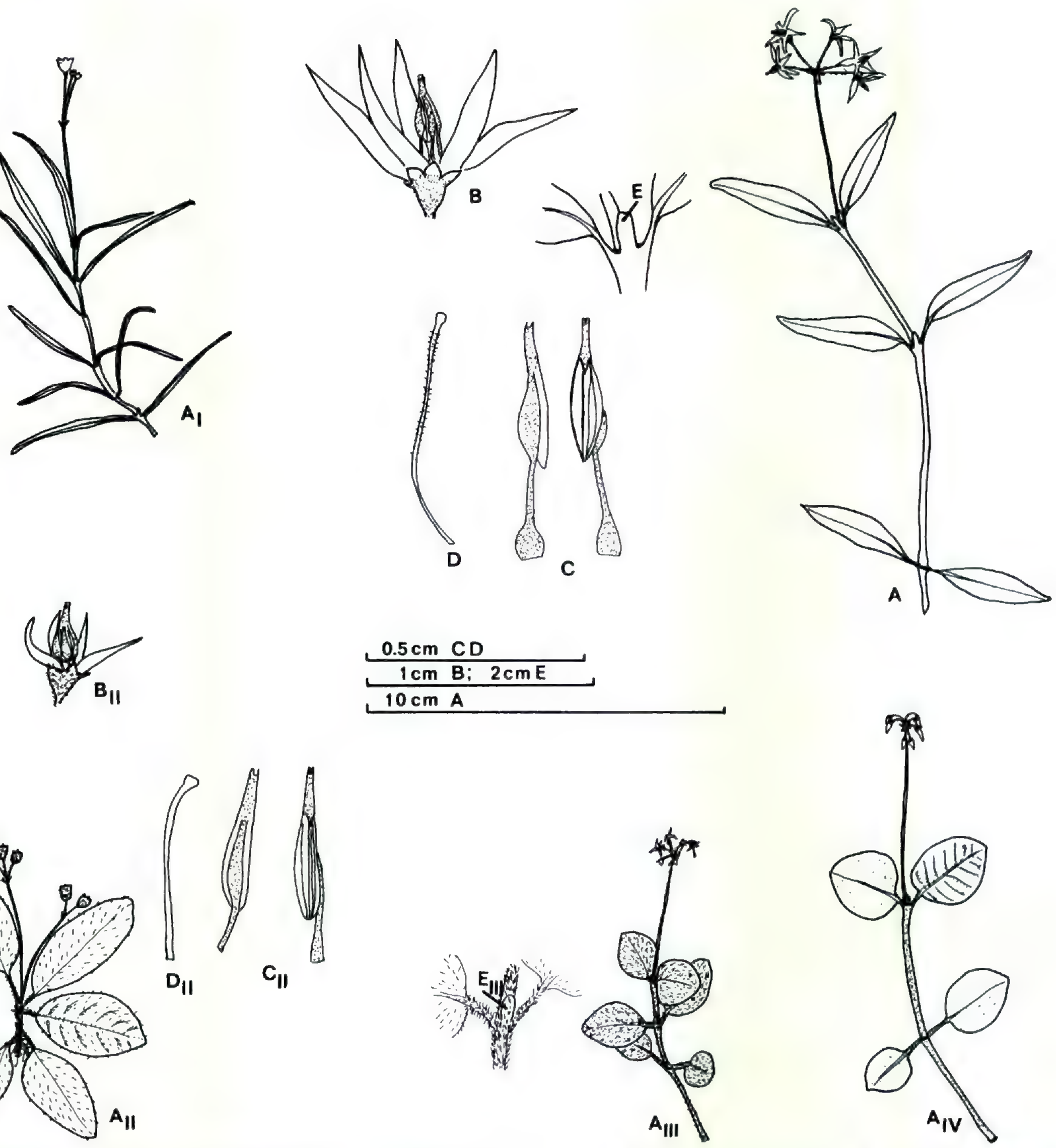


FIGURE 17. *Argostemma moultonii*.—A. Flowering branch.—B. Flower.—C. Anthers.—D. Style.—E. Stipule. A–E from *Burtt & Martin 5326* (E); I from *Chai S34832* (K); II from *Nooteboom 921* (L); III from *Mjöberg 82* (K); IV from *Moulton 6695* (SING).

Div., Bakelalan, 4,000 ft., 1955, *Brooke 10448* (BM, L); 7th Div., Sungei Mengiong, a tributary to Ulu Balleh, 1979, *Bremer 1747* (S, SAR); 7th Div., Sungei Putai, a tributary to Ulu Balleh, 1979, *Bremer 1725* (S, SAR); 7th Div., Bukit Tibang, 3,700 ft., 1969, *Anderson S28735* (K, L); 7th Div., Wong Pelagus, 1954, *Brooke 8984* (BM, K); 7th Div., Teneong, 1954, *Brooke 9128* (BM, L); 7th Div., Giam Pasang, 1954, *Brooke 9258* (BM, L); 7th Div., Ulu Melinau, 1980, *Burtt 12896* (E); 7th Div., Bukit Dema, 1978, *Burtt 11338* (E, S); 7th Div., Sungei Nawai, 2,600 ft., 1978, *Burtt 11461* (E, S); 7th Div., Sungei Linau, 1978, *Burtt 11274* (E, S); low alt., 1975, *Chai S36485* (L, SAR). KALIMANTAN: W Prov., Liang Gagang, 1893–1894, *Hallier 2779* (L); W Prov., Amai Ambit, 1893–1894, *Hallier 3230* (BO, L); E Prov., between Long Bawan and Pando, 1,200 m, 1891, *Geesink 9036* (L); E Prov., between Papadi and Pamilau, 700 m, 1981, *Geesink 9226* (L); E Prov., Banyankara, 1982, *Axelius 198* (S); E Prov., Nanukan Island, southern part, 1954, *Kostermans 9216* (K, L); Sungei Simengkadu, few m alt., 1953, *Meijer 2343* (L); E Prov., W Kutei, near Kemoel, 1,500 m, 1925, *Endert 4172* (A, BO, K, L); E Prov., Kutei, near Tabang, 50 m, 1955, *Kostermans 10570* (L).

14. Argostemma moultonii Ridley, J. Bot. 65: 36. 1927. TYPE: Borneo. Gunong Semapok, Upper Baram, 3,000 ft., 1920, *Moulton 6695* (lectotype, K; Bakh. f. in herb., confirmed here; isolectotype, SING). Figure 17.

A. moultonii var. *hirta* Ridley, J. Bot. 65: 36. 1927. TYPE: Borneo: Gunong Semapok, Upper Baram, 1,000 ft., 1920, *Moulton 6654* (holotype, K; isotype, SING).

A. parvulum Ridley, J. Bot. 65: 36. 1927. TYPE: Borneo: Lio Matu, Upper Baram, 500 ft., 1920, *Moulton 6726* (holotype, K).

A. velutinum Ridley, J. Bot. 65: 35. 1927. TYPE: Borneo: Serapi, 2,800 ft., *Haviland 684* (lectotype, K; Bakh. f. in herb., confirmed here).

A. mjoebergii Merr., Sarawak Mus. J. 3: 534. 1928. TYPE: Borneo. Sarawak: Mt. Poi, 4,500–5,500 ft., 1924, *Mjöberg s.n.* (holotype, UC).

A. murudense Merr., Sarawak Mus. J. 3: 535. 1928. TYPE: Borneo. Sarawak: Mt. Murud, 1,900–2,400 m, 1922, *Mjöberg 82* (holotype, UC; isotype, K).

Creeping to erect, isophyllous herb. Stem 2–40 cm, unbranched or slightly branched, glabrous to densely pubescent, rarely with corky or papery bark; internodes 5–60 mm. Leaves opposite, equal; stipules deciduous, 2–12 mm long, ovate to lanceolate, entire or slightly bifid, obtuse to acuminate at apex; petiole 3–11 mm long, glabrous to pubescent; lamina 1.2–6.5 × (0.2–)0.6–3.1 cm, linear to broadly ovate, basally rounded to attenuate, with the lobes equal or oblique, marginally entire or serrulate, apically obtuse with a short point or acute or acuminate, herbaceous, pubescent on both surfaces to glabrous; midrib distinct, the primary veins (4–7 pairs) distinct to obscure. Inflorescences 1–9-flowered, umbelliform, generally solitary; peduncle (1–)3–8 cm, glabrous; bracts to 5 mm long, ovate to lanceolate; pedicels 0.2–1.2 cm, pubescent. Flowers 5(–6)-merous. Calyx lobes ca. 1 mm long, triangular to ovate, acute, pubescent at least in lower parts. Corolla 3–9(–18) mm long, cleft to near the base, generally glabrous on both surfaces; lobes lanceolate, spreading to reflexed. Stamens 3–6 mm long, coherent; anther cells and apical appendages connate except for the most apical parts, these free and incurved, forming an open cylinder; anther cone ovoid, straight; filaments generally long, equal, straight or bent; sacs opening completely longitudinally; apical appendage ca. ⅓–½ of the anther length, thin and smooth; connective distinct, generally smooth. Style 3.5–6.5 mm long, pubescent or rarely glabrous, with a capitate stigma, shortly exserted. Fruit without furrows or ribs.

Bakhuizen f. (pers. comm. and on herbarium labels) treated *A. parvulum* as a synonym of *A. hameliifolium*; he believed it to be a dwarf form. However, I have found that *A. parvulum* is better accommodated as a synonym of *A. moultonii*.

Argostemma moultonii grows in wet, damp places among mosses on tree trunks, on cliffs, or on sandy or clayey soil, and a few collections are from limestone. It grows from low altitude up to ca. 2,000 m; most specimens are from ca. 1,000 m.

Ridley based *A. moultonii* on two collections by *Moulton*, in K. Both are suitable for lectotypification. Bakhuizen f. (in herb.) selected one of the specimens, *Moulton 6695*, and I follow his choice.

Ridley based *A. velutinum* on three collections, in K, by *Haviland*, *Moulton*, and himself. All are suitable for lectotypification. Bakhuizen f. (in herb.) selected the *Haviland* specimen, and I follow his choice.

Argostemma moultonii and *A. hameliifolium* form a complex in which a number of species have been recognized (see above). This complex is well defined as a group by unique characters: equal, opposite leaves; long, glabrous peduncles; pubescent pedicels; corolla cleft to near the base and with narrow, spreading or reflexed lobes; and connate anthers with distinct apical appendages which are free in the upper part and have margins longer than the central parts and incurved to form an open cylinder. There are at least two species (*A. hameliifolium* and *A. moultonii*) involved in the complex. I cannot recognize more in spite of the fact that this group is the most widely collected in Borneo. There are a few specimens similar in habit to the highly variable species *A. aequifolium* Ridley (1901) from the Malay Peninsula and Sumatra, but this species does not have the unique stamen characters. Specimens similar to the type of *A. hameliifolium*, erect, large plants, are referred to *A. hameliifolium*, but the rest could be separated into several variable groups within *A. moultonii*. There would be many specimens that could not be placed with certainty.

Argostemma moultonii needs further study. I have dealt with it in a manner similar to Dr. Bakhuizen f. (pers. comm.). *Argostemma moultonii* generally can be characterized and separated from *A. hameliifolium* by having a smaller, creeping habit, generally longer internodes, smaller stipules, and anthers with long filaments and long apical appendages. Within *A. moultonii* at least six local populations with distinct morphological characters can be identified. From some localities different populations are found without continuous variation between them. Characters separating these populations are indumentum of the stems, leaves, and floral parts and the shape, texture, and nervation of the leaves. The following examples illustrate this. At the summit of Mt. Matang the plants (including the type of *A. velutinum*) have ovate leaves with acuminate apices, distinct primary veins, and long petioles, and the plants are covered by long hairs. Close to that locality, at Lundu and Berumput, the collections (including the type of *A. mjoebergii*) are similar in habit but less pubescent and have shorter petioles and less distinct veins. At Gunong Murud several different populations occur. One is

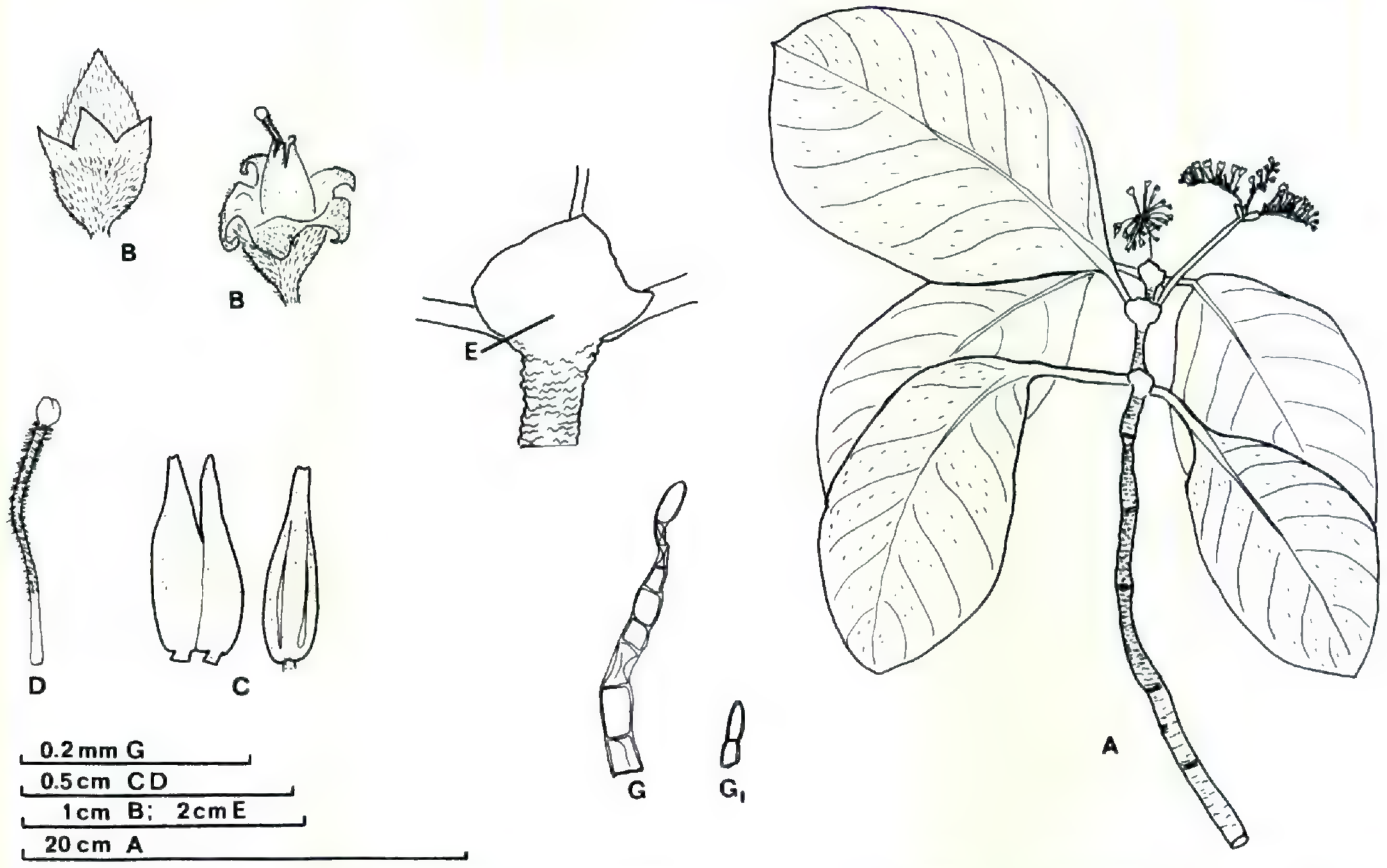


FIGURE 18. *Argostemma borragineum*.—A. Flowering branch.—B. Flower.—C. Anthers.—D. Style.—E. Stipule.—G. Hair from outer surface of the corolla.—G_1. Hair from inner surface of the corolla. From *Bremer 1668* (S).

almost glabrous (dry specimens) with very thick, veinless, elliptic, acuminate leaves and with very long internodes (*Burtt & Martin 5326, Nooteboom & Chai 1935*). Except for the very long internodes, they are similar to the type of *A. parvulum* from Baram. Another population includes the type of *A. murudense* with small, broad, ovate to rounded, obtuse to acute, densely pubescent leaves. These specimens are similar to the type of *A. moultonii* from the upper Baram. *Martin 38848* represents a different population with glabrous, obovate leaves with distinct prominent veins. From Ulu Tinjar in Baram, there is a collection (*Chai 34832*) with glabrous linear leaves. From Mt. Kinabalu, there are several different populations—one (*Gardner 88*) is glabrous with thick, veinless leaves but different from the glabrous specimens from Gunong Mulu. There are also specimens with ovate to obovate, slightly pubescent leaves. Plants from Kutei and Gunong Tapa Sia in Kalimantan (*Endert 3614, 4238* and *Axelius 112B*) are small rosettes with ovate, obtuse leaves having very long hairs. These collections are similar to *Nooteboom 921* from Gunong Alab in Sarawak. Perhaps these represent something different and distinct from *A. moultonii*, but based on the scanty material available, it is impossible to decide.

Additional specimens examined. BORNEO. BRUNEI: Kuala Belalong, 1959, *Ashton 199* (K). SABAH: W Coast Res., Kinabalu, Silau Silau trail, 1,400 m, 1979, *Anderson 4349* (MO, UC); Bebangan River, 5,000 ft., 1964, *Chew & Corner RSNB4618* (K); Tenompok, 5,000 ft., 1932, *Clemens 28250* (BM, BO, K); Tenompok, 5,500 ft., 1932, *Clemens 29499* (BM, K); Columbon basin, 4,500 ft., 1933, *Clemens 40049* (BM, BO, NY); Masilau, 6,000–8,000 ft., 1933, *Clemens 51670* (BM, NY); Marai Parai, 6,000 ft., 1958, *Collenette 60* (BM); 1937, *Grieswold 27* (GH); Lumu-Lumu, 1957, *Sinclair 9212* (E, L); W Coast Res., Gunong Alab, Crocker range, 1,600 m, 1980, *Argent 1308* (E); 1,400 m, 1969, *Nooteboom 921* (B, L); 1,600 m, 1969, *Nooteboom 1035* (L); Sandakan Res., Tawau Plateau, 50 m, 1977, *Gardner 88* (E, L); Interior Res., Sipitang, Ulu Moyah, 2,750 ft., *Wood SAN16695* (L, SING). SARAWAK: 1st Div., Mt. Matang (= Gunong Serapi), near summit, 2,700 ft., 1966, *Anderson S25106* (K); 1865, *Beccari 1716* (L); near summit, 2,700 ft., 1919, *Bremer 1719* (S, SAR); ca. 2,500 ft., 1962, *Burtt & Woods 2516* (E, SAR); near summit, 2,500 ft., 1929, *Clemens 223221* (NY); 2,500–3,000 ft., *Mjöberg s.n.* (UC); 1927, *native collector s.n.* (UC); 1905, *Ridley 12304* (BM, K, SING); 1st Div., Santubong, near summit, 1909, *Brooke 1034* (BM); 1st Div., Gunong Gading, 2,800 ft., 1962, *Burtt & Woods 2682* (E); 1st Div., Mt. Poi, 5,000–6,000 ft., 1929, *Clemens field no. 6891, 6920, 6973* (NY); 1st Div., Gunong Berumput, 4,800 ft., 1954, *Brooke 8564* (BM, L); 300 ft., 1962, *Burtt & Woods 2761* (E); 3,500 ft., 1962, *Burtt & Woods 2845* (E); 2nd Div., E of Bukit Sadon, 1982, *Axelius 112B* (S); 4th Div., Mt. Dulit, Dulit trails, 800 m, 1932, *Richards 1537* (K, L); Dulit ridge, 1,100 m, 1932, *Richards 1790* (K, L); 4th Div., Bario, 1,000 ft., 1970, *Nooteboom & Chai 1744* (B, L, SAR, US); 4th Div., Mt. Murud, 1,900–2,400 ft., 1922, *Mjöberg 85* (UC); 1,900–2,400 ft., 1922, *Mjöberg 88* (NY, UC); 1914, *Moulton 105* (probably cited as 165 in the

protologue of *A. velutinum*) (SING); 1,100 m, 1970, *Nooteboom & Chai 1856* (L, SAR, US); 1,700 m, *Nooteboom & Chai 1935* (B, L, US); 4th Div., Sungei Melinau, 1962, *Burtt & Woods 2293* (E); 4th Div., Gunong Mulu, 4,200 ft., *Anderson S4516* (K, SAR); 1,700 m, *Argent & Jermy 1038* (E), 1,300 m, 1978, *Argent & Coppins 1076* (E); 1962, *Burtt & Woods 2090* (E); 4,500 ft., 1962, *Burtt & Woods 2095* (E, SAR); 4,500 ft., 1962, *Burtt & Woods 2152* (E); 150 m, 1978, *Hansen 187* (K); 1,300 m, 1977, *Martin S38848* (L, SAR); 1,800 m, 1978, *Nielsen 838* (AAU); 5th Div., 1½ days from Maputi, 2,500 ft., *Brooke 10177* (BM, L); 5th Div., Bakelalan, 4,000 ft., 1955, *Brooke 10408* (L); 5th Div., from Bakelalan to Gunong Murud, 6,000 ft., 1967, *Burtt & Martin 5326* (E); 7th Div., Bukit Bakar (= ?Bakak), 980 m, 1975, *Ilias Paie S36357* (L); 7th Div., Sungei Nai Punan Bah, 1973, *Chai et al. S33328* (L, MO); 7th Div., near Punan Bah, 1979, *Tong & Banyeng S33271* (K, L, MO, SAR); 7th Div., Sungei Brearan, 1978, *Burtt 11355* (E, S), *11356* (E); 7th Div., Sungei Dema-nawai, 1978, *Burtt 11431* (E); 7th Div., Sungei Tellini, 2,800 ft., 1978, *Burtt 11401* (E); 2,850 ft., 1978, *Burtt 11409* (E, S); 7th Div., S Hose Mts., Bukit Salong, 1980, *Burtt 12709, 12908* (E); 950 m, 1976, *Chai S37296* (K, L, SAR); 7th Div., S Hose Mts., E of Bukit Sanpandai, 1980, *Burtt 12797* (E); 7th Div., Ulu Mujong, 200 m, 1964, *Ashton S12132* (K, L); 900 m, 1964, *Ashton S21238* (L, SAR); 200 m, 1964, *Ashton S21249* (A, L); 7th Div., Bukit Tibang, 3,000 ft., 1969, *Ilias Paie S28445* (A, E, K, L), *S28566* (K, L). KALIMANTAN: W Prov., ?Goenseng Kenepai, 1893–1894, *Hallier 1720* (BO, L); E Prov., W Kutei, 1925, *Endert 3614* (BO, L); near Kemoel, 1,300 m, 1925, *Endert 3874* (BO, L); near Kemoel, 1,600 m, 1925, *Endert 4238* (BO, L); E Prov., between Papadi and Pamilau, 1,200 m, 1981, *Geesink 9255* (L); E Prov., Gunong Tapa Sia, 1,800 m, 1981, *Geesink 9112* (L).

15. Argostemma borragineum Blume ex DC., Prod. 4: 417. 1830. TYPE: *Blume* in G-DC (holotype, G-DC, not seen; microfiche, LD!). Figure 18.

A. borragineum var. *rotundifolium* Valeton in H. Winkler, Bot. Jahrb. 44: 548. 1910. TYPE: S.O. Borneo: Batu Babi in Lumowia, 1908, *Winkler 2853* (lectotype, L; Bakh. f. in herb., confirmed here; isolectotypes, BM, BO).

A. streblosifolium Valeton, Icones Bogorienses 4: 271. 1914. TYPE: Borneo: Oeloe Tjihan, 1898–99, *Amdjah 319* (lectotype, BO; Bakh. f. in herb., confirmed here).

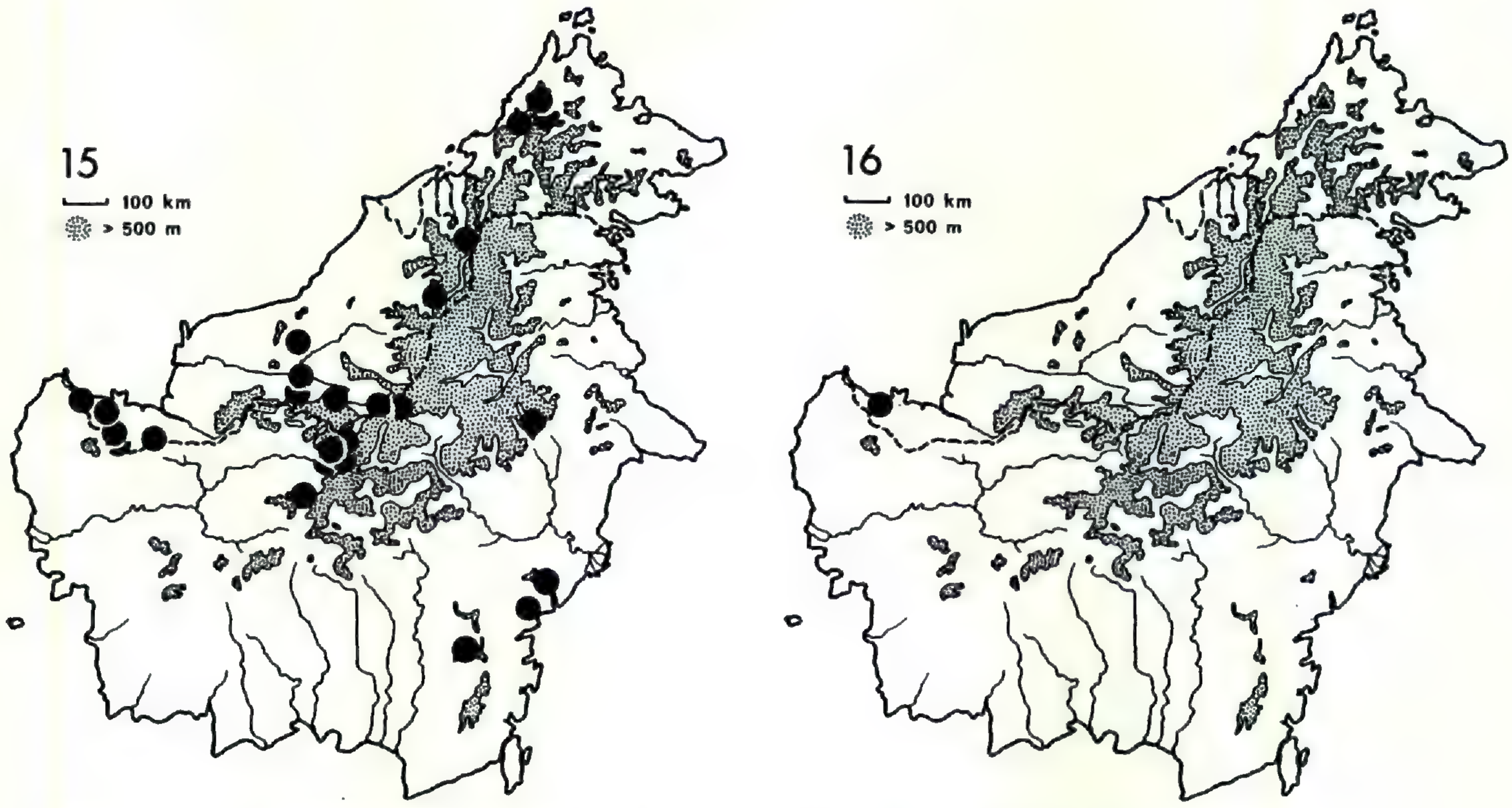
A. nutans var. *borneense* Ridley, J. Bot. 65: 33. 1927. TYPE: Borneo: Gunong Semapok ("Temapok" Ridley, 1927, sphalm.), 1,000 ft., 1920, *Moulton 6653* (holotype, K; isotype, SING).

Large, erect, isophyllous herb. Stem to 100 cm, glabrous to finely pubescent, black, with distinct scars in upper part; internodes 5–45 mm. Leaves opposite, equal; stipules persistent, ca. 10 mm long, broadly ovate, obtuse to acute at apex; petiole 0.5–7 cm, pubescent to glabrous; lamina 4.5–21 × 2.5–13 cm, broadly ovate to broadly obovate, basally rounded or acute to attenuate with the lobes equal, marginally entire or serrulate, apically obtuse, then sometimes with a point, or acute, herbaceous, glabrous to pubescent, most prominently pubescent on the veins below; midrib and primary veins (4–12 pairs) distinct. Inflorescences 25–160-flowered, umbelliform or with 2 or 3 scorpioid branches, solitary or a few together; peduncle 2–8 cm, glabrous to pubescent; bracts to 1 cm long, oblong to ovate; branches, if present, to 5 cm, glabrous to pubescent; pedicels to 2 cm, pubescent. Flowers 5-merous; calyx lobes 1–2 mm long, ovate to triangular or lanceolate, pubescent at least on basal parts; corolla 4–5 mm long, cleft to about middle, externally pubescent, internally glabrous to pubescent on the lobes; lobes ovate to triangular, recurved. Stamens 2–4 mm long, coherent, coriaceous; anther cells and apical appendages connate except for the most apical part; anther cone ovoid or shortly so, straight; filaments very short, equal, straight; sacs opening completely longitudinally; apical appendage ca. ⅓ the anther length, thin and smooth; connective indistinctly passing over to the thecae, smooth. Style 5–6 mm long, pubescent, with a capitate stigma, long-exserted. Fruit without furrows or ribs but covered with emergences.

Winkler based *A. borragineum* var. *rotundifolium* on one collection with several specimens. All specimens are suitable for lectotypification. Bakhuizen f. (in herb.) selected the specimen in L and I follow his choice.

Valeton did not indicate any collection in the protologue of *A. streblosifolium*. In the Bogor herbarium (BO) there is only one specimen (*Amdjah 319*) that fits the picture and the protologue. Bakhuizen f. (in herb.) has selected that specimen, and I follow his choice.

Argostemma borragineum is one of the most common *Argostemma* species from low altitudes to ca. 2,000 m. It often grows near shady streams. All notes concerning its habitat place it on sandy, loamy soil, sandstone, or sedimentary rocks. It is highly variable. The majority of the plants are large, to 1 m high, with black and scarred stems. The opposite leaves are equal, large, and rounded, and the stipules are broad and distinctive. The inflorescences are densely pubescent and generally very large, sometimes with more than 150 flowers. They commonly develop two or three scorpioid branches, which become most prominent after anthesis. The corollas are cleft for about half their length into recurved lobes. The stamens are unique. The entire stamen is coriaceous and (on dry specimens) dark, and no differences can be discerned between the connective and the thecae, at least not from the dorsal side. The apical appendages



MAPS 15, 16. Distributions in Borneo.—15. *Argostemma borragineum.*—16. *A. flavescens.*

are separated in a characteristic way. The style is generally densely pubescent and bears a distinct capitate stigma strongly exserted. There are also plants uniformly smaller in all organs except for the flower, with smooth stems and more densely pubescent inflorescences, but there are also other small plants which have scarred stems. Several different populations have been collected from Mt. Kinabalu. I have not found any correlation between the morphological variation and any pattern of distribution.

Additional specimens examined. BORNEO. SABAH: W Coast Res., Gunong Alab, 1,500 m, 1969, *Nooteboom 1031* (B, L, US); W Coast Res., Kinabalu, below Kambarangan, 6,000 ft., 1962, *Bogle 545* (GH); Kiau, 1915, *Clemens 10058* (BO, UC); Penibukan, 4,000–5,000 ft., 1932, *Clemens s.n.* (BM); ridge above Pina Taki, 4,000–5,000 ft., 1933, *Clemens 31077* (BM, BO, GH, NY); Marai Parai spur, 5,000 ft., *Clemens 32962* (A, BO); Marai Parai, Gigisan Creek, 4,500 ft., 27 Mar. 1933, *Clemens 33962* (BM, G, L, UC); headwater of Sadikan, 5,000 ft., 5 May 1933, *Clemens 33962* (NY, must be wrongly numbered cf. the one before); Lumu-Lumu, 6,100 ft., 1957, *Sinclair et al. 9215* (E, L, US); between Kinabalu and Ranau, 5,000 ft., 1954, *Darnton 568* (BM). SARAWAK: 1st Div., Sungei Lundu below Gunong Perigi, 1962, *Burtt & Woods 2710* (E, SAR); 1st Div., Mt. Matang, near summit, 2,300 ft., 1979, *Bremer 1720* (S, SAR); 1955, *Brooke 9749* (BM, L, SAR); 1,500 ft., 1929, *Clemens 22372* (NY, SAR); 1,000 ft., 1924, *Mjöberg s.n.* (UC); 1913, *Moulton's native collectors 365* (BM); 2,000 ft., 1960, *Sinclair 10355* (E); 1st Div., Kampong Grumbing, Padawan, 30 m, 1975, *Othman Ismawi S37437* (L, MO, SAR); 1st Div., Mt. Penrissen, 4,400 ft., 1924, *Mjöberg 218* (NY, UC); 1st Div., Sabal, 500 m, 1979, *Bremer 1668* (S, SAR); above the forestry office, 1979, *Bremer 1673* (S, SAR); 4th Div., Bukit Mersing, 3,000 ft., 1956, *Purseglove 5282* (A, K, L, SAR, SING); 5th Div., route from Bakelalan to Gunong Murud, 3,800 ft., 1967, *Burtt & Martin 5216* (E); 7th Div., Sungei Bena area, 1980, *Burtt 13003* (E); 7th Div., Bukit Goram, 1975, *Chai S36137* (L, MO); 7th Div., junction of Sungei Tekalit and Sungei Mengiong, 1979, *Bremer 1742, 1743* (S, SAR); 7th Div., Ulu Sungei Sadampa, 1,500 ft., 1969, *Anderson & Ilias Paie S28295* (E, L); 7th Div., foothills of Bukit Batu Tibang, 3,100 ft., 1969, *Anderson S28396* (A, K, L); 7th Div., Sungei Balang, 1969, *Anderson & Ilias Paie S28881* (A, E, K, L, SAR). KALIMANTAN: E Prov., Balikpapan District, Mentawir region, 1955, *Kostermans 10121* (L); S of Gunong Balikpapan, 1985, *Axelius 217* (S); E Prov., W Kutei, near Laih Leng, 200 m, 1925, *Endert 2952* (BO, L); W Prov., Bukit Raja, 1,250 m, 1924, *Winkler 879* (HBG, NY); 1,400 m, 1924, *Winkler 1007* (HBG, NY); W Prov., Sungei Malang, 70 m, 1925, *Winkler 1282* (HBG, NY); W Prov., Bukit Obat, 150 m, *Winkler 1353* (HBG); W Prov., Nanga Era, 100 m, 1925, *Winkler 1562* (HBG); W Prov., Liang Gagang, 1893–1894, *Hallier 2686* (BO, L).

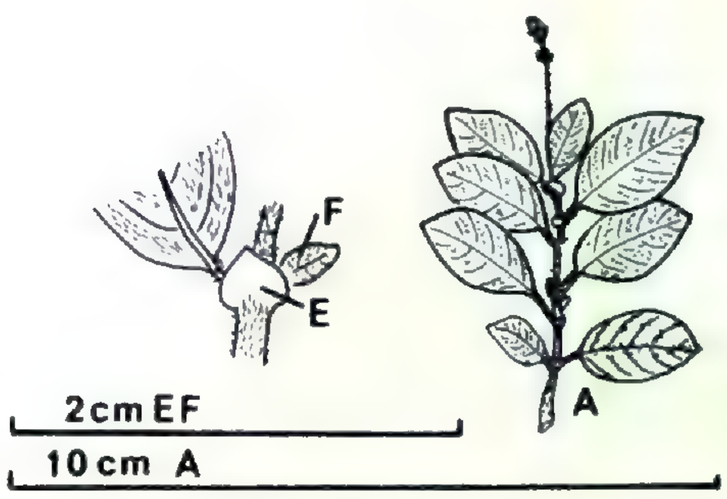


FIGURE 19. *Argostemma flavescens.*—A. Flowering branch.—E. Stipule.—F. Nanophyllous leaf. From *Haviland 84/75* (SING).

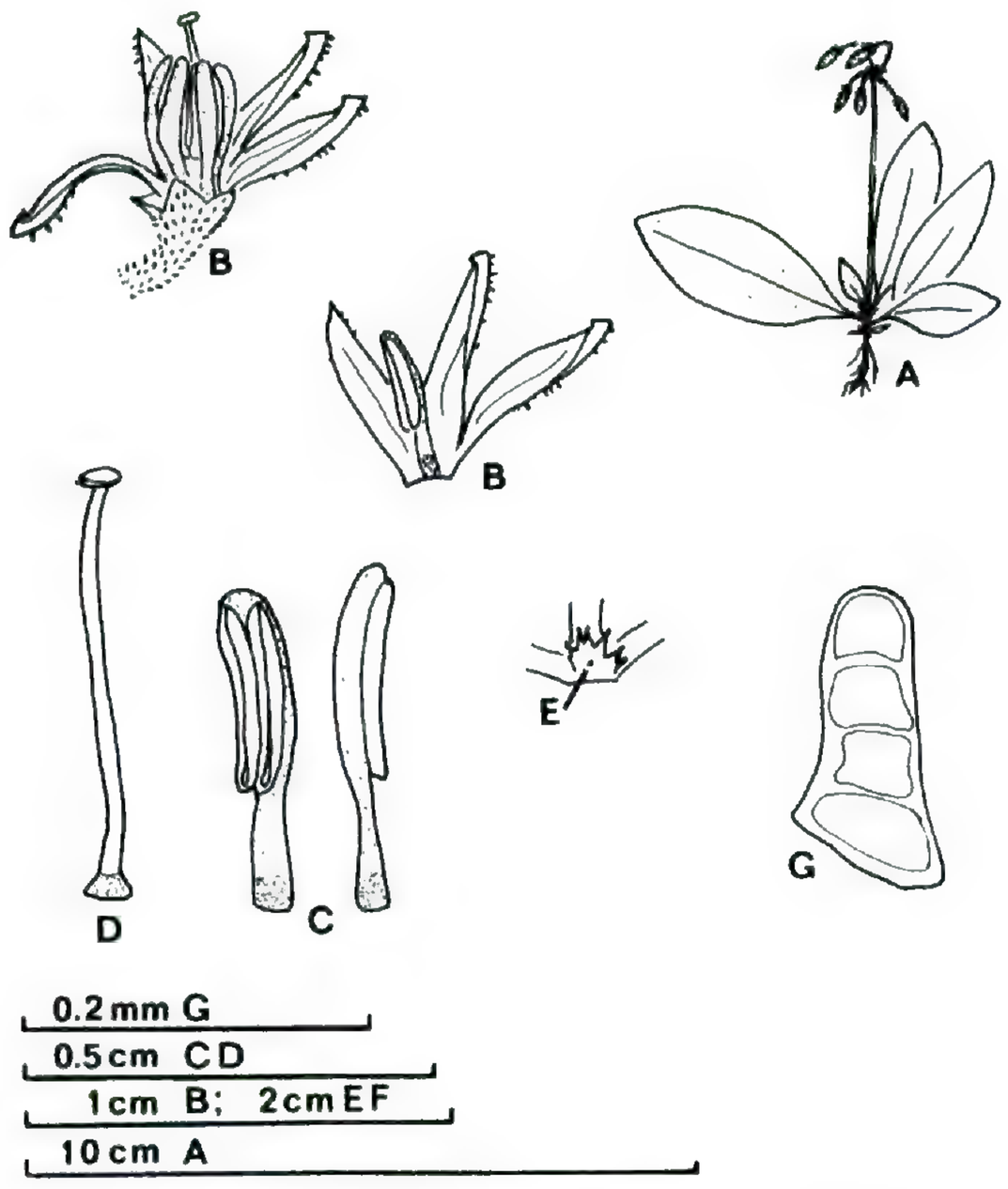


FIGURE 20. *Argostemma chaii*.—A. Habit.—B. Flower.—C. Anthers.—D. Style.—E. Stipule.—G. Hair from outer surface of the corolla. From *Brooke 10268* (L).

16. Argostemma flavescens Bakh. f., Blumea 7: 331. 1953. TYPE: Borneo. Path to Matang, *Haviland 84/75* (holotype, SING). Figure 19.

Creeping, anisophyllous herb. Stem ca. 10 cm, branched, pubescent; internodes 4–8 mm. Leaves opposite, very unequal; stipules persistent, to 3 mm long, ovate to cordiform, acute at apex; larger leaves of the anisophyllous pairs with pubescent petioles 3–8 mm long; lamina 1–3 × 0.1–1.5 cm, obovate to ovate or elliptic, basally obtuse to acute and oblique, marginally entire to serrulate, apically acute, herbaceous, pubescent between the veins; midrib and primary veins (5–7 pairs) distinct. Nanophyllous leaves persistent, ca. 3 mm long, ovate. Inflorescences 1–3-flowered, solitary; peduncle 1–2 cm, pubescent; bracts to 0.3 cm, lanceolate; pedicels 0.5–0.8 cm, pubescent. Flowers 5-merous; calyx lobes ca. 1 mm long, broadly ovate, acute, pubescent in lower part; corolla 4 mm long. Stamens 5. Style pubescent, with an elliptic stigma, long-exserted.

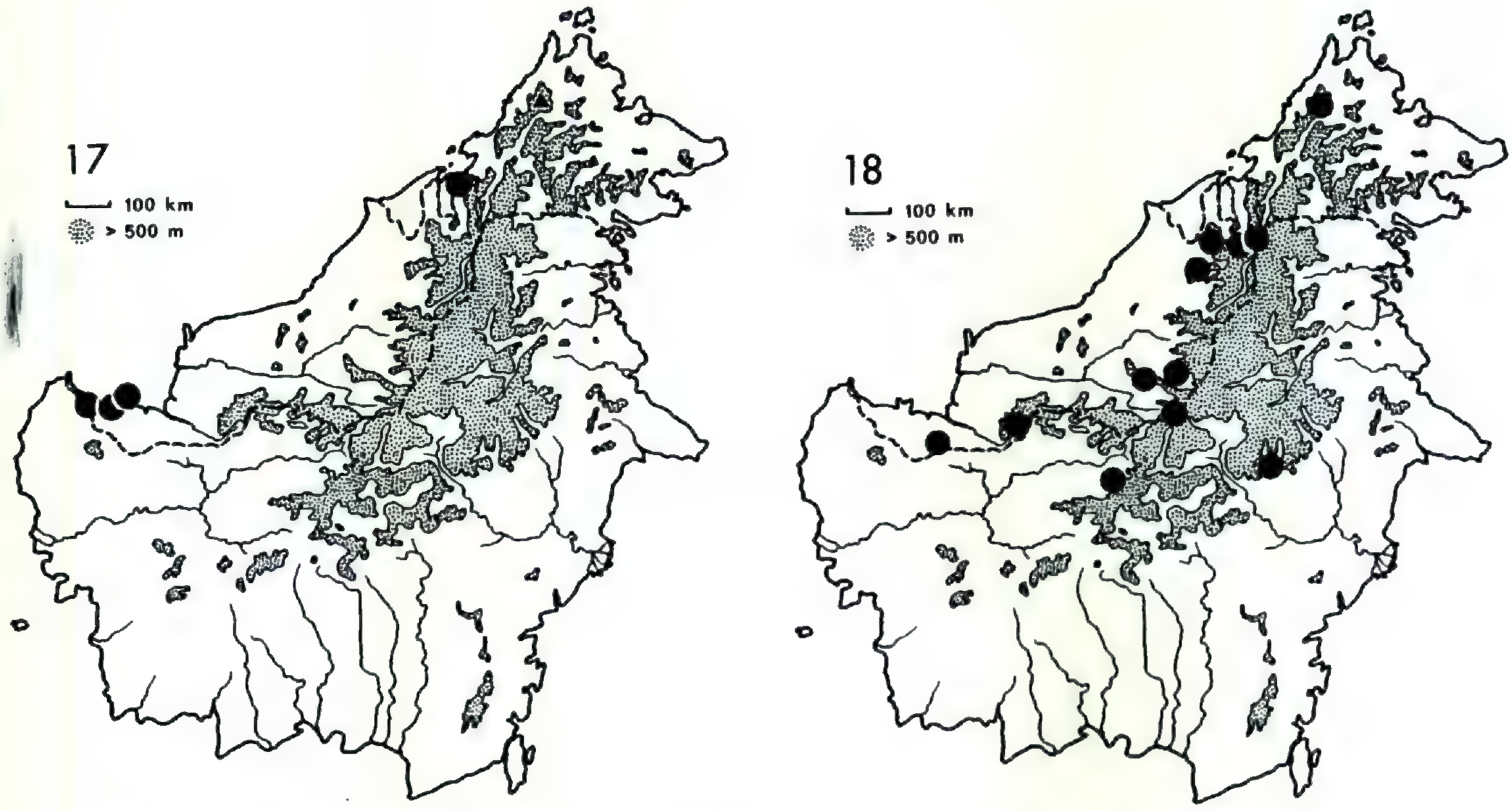
Argostemma flavescens is known from only two very poor collections. Both were examined, but there is still a great deal of information missing about the species. It has a characteristic habit, and its leaves are densely pubescent, particularly between the veins. In all other Borneo species the indumentum is more dense on the veins. The information on the flowers in the description is taken from Bakhuizen f. (1953, and pers. comm.). He placed *A. flavescens* close to *A. borragineum* because of its stamens. In my opinion it is not possible to determine its closest relatives within *Argostemma* at this time.

Additional specimen examined. BORNEO. SARAWAK: 1st Div., Mt. Matang, *Beccari 621* (L).

17. Argostemma chaii B. Bremer, nom. nov. *Argostemma enerve* Ridley (non Ridley 1912), nom. illeg., J. Bot. 65: 28. 1927. TYPE: Borneo. Sarawak: *native collector 1227* (holotype, K). Figure 20.

Small, erect, isophyllous herb. Stem very short to 11 cm, unbranched or slightly branched, glabrous; internodes very short to 10 mm long. Leaves opposite, subequal; stipules persistent, ca. 1 mm long, broadly ovate to cordiform, apically fringed with each point ending in a gland; petiole 3–9 mm long, glabrous; lamina 1.2–7 × 0.8–4.5 cm, ovate or elliptic or rarely lanceolate, basally acute to attenuate with the lobes equal, marginally entire, apically acute to obtuse, herbaceous to coriaceous, glabrous or with a few hairs above; midrib distinct, the primary veins obscure or absent. Inflorescences 2–15(–25)-flowered, umbelliform, solitary or a few together; peduncle 2–10 cm, glabrous; bracts to 0.6 cm long, ovate to lanceolate; pedicels 0.3–1.2 cm, pubescent or glabrous. Flowers 5-merous; calyx lobes 0.5–1 mm long, ovate to triangular, acute, glabrous to pubescent; corolla 3–5 mm long, cleft to near the base, externally pubescent or glabrous, internally glabrous; lobes lanceolate to oblong, erect-spreading. Stamens 3–4 mm long, at anthesis probably free; anther cells free, the apical appendage first connate then free, not forming a cone; filaments ca. ½ as long as the anthers, equal, straight; sacs opening completely longitudinally; apical appendages very short, thick and smooth; connective distinct, smooth. Style ca. 3–6 mm long, glabrous, with a discoid stigma, long-exserted. Fruit without furrows or ribs.

This species is named after Mr. Paul Chai of the Forest Department, Sarawak. *Argostemma chaii* grows on dead wood, wet rocks, or wet ground in the lowland rainforest, to 300 m. This species is a very small herb, with leaves more or less condensed into rosettes. Its primary veins are obscure, and the stipules are broad and fringed apically with colleters. The flowers are characteristic, with thick corolla lobes and free anthers. The filaments are wide, fixed at the base of the corolla, and adnate with it for a short distance. The stigma is discoid.



MAPS 17, 18. Distributions in Borneo.—17. *Argostemma chaii.*—18. *A. gracile.*

Argostemma chaii is a rare species collected from two different areas in Sarawak. The collections from the 5th Division are hairy on the pedicels, calyx, and on the outside of the corolla. The leaves also have scattered hairs. From the 1st Division the plants (including the type specimen) are glabrous in all parts. From Mt. Matang in the 1st Division the leaves are distinctly larger than from other localities.

Bakhuizen f. (pers. comm.) has treated this taxon as a synonym of *A. inaequale* (Bennett, 1838). Their habits are similar, but their flowers are different. *Argostemma inaequale* does not have the thick corollas nor the discoid stigma, and its anthers have long apical appendages, while the anther appendages of *A. chaii* are very short.

Additional specimens examined. BORNEO. SARAWAK: 1st Div., Bako, Telok Asam, 100 ft., 1956, *Purseglove 5096* (SING); 1st Div., Mt. Matang, 800 ft., 1954, *Brooke 9474* (L), *9478* (BM, L); 1st Div., Krangi, 1954, *Brooke 8502, 8512* (BM, L); 4th Div., G. Mulu, 120 m, 1978, *Nielsen 368* (AAU); 5th Div., Lawas, 1955, *Brooke 10542, 10268* (BM, L).

18. Argostemma gracile Stapf, Trans. Linn. Soc. London Bot. 4: 168. 1894. *Argostemella gracilis* (Stapf) Ridley, J. Bot. 65: 41. 1927. TYPE: Borneo. Kinabalu, Penokok, 3,500 ft., *Haviland 1325* (holotype, K; isotypes, SAR, SING). Figure 21.

A. podochiloides Merrill, Mitt. Inst. Allg. Bot. Hamburg 7: 279. 1937. Type: West Borneo: Bukit Tilung, 750 m, 1925, *Winkler 1479* (holotype, HBG; isotype, NY).

Small, creeping, anisophyllous herb. Stem 5–20 cm, slightly branched or unbranched, glabrous;

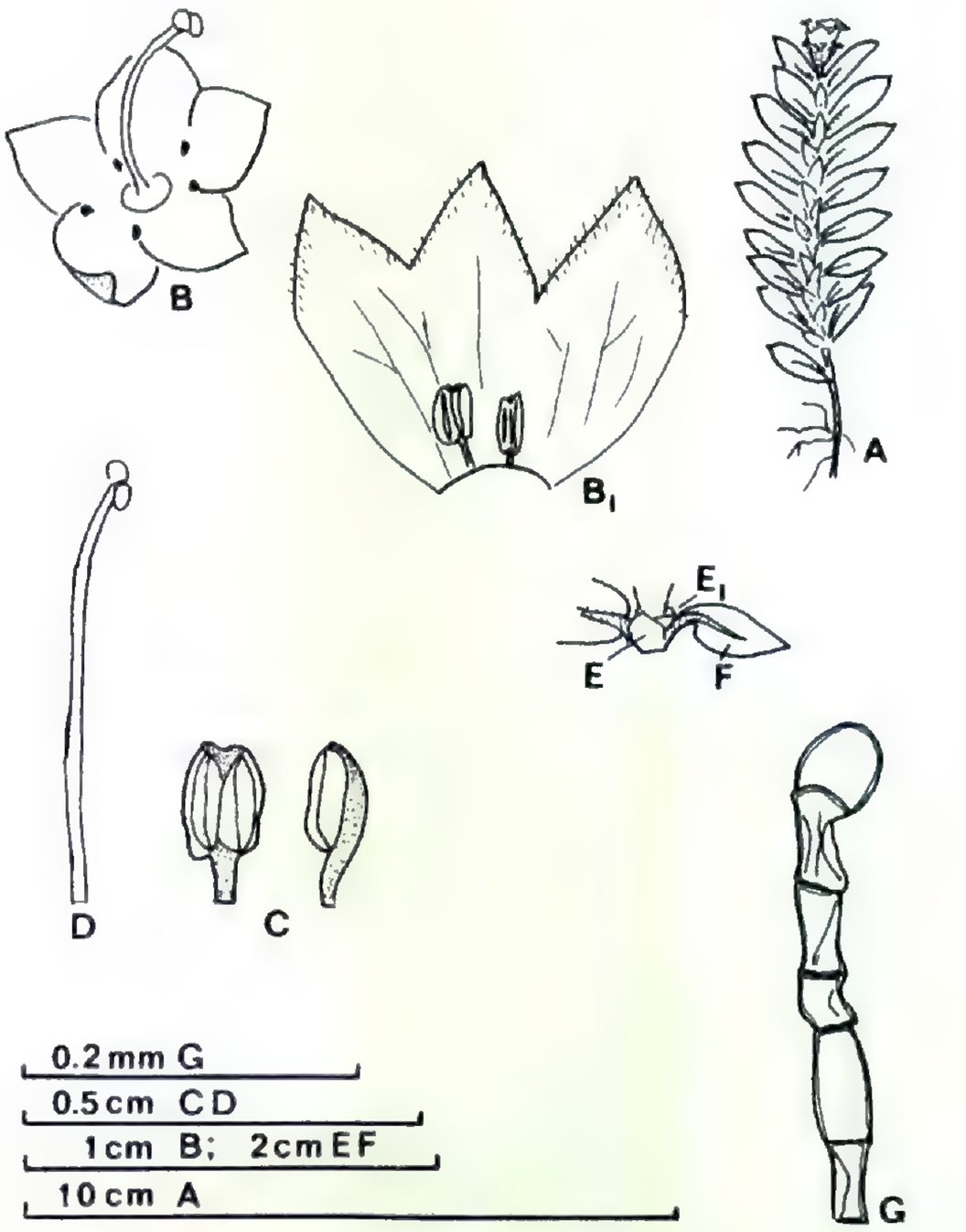


FIGURE 21. *Argostemma gracile.*—A. Habit.—B. Flower, inner surface of calyx.—B_1. Inside view of part of a corolla.—C. Anthers.—D. Style.—E. Stipule.—E_1. Amplexicaul sheath.—F. Nanophyllous leaf.—G. Hair from outer surface of the corolla. A from *Bremer 1667* (S); B–G from *Argent & Coppins 1142* (E).

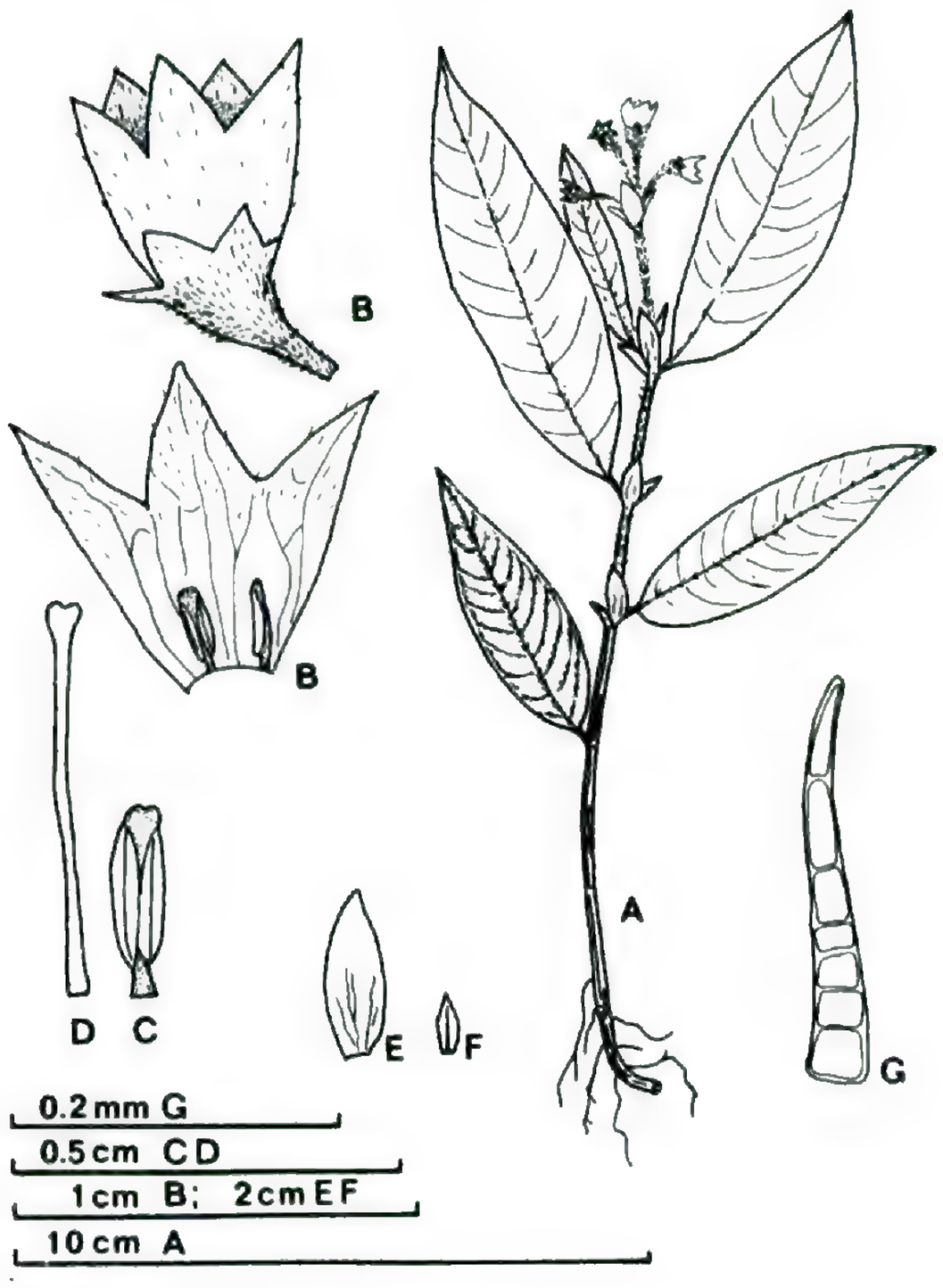


FIGURE 22. *Argostemma brachyantherum*. —A. Habit.—B. Flower.—C. Anther.—D. Style.—E. Stipule.—F. Nanophyllous leaf.—G. Hair from outer surface of the corolla. A from *Bogle et al. 389* (GH); B–G from *Hou 225* (L).

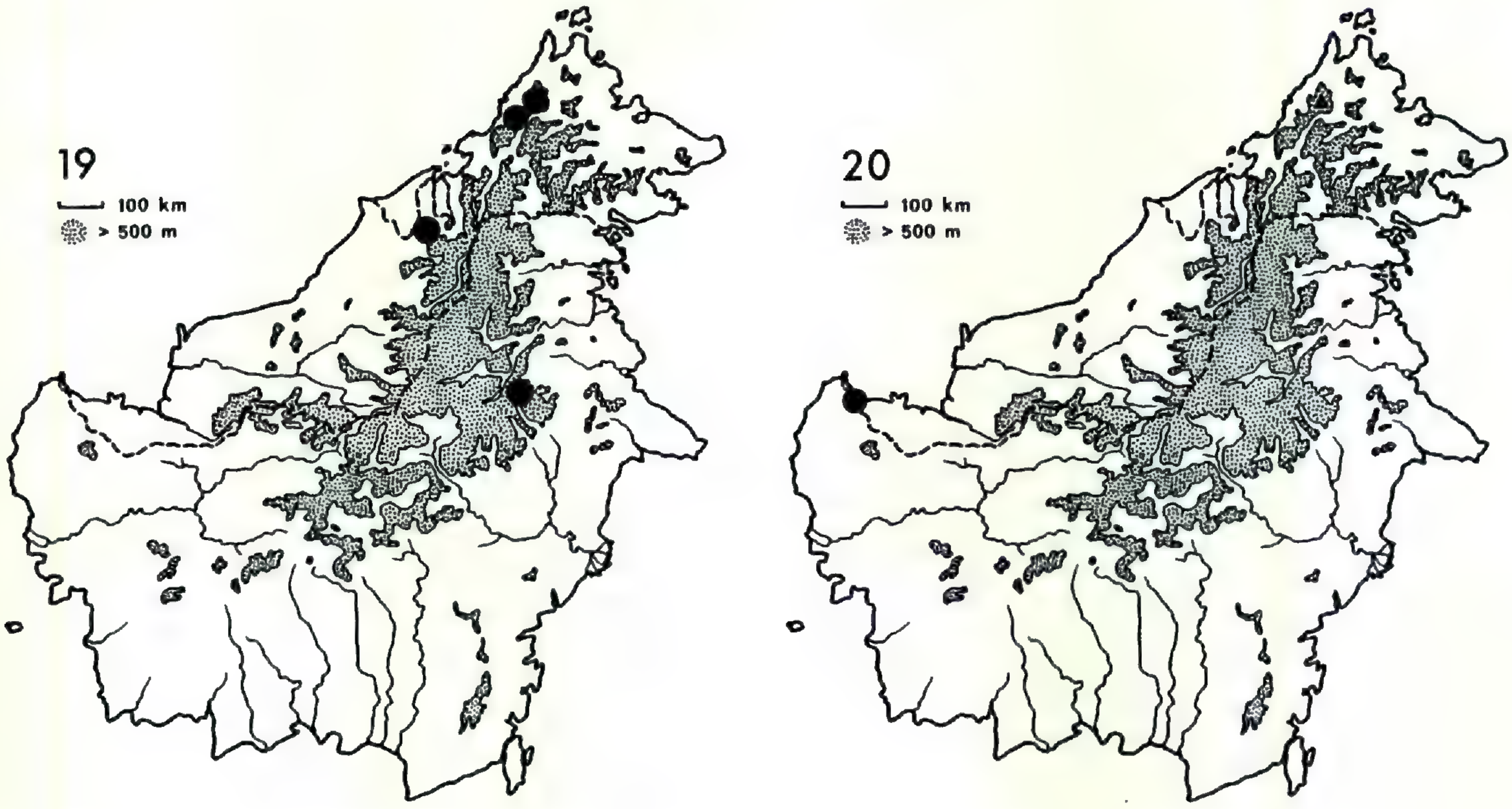
internodes 2–5 mm. Leaves opposite, very unequal, distichous, pale silvery underneath; stipules persistent, ca. 2 mm long, broadly ovate or cordiform to auriculiform, ending apically in a distinct point; stipules and petioles ± fused into an amplexicaul sheath. Larger leaves of the anisophyllous pairs with pubescent petioles 0.5–1.5 mm long; lamina 0.6–1.7 × 0.3–0.7 cm, oblong to narrowly oblong or rarely obovate, basally rounded or acute with the lobes equal or oblique, marginally entire, apically obtuse or obtuse with a point, or acute, herbaceous to coriaceous, glabrous or with scattered hairs somewhat concentrated along the midrib on both sides; midrib distinct but without primary veins. Nanophyllous leaves persistent, 4–5 mm long, ovate. Inflorescences 1-flowered, solitary, without peduncle; pedicel 0.2 cm, pubescent. Flowers 5(or 6)-merous; calyx lobes 2–3 mm long, triangular to cordiform, pubescent in lower parts; corolla ca. 8 mm long, cleft less than ⅓ its length, externally glabrous and internally pubescent only along the margins of the lobes; lobes broadly triangular, spreading. Stamens ca. 2.5 mm long, free; anther cells and apical appendage free, not forming a cone; filaments ca. ⅓–½ as long as the anthers, equal, straight; sacs opening completely longitudinally; apical appendages almost absent, thick and slightly papillose; connective distinct, smooth. Style ca. 5 mm long, glabrous, with a discoid, bifid stigma, long-exserted. Fruit without furrows or ribs.

Argostemma gracile grows on fallen rotten logs or on rocks among mosses in submontane or montane forests from 1,000 to 1,600 m. One collection (*Bremer 1667*) is from low elevation, 350 m, in an area of lowland rainforest with big boulders covered by mosses.

Argostemma gracile is easily recognized, with its creeping habit and distichous, anisophyllous leaves, the nanophyllous leaves above the larger leaves. The leaves are thick with a distinct midrib but without other visible veins. They are silvery white beneath. The petiole and midrib have a few hairs on both surfaces, but one exception is the type specimen of *A. podochiloides* with completely glabrous leaves. The stipules and petioles are more or less connate with the amplexicaul sheath. This character, combined with the glabrous leaves, has been used for recogniton of *A. podochiloides*, a species not accepted here. Flowers in *A. gracile* are solitary on very short pedicels and without peduncles. The corolla is campanulate with spreading lobes. The stamens are free, and there are practically no apical appendages. The stigma is distinctly bifid and discoid.

Additional specimens examined. BORNEO. SABAH: W Coast Res., Kinabulu, Ulu Langanani, 3,800 ft., 1961, *Chew et al. 1713* (A, K, L, SAR, SING); Tenompok, 5,000 ft., 1932, *Clemens 26926A* (BM, BO, K, L, NY); Columbon River, 4,500 ft., 1933, *Clemens 34110* (BM, BO, GH, L, NY, UC); Penibukan, 4,000 ft., 1933, *Clemens 32113* (B, BO, BM, G, GH, K, NY, UC); Penibukan, 4,000–5,000 ft., 1932, *Clemens s.n.* (BM, NY); Marai Parai spur, 1915, *Clemens 11076* (UC). SARAWAK: 1st Div., Sabal, 350 m, 1979, *Bremer 1667* (S, SAR); 2nd Div., Lubok Antu District, near Bukit Sengkajang, 1974, *Chai S34006* (K, L, SAR); 4th Div., Gunong Mulu, W ridge near camp 3, 1,300 m, 1978, *Argent & Coppins 1142* (E); near camp 4, 4,000 ft., 1962, *Burtt & Woods 2176* (E, SAR); 1,180 m, 1976, *Martin S38185* (L, SAR); 4th Div., Mt. Dulit ridge, 1,200 m, 1932 *Richards 1689* (K, L); S slope, 1,800 m, *Nielsen 833* (AAU); 5th Div., Bakelalan, 4,000 ft., 1955, *Brooke 10461* (BM, L); 5th Div., route from Bakelalan to Gunong Mulu, 3,800 ft., 1967, *Burtt & Martin 5211* (E); 7th Div., Belaga District, 2,900 ft., 1978, *Burtt 11444* (E); 7th Div., S Hose Mts., W of Bukit Sanpandai, 1980, *Burtt 12750A* (E); camp 6, 4,600 ft., 1980, *Burtt 12848* (E); 7th Div., summit ridge of Bukit Tibang, 5,000 ft., 1069 *Anderson & Ilias Paie S28667* (KLU, L, SAR). KALIMANTAN: E Prov., W Kutei, near Tabang, 600 m, 1956, *Kostermans 12851* (L).

19. Argostemma brachyantherum Stapf, Trans. Linn. Soc. London Bot. 4: 168. 1894. *Argostemmella brachyanthera* (Stapf) Ridley, J. Bot. 65: 41. 1927. TYPE: Borneo. Kin-



MAPS 19, 20. Distributions in Borneo.—19. *Argostemma brachyantherum.*—20. *A. brookei.*

abalu, 3,000 ft., *Haviland 1326* (holotype, K). Figure 22.

A. kinabaluense Wernham in Gibbs, J. Linn. Soc. Bot. 42: 88. 1914. TYPE: British North Borneo. Kinabalu, near Dahobang and Kinitaki rivers, 4,000–5,000 ft., 1910?, *Gibbs 4056* (holotype, BM; isotype, K).

Erect, anisophyllous herb. Stem 3–40(–80) cm, slightly branched or unbranched, densely pubescent in upper part, in lower part with corky or papery bark; internodes 2–20(–45) mm. Leaves opposite, very unequal; stipules deciduous or persistent, 4–10 mm long, oblong to lanceolate, acute to acuminate at apex; larger leaves of the anisophyllous pairs with pubescent petioles 2–5 mm long; lamina 2.5–9 × 1–3 cm, obovate or oblanceolate or elliptic to narrowly elliptic, basally acute to obtuse with the lobes equal or oblique, marginally entire or serrulate, apically acute to acuminate, herbaceous, glabrous or with scattered hairs above, pubescent on the veins below; midrib and primary veins (6–14 pairs) distinct. Nanophyllous leaves deciduous or persistent, 3–10 mm long, ovate to lanceolate, acute to acuminate. Inflorescences 1–6(–12)-flowered, umbelliform, solitary or a few together; peduncle 1–3 cm, pubescent; bracts 0.2–0.7 cm long, ovate to lanceolate; pedicels 0.5–1.5 cm long, pubescent. Flowers 5-merous; calyx lobes 2–5 mm long, ovate to triangular, acute, sparsely pubescent; corolla campanulate, cleft less than ⅓ their length, externally pubescent, internally papillose to pubescent only on the lobes; lobes triangular, acute, erect(?). Stamens 2–3(–4) mm long, free; anther cells and apical appendages free, not forming a cone; filaments short, equal, straight; sacs opening completely longitudinally; apical appendage ¼–⅕ the anther length, thick and slightly papillose; connective distinct, smooth. Style 3–6 mm long, glabrous, with a capitate stigma, long-exserted. Fruit without furrows or ribs.

Argostemma brachyantherum grows in submontane or montane forest between 1,000 and 2,100 m in northeastern Borneo.

This species is generally small to medium sized with anisophyllous leaves and a few large, campanulate flowers with free, very short anthers. The indumentum, particularly on the leaves, differs among the collections, otherwise the species is rather uniform. The specimen *Argent & Coppins 1081* is much larger than those of other collections and also has many more flowers. Some characters of this specimen deviate from the typical range for the species and are enclosed in parentheses in the description.

Additional specimens examined. BORNEO. SABAH: W Coast Res., Kinabalu, vicinity of Kambaranga, 7,040 ft., 1962, *Bogle et al. 389* (GH); Tenompok, 5,000 ft., 1932, *Clemens 28179* (BM, BO, G, K, L, NY); Marai Parai, 5,000 ft., 1933, *Clemens 35136* (BM, BO, L, NY, UC); Marai Parai spur, 1915, *Clemens 10981* (UC); Upper Kinabalu, 6,000 ft., 1933, *Clemens 51020* (BM, G, K, NY); Marai Parai, 5,000 ft., 1958, *Collenette A77* (BM); on ridge parallel to Kinataki River, 45 ft., *Collenette A103* (BM); 1,650 m, 1966, *Ding Hou 225* (K, L); Kamarangoh, 7,000 ft., 1967, *Price 194* (K); W Coast Res., Gunong Alab, 1,400 m, 1969, *Nooteboom*

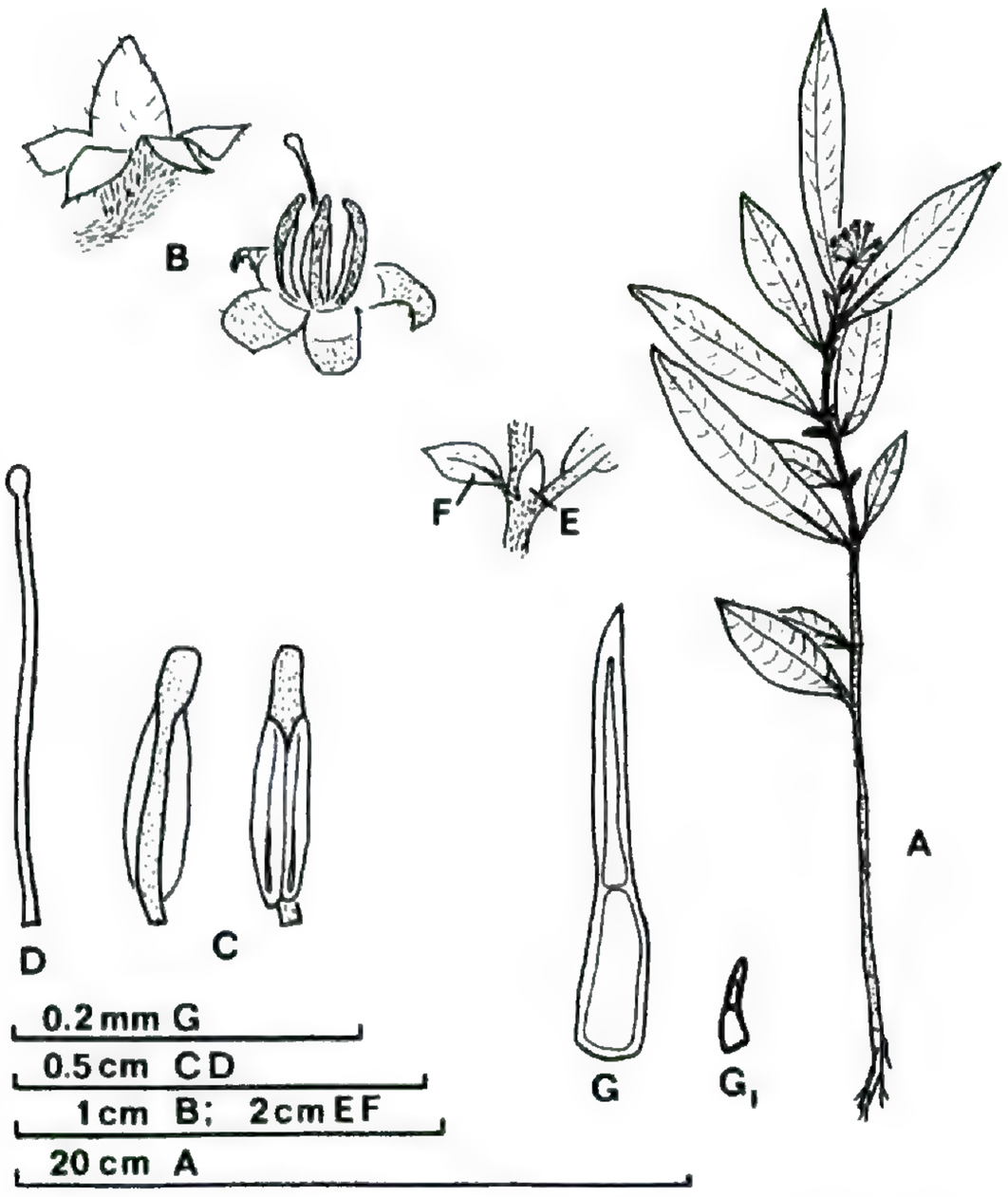


FIGURE 23. *Argostemma brookei*.—A. Habit.—B. Flower.—C. Anthers.—D. Style.—E. Stipule.—F. Nanophyllous leaf.—G. Hair from outer surface of the corolla.—G_1. Hair from inner surface of the corolla. A from *Brooke 8562* (G); B–G from *Clemens 20064* (NY).

922 (L). SARAWAK: 4th Div., Gunong Mulu, west ridge, 1,800 m, 1978, *Argent & Coppins 1081* (E); ridge at about 5,000 ft., 1962, *Burtt & Woods 2150* (E); 4,000 ft., 1962, *Burtt & Woods 2178, 2187* (E); path from Milinau Paku, 4,200 ft., 1961, *Anderson 4516* (K, L). KALIMANTAN: E Prov., W Kutei, 1925, *Endert 4171* (A, BO, K, L).

20. Argostemma brookei B. Bremer, sp. nov. TYPE: Borneo. Sarawak: 1st Div., Berumput, 4,800 ft., 1954, *Brooke 8562* (holotype, L; isotypes, BM, G, UC). Figure 23.

Herba inflorescentiis valde pubescentibus, staminibus liberis. Folia opposita, illis parium inaequalissimis. Inflorescentia umbelliformis, floribus pusillis. Lobi calycis ovati ad triangulares, acuti, patentes. Corolla profunde fissa. Lobi corollae recurvi. Stamina libera, sed approximata. Appendix apicalis ¼ longitudinem antherae aequans, crassa, laevis. Connectivum distinctum. Stylus glaber, stigmate leviter capitato.

Argostemma havilandii, A. calcicolum, A. trichosanthes, A. humifusum, A. psychotrioides, A. variegatum simile sed lobis corollae profunde fissis, staminibus liberis differt.

Erect, anisophyllous herb. Stem 5–22 cm, slightly branched or unbranched, finely pubescent; internodes 3–15 mm. Leaves opposite, generally very unequal; stipules deciduous or persistent, 4–6 mm long, ovate, acuminate at apex; larger leaves of the anisophyllous pairs with pubescent petioles 2–35 mm long; lamina 3–70 × 0.8–2.2 cm, oblanceolate to narrowly elliptic, basally acute with the lobes equal, marginally entire, apically acuminate, rarely acute or obtuse, herbaceous, glabrous above, pubescent on the veins below; midrib and primary veins (6–10 pairs) distinct. Nanophyllous leaves deciduous or persistent, 4–10 mm long, ovate to lanceolate, acute to acuminate. Inflorescences 5–16-flowered, umbelliform, solitary or a few together; peduncle 0.8–1.7 cm, pubescent; bracts ca. 0.5 cm long, lanceolate; pedicels 0.6–1.0 cm, pubescent. Flowers 5-merous; calyx lobes ca. 2 mm long, ovate to triangular, acute, sparsely pubescent, spreading; corolla cleft to near the base, externally with a few hairs, internally pubescent only on the distal part of the lobes; lobes ovate to triangular, recurved. Stamens ca. 3 mm long, free but close together; anther cells and apical appendage free; no true cone; filaments short, equal, straight; sacs opening completely longitudinally; apical appendage ca. ¼ the anther length, thick and smooth; connective distinct, smooth. Style ca. 6 mm long, glabrous, with a slightly capitate stigma, long-exserted. Fruit without furrows or ribs.

Argostemma brookei has been collected from the ground in the forest in the Poi (= Pueh) range at elevations of 1,000 to 2,000 m.

It is medium sized with oblanceolate, anisophyllous leaves. The upper part of the stems, the peduncles, and the whole inflorescences are covered by rather stiff hairs. The length of the calyx lobes is intermediate between the short ones, most common among the Borneo species, and the long lobes of *A. psychotrioides*.

Most specimens of this taxon have been determined as *A. brachyantherum*, another mountain species, which occurs mainly at Kinabalu. In habit they are similar, but *Argostemma brookei* has many small flowers with deeply cleft corollas having evidently recurved lobes. The free anthers are longer and stand close together, like a cone; the apical appendages are much longer, and the filaments are shorter than in *A. brachyantherum*.

Additional specimens examined. BORNEO. SARAWAK: 1st Div., Mt. Poi (= Pueh), summit ridge, northern end, 4,400 ft., 1956, *Bell 2068* (BM); 6,000 ft., 1929, *Clemens 20064* (K, NY); forested slopes, 1929, *Clemens 20331* (NY); 4,500–5,500 ft., 1924, *Mjöberg s.n.* (UC); 1st Div., Gunong Berumput, 3,000 ft., 1954, *Brooke 8599* (L); 4,870 ft., 1962, *Burtt & Woods 2800* (E).

21. Argostemma havilandii Ridley, J. Straits Branch Roy. Asiat. Soc. 61: 13. 1912. TYPE: Borneo: Kuching, 1893, *Haviland 2958* (holotype, SING; isotypes, BM, BO, K). Figure 24.

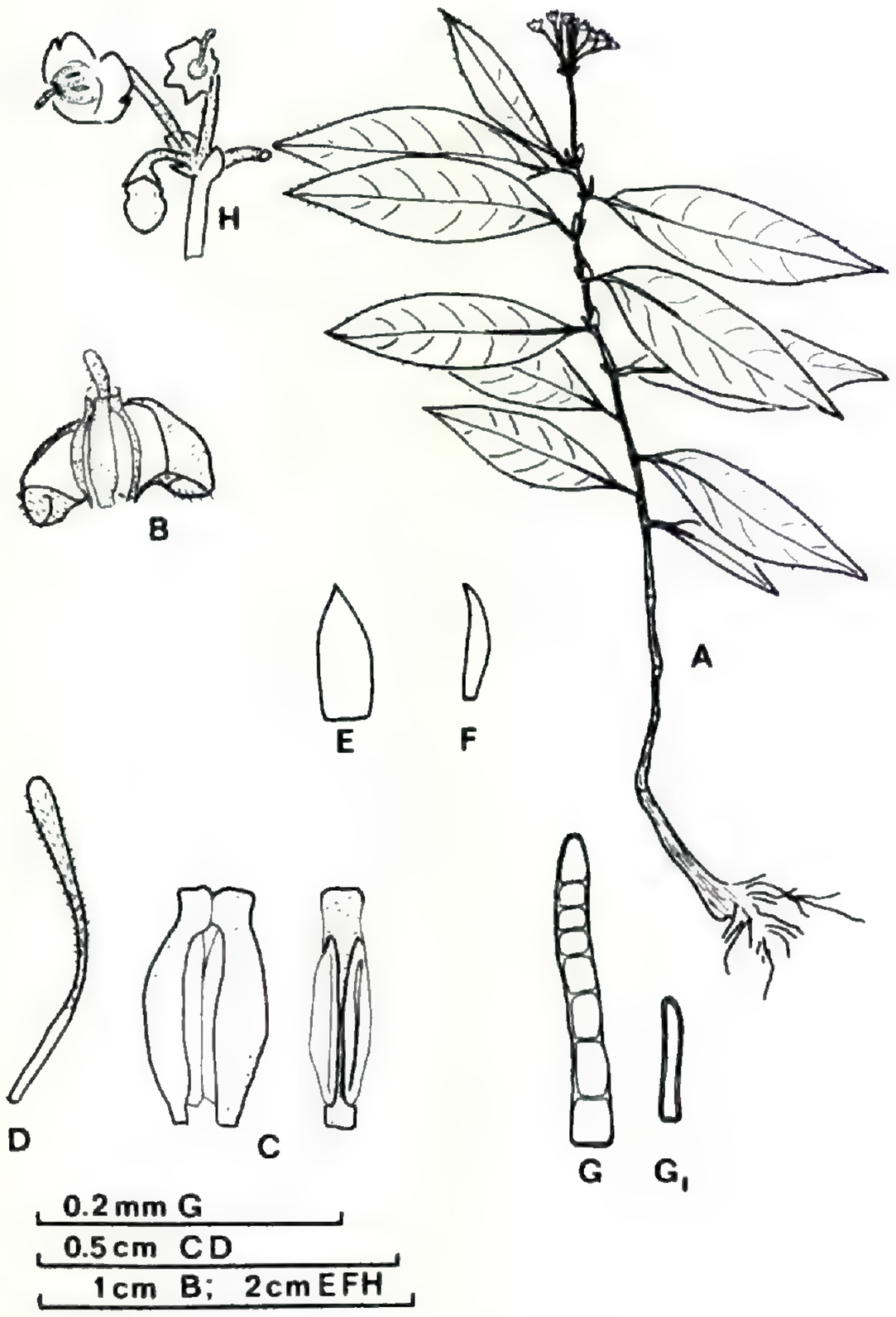


FIGURE 24. *Argostemma havilandii*.—A. Habit.—B. Flower.—C. Anthers.—D. Style.—E. Stipule.—F. Nanophyllous leaf.—G. Hair from outer surface of the corolla.—G_1. Hair from inner surface of the corolla.—H. Inflorescences. A, E, F from *Bremer 1689* (S); C, D, G, H from *Bremer 1662* (S).

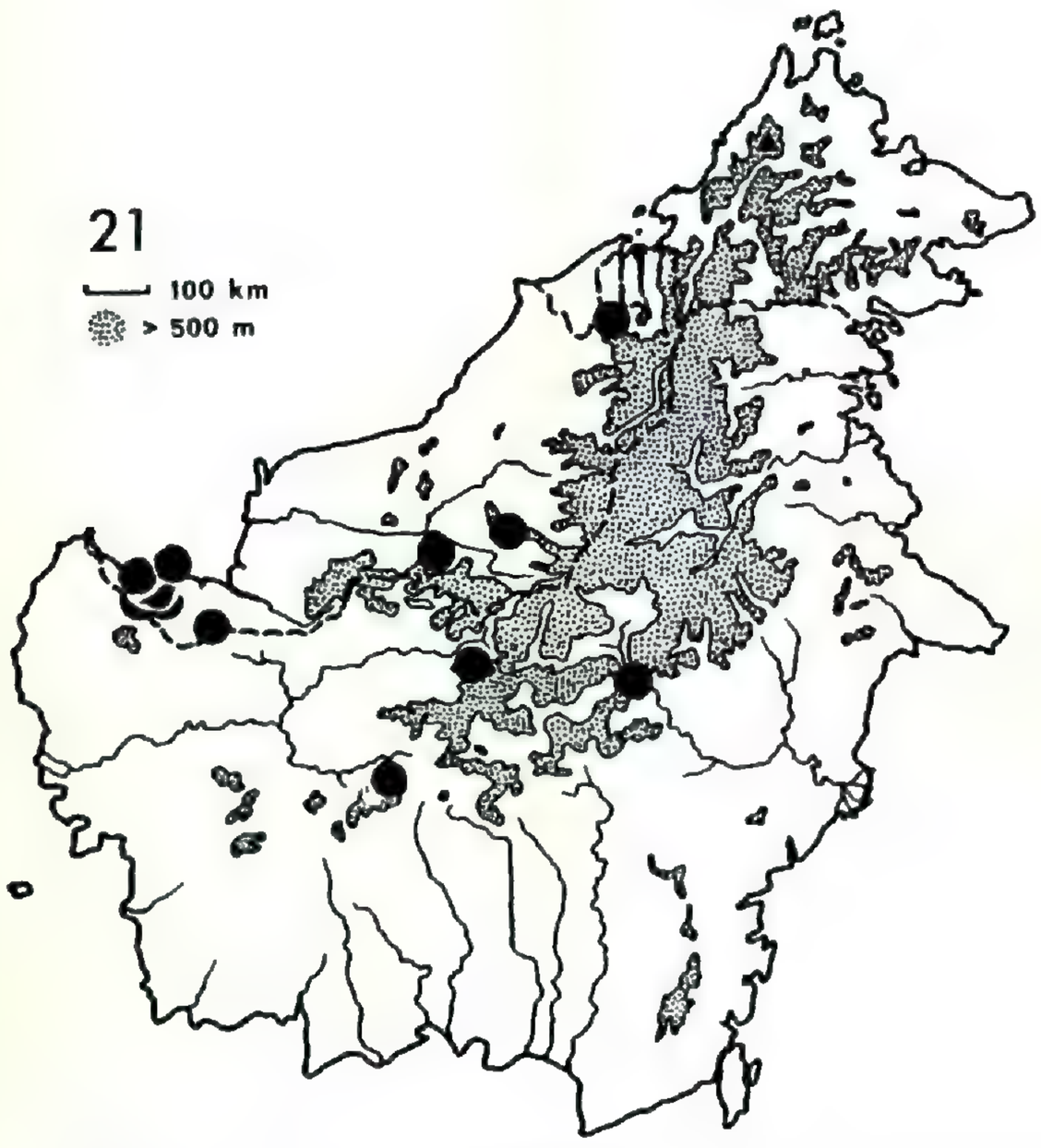
A. hallieri Valeton, Icones Bogorienses 4: 267. 1914. TYPE: Borneo: Amai Ambit, *Hallier B3228* (holotype, BO; isotypes, BO, L).

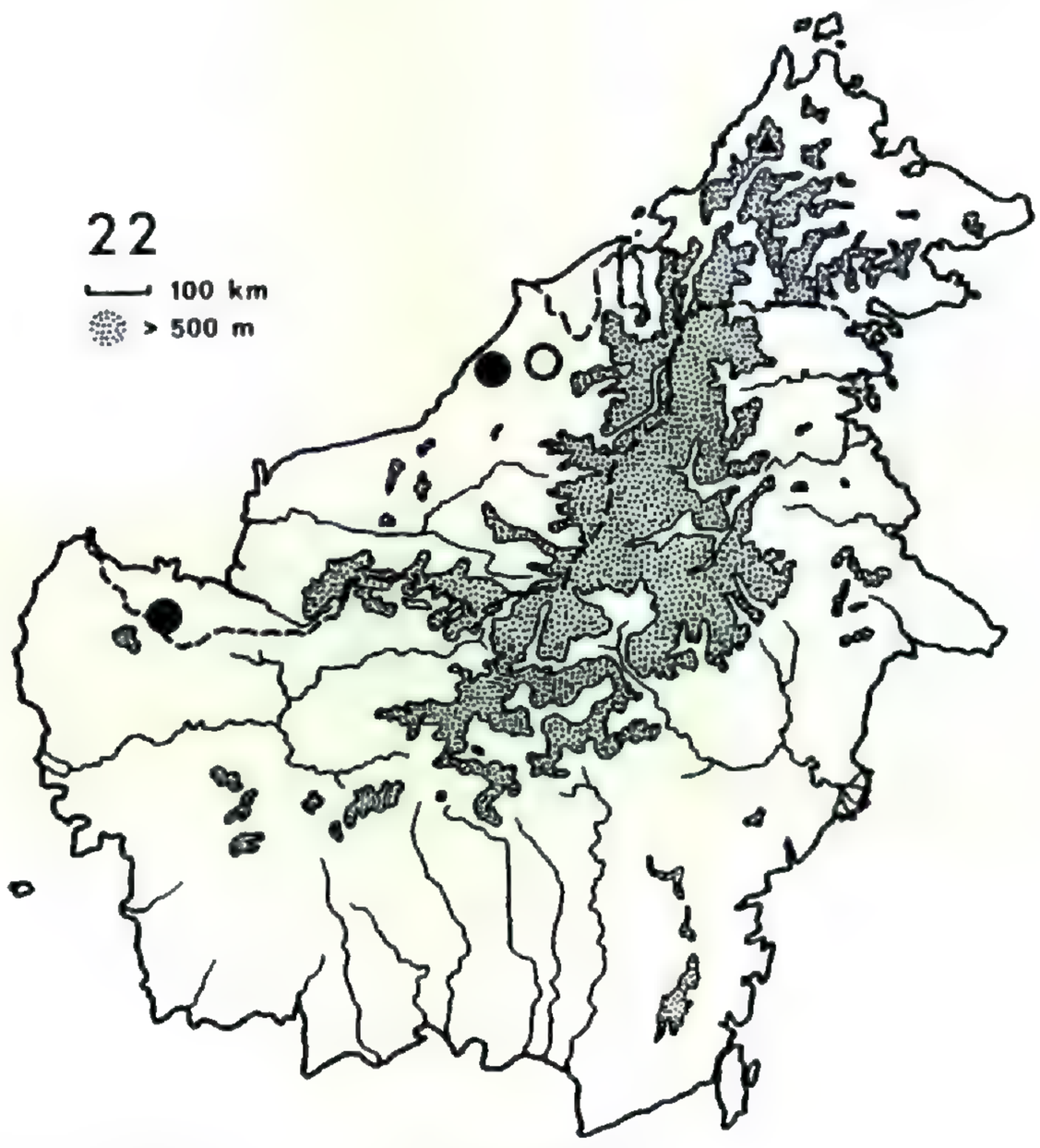
A. lanceolatum Valeton, Icones Bogorienses 4: 269. 1914. TYPE: Borneo: *Teysmann 11292* (lectotype, L; Bakh. f. in herb., confirmed here).

A. sarawakense W. Smith, Notes Roy. Bot. Gard. Edinburgh 8: 318. 1915. TYPE: Borneo. Sarawak: 1913, *native collector 85* (holotype, E).

A. hallieri var. *sparsipilum* Merr., Mitt. Inst. Allg. Bot. Hamburg 7: 279. 1937. TYPE: West Borneo: Sungei Bika, 50 m, 1925, *Winkler 1428* (holotype, HBG; isotypes, HBG, NY).

Erect, anisophyllous herb. Stem 10–60 cm, unbranched or slightly branched, glabrous or rarely slightly pubescent, lower and older parts pale brown with elevated corky to papery longitudinal ridges and/or with transverse bars; internodes 9–30 mm. Leaves opposite, very unequal; stipules deciduous, 4–7 mm long, ovate to broadly ovate, obtuse at apex. Larger leaves of the anisophyllous pairs with glabrous or finely pubescent petioles 4–8 mm long; lamina 4–13 × 1.2–5 cm, obovate or oblanceolate to ovate to lanceolate, basally cuneate to acute or attenuate with the lobes equal, marginally entire, apically acuminate or rarely acute to obtuse, herbaceous to coriaceous, glabrous above or with a few hairs on the veins and margins, glabrous or generally pubescent on the veins below; midrib distinct, primary veins (6–11 pairs) generally distinct. Nanophyllous leaves deciduous, 4–10 mm long, lanceolate to linear. Inflorescences 4–18-flowered, umbelliform, solitary or a few together; peduncle 1.7–4.5 cm, glabrous; bracts to 0.6 cm long, ovate to broadly ovate; pedicels 0.7–1.8 cm,





MAPS 21, 22. Distributions in Borneo.—21. *Argostemma havilandii*.—22. *A. calcicolum*.

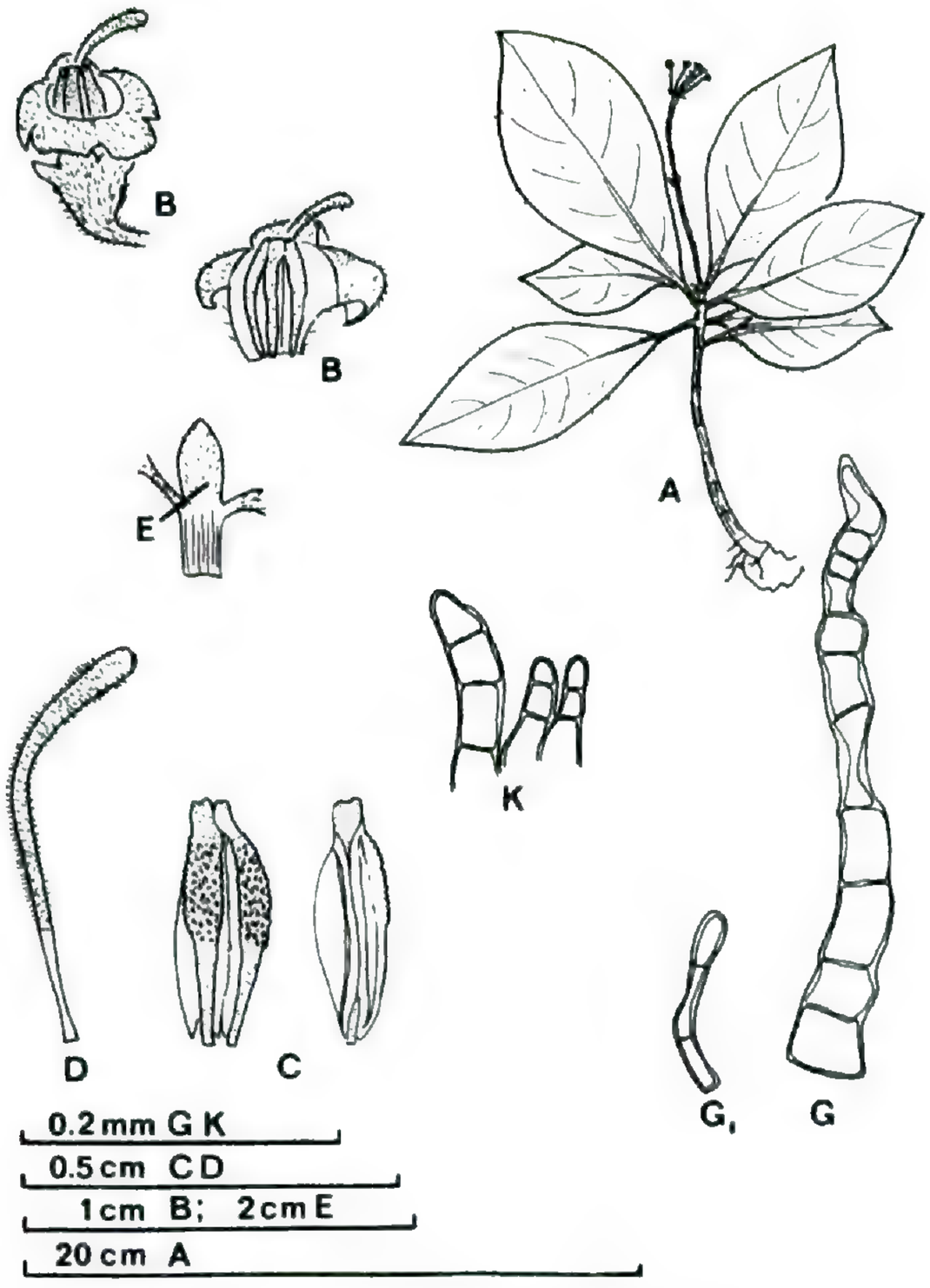


FIGURE 25. *Argostemma calcicolum.*—A. Habit.—B. Flower.—C. Anthers.—D. Style.—E. Stipule.—G. Hair from outer surface of the corolla.—G_1. Hair from inner surface of the corolla.—K. Hairs from the connectives. A, E from *Burtt & Woods 2005* (E); B–D, G, I from *Bremer 1707* (S).

pubescent or rarely glabrous. Flowers 5-merous; calyx lobes ca. 1 mm long, ovate to orbicular, obtuse or acute, pubescent; corolla 3–4 mm long, cleft to about ½, externally pubescent, internally papillose to pubescent only on the lobes; lobes ovate to triangular, recurved. Stamens 3–4 mm long, coherent; anther cells free, the apical appendages connate; anther cone ovoid to shortly so, straight; filaments very short, equal, straight; sacs opening completely longitudinally; apical appendage ¼–⅛ the anther length, thick, coriaceous, smooth; connective coriaceous, distinct, generally smooth. Style ca. 3–6 mm long, pubescent, with a clavate stigma, long-exserted. Fruit without furrows or ribs.

Valeton based *A. lanceolatum* on four collections by *Teysmann* and *Hallier*, in BO and L. All are suitable for lectotypification. Bakhuizen f. (in herb.) has selected *Teysmann 11292* in L, and I follow his choice.

Bakhuizen f. selected the K specimen of *A. havilandii* as the type (= holotype). This is a mistake because Ridley (1912) stated that the plants are preserved in the Singapore Botanical Gardens (note under *A. ophirense*).

Argostemma havilandii has a scattered distribution. Most, if not all, collections are from limestone. It grows from 50 to 1,100 m elevation on litter or more or less as an epiphyte on tree trunks, usually in lowland rainforest.

It is easily distinguished. The stem is black on the upper part (on dry specimens), and the lower part is pale brown to gray and papery to corky with elevated ridges and with more or less distinct transverse bars. The corolla is cleft to about its middle into recurved lobes. The anther cone is low and pale yellow to creamish. The connectives are distinct, and the thecae are separated from each other at anthesis. The broad, thick apical appendages are connate along their whole length.

Argostemma havilandii is easily circumscribed. There is little variation among the populations except for width and hair cover of the leaves. From around Gunong Api there is a population with a very dense hair cover, even more distinctive than the densely pubescent specimens from Sungei Bika in Kalimantan, where they have been described as *A. hallieri* var. *sparsipilum*.

Additional specimens examined. BORNEO. SARAWAK: 1st Div., Mt. Matang: 500 ft., 1954, *Brooke 9487* (L); 1,400 ft., 1927–1928, *native collector 5181* (NY, UC); 1st Div., Bau, Seburan, 200 ft., 1960, *Anderson 8982* (K, L, SAR); Seburan, 300 ft., 1960, *Anderson 12915* (K, L, SAR); Seburan, 200 ft., 1960, *Anderson 14600* (K, L, SAR); Jambusan, 100 ft., 1960, *Anderson 12581* (K, L, SAR); Bidi Gunong Umbut, 1979, *Bremer 1717* (S, SAR); 1st Div., Sabal, 1979, *Bremer 1662* (S, SAR); 1st Div., Setapok, mi. 4½ Batu Kawa Road, 1975, *James Mamit S35046* (L); 1st Div., Bako, 1979, *Bremer 1689* (S, SAR); 1st Div., Kuching, 1955, *Brooke 9770, 10792* (BM, L); 1893, *Haviland s.n.* (BM, L); 1913, *native collector s.n.* (E); 1st Div., Semengoh, 300 ft., 1958, *Anderson 9106* (L, SAR); 1979, *Bremer 1647* (S, SAR); 4th Div., Gunong Mulu, 1975, *Burtt 8300* (E); 4th Div., Gunong Api, 2,900 ft., 1971, *Anderson S30826* (E, K, L); 1,000 ft., 1977, *Argent et al. 666* (E); 3,500 ft., 1970, *Chai S30085* (K, L, SAR); 7th Div., Bukit Salong, 1980, *Burtt 12734* (E); without loc., *native collector 1232* (A); 1914, *native collector 2403* (A). KALIMANTAN: E Prov., W Kutei, near Tabang, 1956, *Kostermans 12845* (L); without loc., *Teysmann 11921* (BO, K).

22. Argostemma calcicolum B. Bremer, sp. nov. TYPE: Borneo. Sarawak: 1st Div., Bukit Manok, halfway between Teng Bukap and Padawan, low alt., 1979, *Bremer 1707* (holotype, S; isotypes, K, L, SAR). Figure 25.

Herba caulibus porcatis et suberosis ad papyraceis. Folia opposita, illis parium aequalibus. Inflorescentiae umbelliformes aut ramis duobus scorpioides. Lobi calycis triangulares ad ovati, acuti. Corolla ad dimidio fissa. Lobi corollae recurvi. Antherae liberae. Appendices apicales connatae, ¼–⅕ longitudinem antherarum aequans, cras-

sae, coriaceae, laeves. Connectivum distinctum, papillosum. Stylus pubescens, stigmate clavato.

Argostemma havilandii simile, sed planta plus pubescens, foliis oppositis aequalibus differt.

Erect, isophyllous herb. Stem 5–30 cm, slightly branched or unbranched, slightly pubescent, the lower and older parts pale brown with elevated corky to papery longitudinal ridges and/or with transverse bars; internodes 4–10 mm. Leaves opposite, equal or subequal; stipules deciduous, 5–10 mm long, ovate to oblong, acute to obtuse at apex; petiole 3–14 mm long, pubescent; lamina 5–17 × 2–7 cm, obovate to elliptic, basally cuneate to attenuate with the lobes equal, marginally entire or serrulate, apically acuminate, herbaceous, pubescent on both surfaces; midrib and primary veins (7–9 pairs) distinct. Inflorescences 3–30-flowered, umbelliform or with 2 scorpioid branches, solitary or a few together; peduncle 3–4.5 cm, pubescent, the bracts to 0.5 cm long, lanceolate; pedicels 0.5–0.7 cm, pubescent. Flowers 5-merous; calyx lobes ca. 1 mm long, triangular to ovate, acute, pubescent; corolla ca. 4 mm long, cleft to about ½, externally pubescent, internally papillose to pubescent only on the lobes; lobes ovate to triangular, recurved. Stamens ca. 3.5 mm long, coherent; anther cells free, the apical appendages connate; anther cone ovoid to shortly so, straight; filaments very short, equal, straight; sacs opening completely longitudinally; apical appendage ¼–⅕ the anther length, thick, coriaceous, smooth; connective coriaceous, distinct, papillose. Style 5–6 mm long, pubescent, with a clavate stigma, long-exserted. Fruit without furrows or ribs.

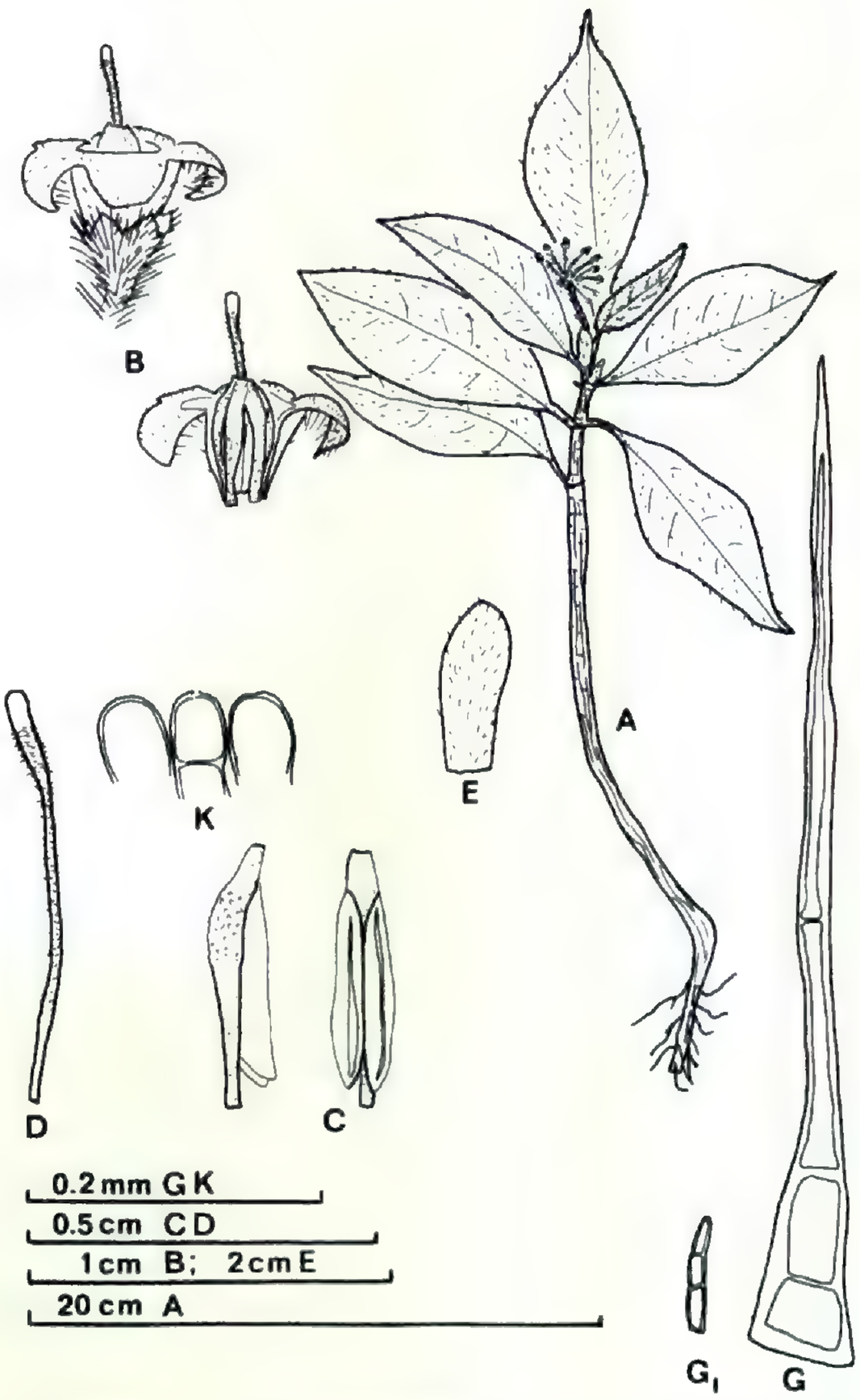


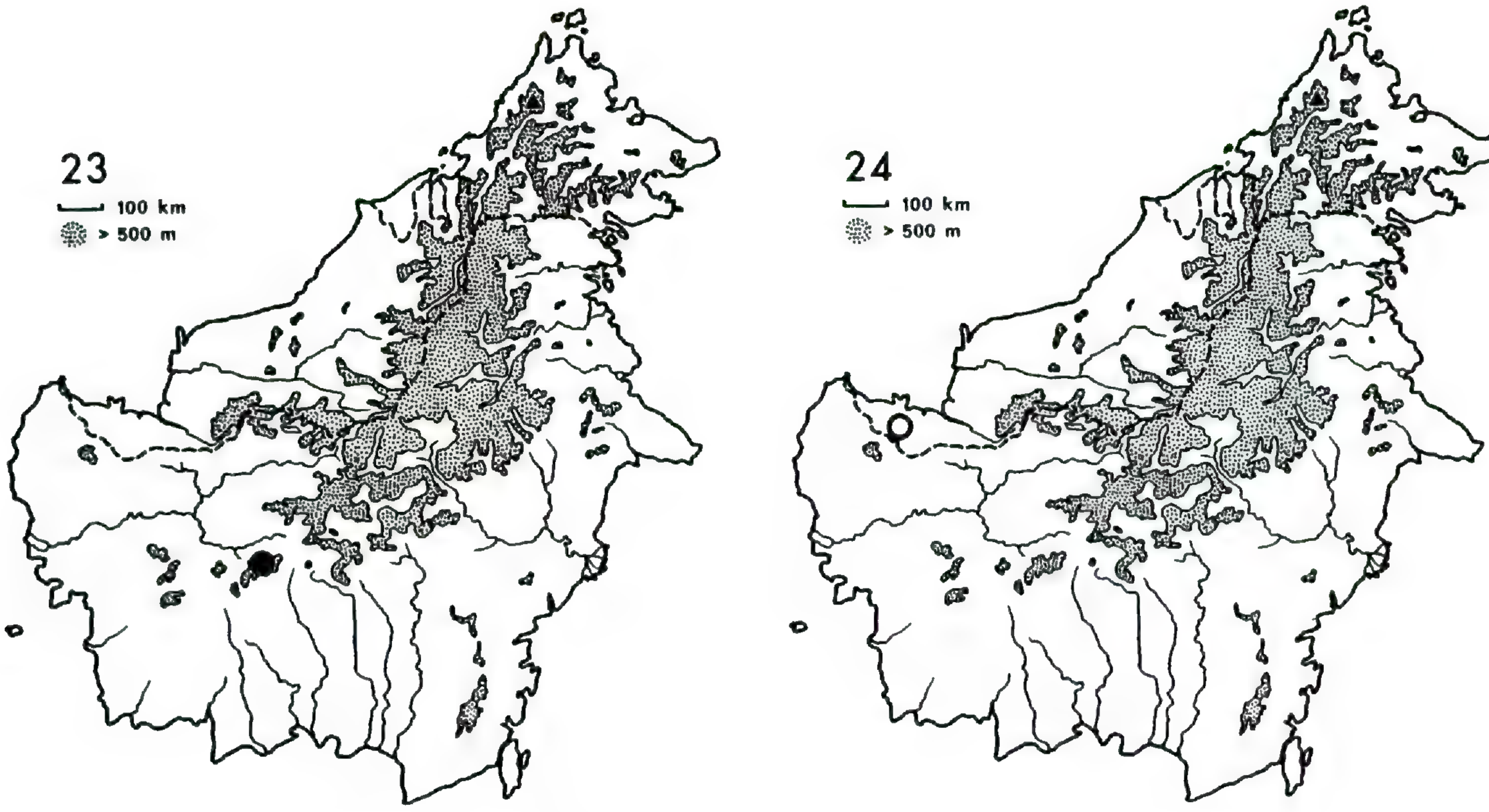
FIGURE 26. *Argostemma trichosanthes*.—A. Habit.—B. Flower.—C. Anthers.—D. Style.—E. Stipule.—G. Hair from outer surface of the corolla.—G_1. Hair from inner surface of the corolla.—K. Papillae or hairs from the connectives. From *Winkler 781* (NY).

This rare species has been collected only four times. Haviland and Hose made the first collection, noting only the locality as Baram. Different collectors recorded it as growing on limestone. Anderson said "frequent in crevices on vertical limestone rocks." My collection is from low altitude in a limestone area. The earlier collections were all determined as *A. borragineum* because of the equal, opposite leaves. However, the stems, stipules, anthers, and style are quite different. It is close to *A. havilandii* and shares various characters with this species: lower stems pale brown to grayish, these having papery to corky surfaces and elevated ridges; anther shape; and clavate pubescent styles. However, *Argostemma calcicolum* differs from *A. havilandii* by its denser pubescence even on the peduncles and stipules, isophyllous leaves, and the upper part of the connectives distinctly papillose to hairy. The hairs on the connectives are not homologous to those on the anthers of *A. psychotrioides*, which has smooth connectives but papillose to hairy thecae and apical appendages. In *A. calcicolum* these parts are smooth.

Additional specimens examined. BORNEO. SARAWAK: 4th Div., Gunong Subis, 1972, *Anderson S31672* (A); 4th Div., Penkalan Lobang Niah Caves, *Burtt & Woods 2005* (E); 4th Div., Baram, 1894, *Haviland & Hose 3409* (K).

23. Argostemma trichosanthes Merr., Mitt. Inst. Allg. Bot. Hamburg 7: 280. 1937. TYPE: West Borneo. Bidang Menabei, 700 m, 1924, *Winkler 781* (holotype, HBG; isotype, NY). Figure 26.

Erect, densely pubescent, isophyllous herb. Stem ca. 25 cm, unbranched, densely pubescent, lower and older parts pale brown with elevated corky to papery longitudinal ridges and/or with transverse bars; internodes 7–15 mm. Leaves opposite, equal; stipules deciduous, 8–10 mm long, ovate, obtuse at apex; petiole 5–12 mm long, pubescent; lamina



MAPS 23, 24. Distributions in Borneo.—23. *Argostemma trichosanthes.*—24. *A. humifusum.*

6–11 × 3–5 cm, obovate to elliptic, basally cuneate to attenuate with the lobes equal, marginally serrulate, apically acuminate, herbaceous, pubescent on both sides; midrib and primary veins (ca. 8 pairs) distinct. Inflorescences 10–20-flowered, umbelliform, solitary; peduncle 1.5–3.2 cm, pubescent; bracts to 0.6 cm long, lanceolate to linear; pedicels 0.5–0.7 cm, pubescent. Flowers 5-merous; calyx lobes less than 1 mm long, triangular or ovate, acute, pubescent; corolla 3–5 mm long, cleft to about ½, externally pubescent, internally papillose to pubescent only on the lobes; lobes ovate to triangular, recurved. Stamens ca. 3.5 mm long, coherent, the anther cells free, the apical appendages connate; anther cone ovoid to shortly ovoid, straight; filaments very short, equal, straight; sacs opening completely longitudinally; apical appendage ¼–⅕ the anther length, thick, coriaceous, smooth; connective coriaceous, distinct, papillose in upper part. Style ca. 6 mm long, pubescent, with a clavate stigma, long-exserted. Fruit without furrows or ribs.

Argostemma trichosanthes is known only from the type. It was collected at Bidang Menabei on Kalimantan at 700 m.

Argostemma trichosanthes is close to *A. havilandii* and *A. calcicolum*, with which it shares the stem characters pale brown to gray, papery to corky, and with elevated ridges on the lower stems. With *A. calcicolum* it shares opposite isophyllous leaves. *Argostemma trichosanthes* is easily distinguished by its dense indumentum. The upper part of the stems, particularly the younger leaves and most parts of the inflorescences, are densely covered by stiff, long, thick-walled hairs.

24. Argostemma humifusum W. Smith, Notes Roy. Bot. Gard. Edinburgh 8: 317. 1915. TYPE: Borneo. Sarawak: Gunong Bayat (= ?Gunong Sebayat near Kuching), 1914, *native collector D131* (holotype, E; isotypes, E, K, SAR). Figure 27.

Erect, anisophyllous herb. Stem 6–16 cm, slightly branched or unbranched, glabrous; internodes 4–15 mm. Leaves opposite, very unequal; stipules persistent, 6–8 mm long, cordiform or broadly ovate, acuminate at apex. Larger leaves of the anisophyllous pairs with finely pubescent petioles 5–16 mm long; lamina 4–9 × 2–4.5 cm, obovate, basally acute to obtuse with the lobes unequal, marginally serrulate, apically shortly acuminate, membranaceous to herbaceous, pubescent on both surfaces; midrib and primary veins (6–10 pairs) distinct. Nanophyllous leaves persistent, 5–10 mm long, ovate. Inflorescences 5–10-flowered, umbelliform, solitary or a few together; peduncle 1.7–2.5 cm, glabrous; bracts very small, ovate to linear; pedicels 0.3–0.6 cm, with a few hairs. Flowers 5-merous; calyx lobes less than 1 mm long, ovate, acute, pubescent; corolla ca. 4 mm long, externally pubescent, internally glabrous(?). Stamens ca. 3 mm long, coherent; anther cells free,

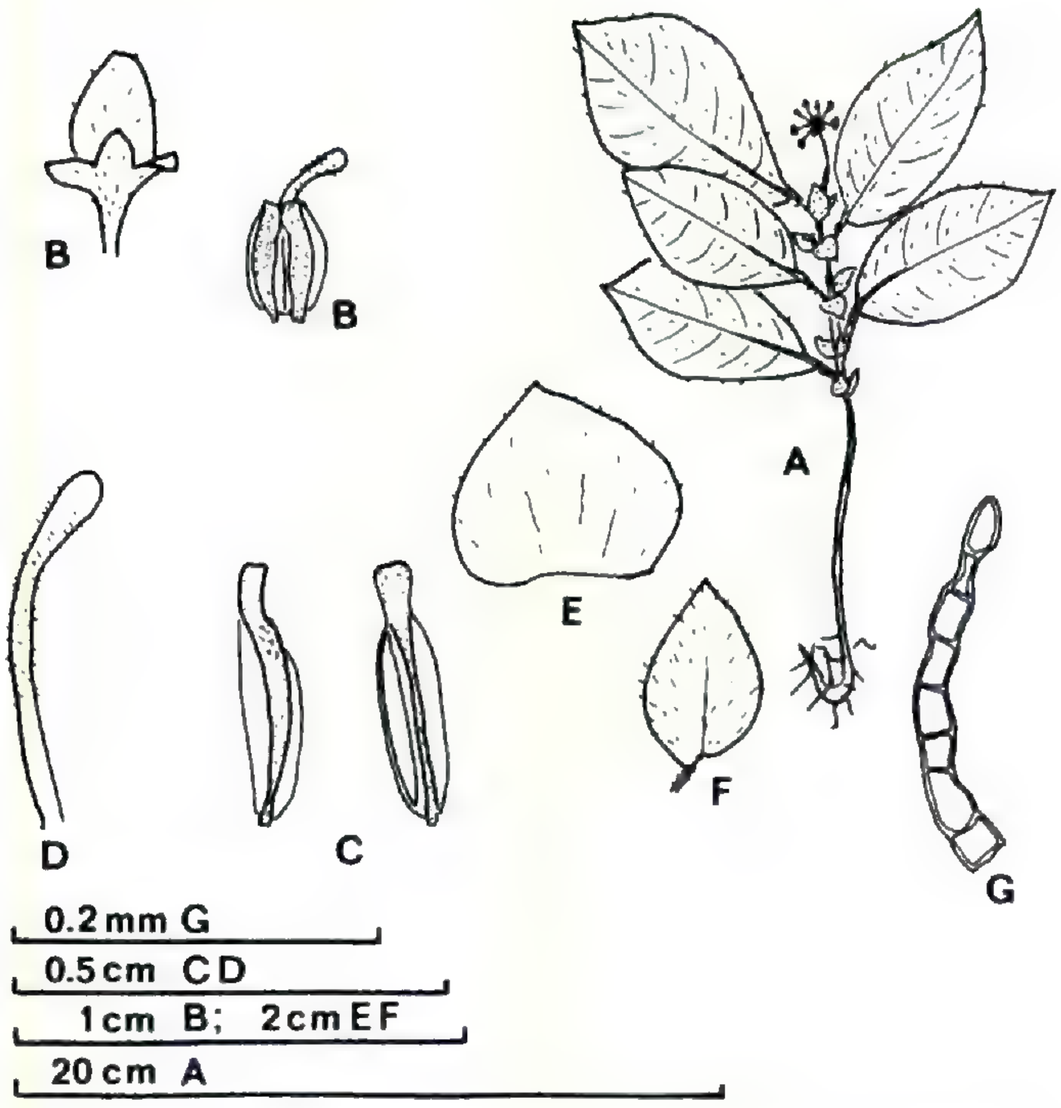


FIGURE 27. *Argostemma humifusum*.—A. Habit.—B. Flower bud, and anther cone.—C. Anthers.—D. Style.—E. Stipule.—F. Nanophyllous leaf.—G. Hair from outer surface of the corolla. From *native collector D131* (E, K).

the apical appendages connate; anther cone ovoid to shortly ovoid, straight; filaments very short, equal, straight; sacs opening completely longitudinally; apical appendage ¼–⅕ the anther length, thick, coriaceous, smooth; connective coriaceous, distinct, papillose in upper part. Style ca. 5 mm long, glabrous to pubescent, with a clavate stigma, long-exserted. Fruit without furrows or ribs.

Argostemma humifusum has been collected twice, but nothing was recorded about its habit or habitat.

This species is characterized by its broad, obovate leaves and large cordiform stipules. Because of incomplete material, I do not know the shape of the corolla. It has a thin corolla similar to those generally cleft halfway into recurved lobes. Internally the corolla seems to be glabrous, but among the other species with thin corollas, the lobes are usually pubescent. The upper part of the connective is probably papillose to pubescent as in *A. calcicolum* and *A. trichosanthes*.

Additional specimen examined. BORNEO. SARAWAK: Kutein, 1865–1867, *Beccari 150* (K, L).

25. Argostemma psychotrioides Ridley, J. Bot. 65: 38. 1927. TYPE: Borneo: *Haviland 689* (holotype, K; isotype, SAR). Figure 28.

Erect, anisophyllous herb. Stem 10–100 cm, slightly branched or unbranched, finely pubescent

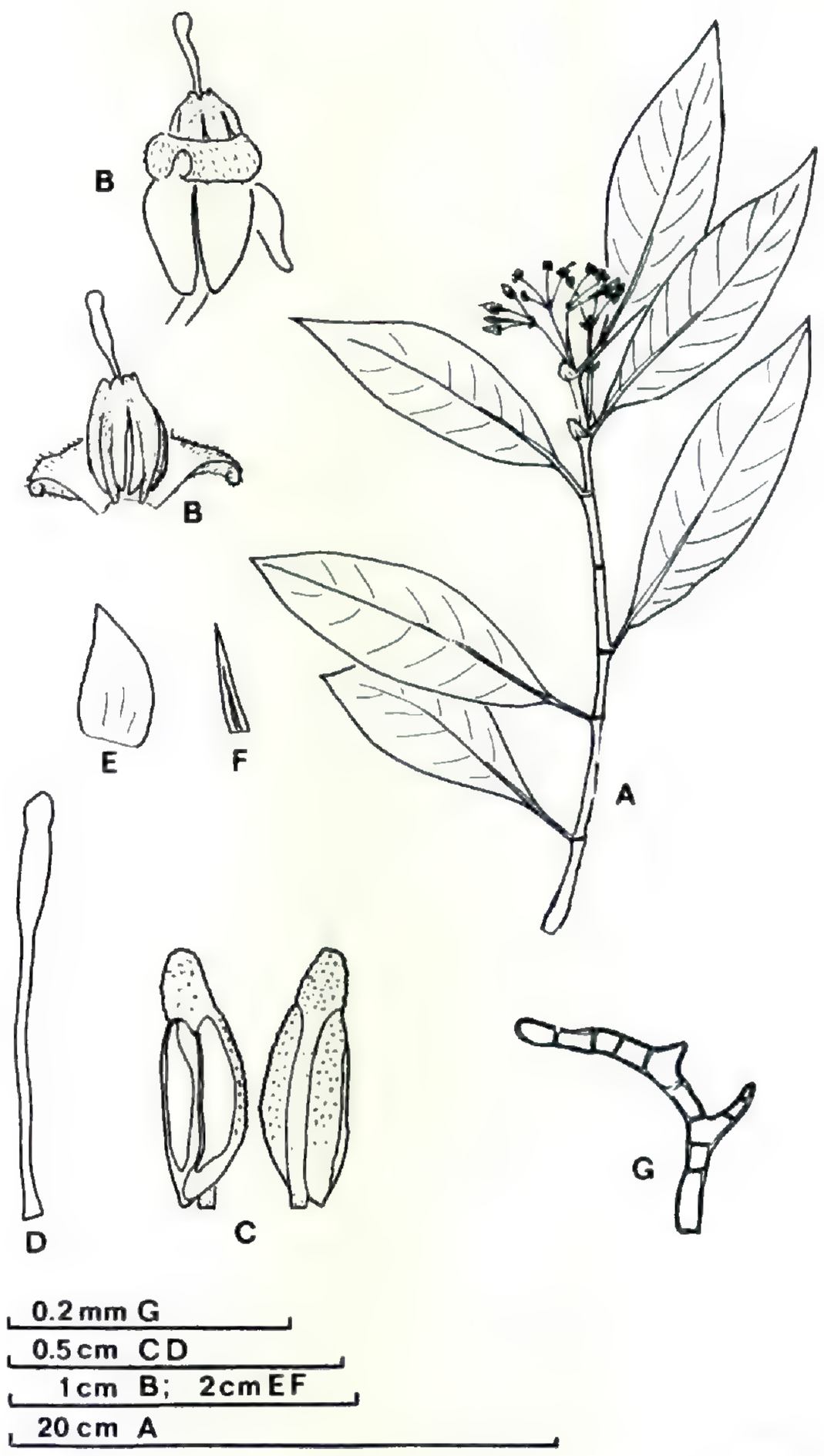
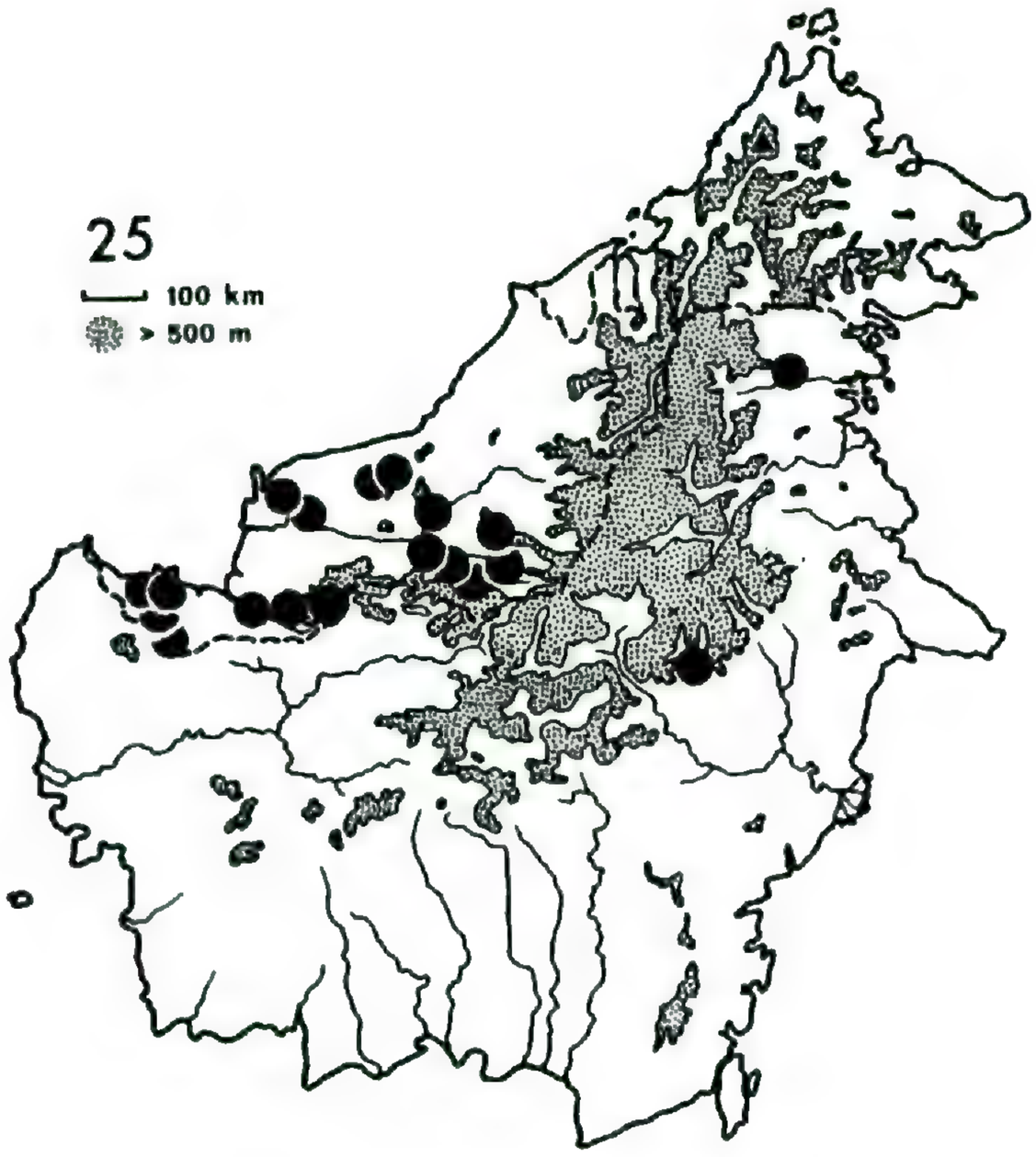
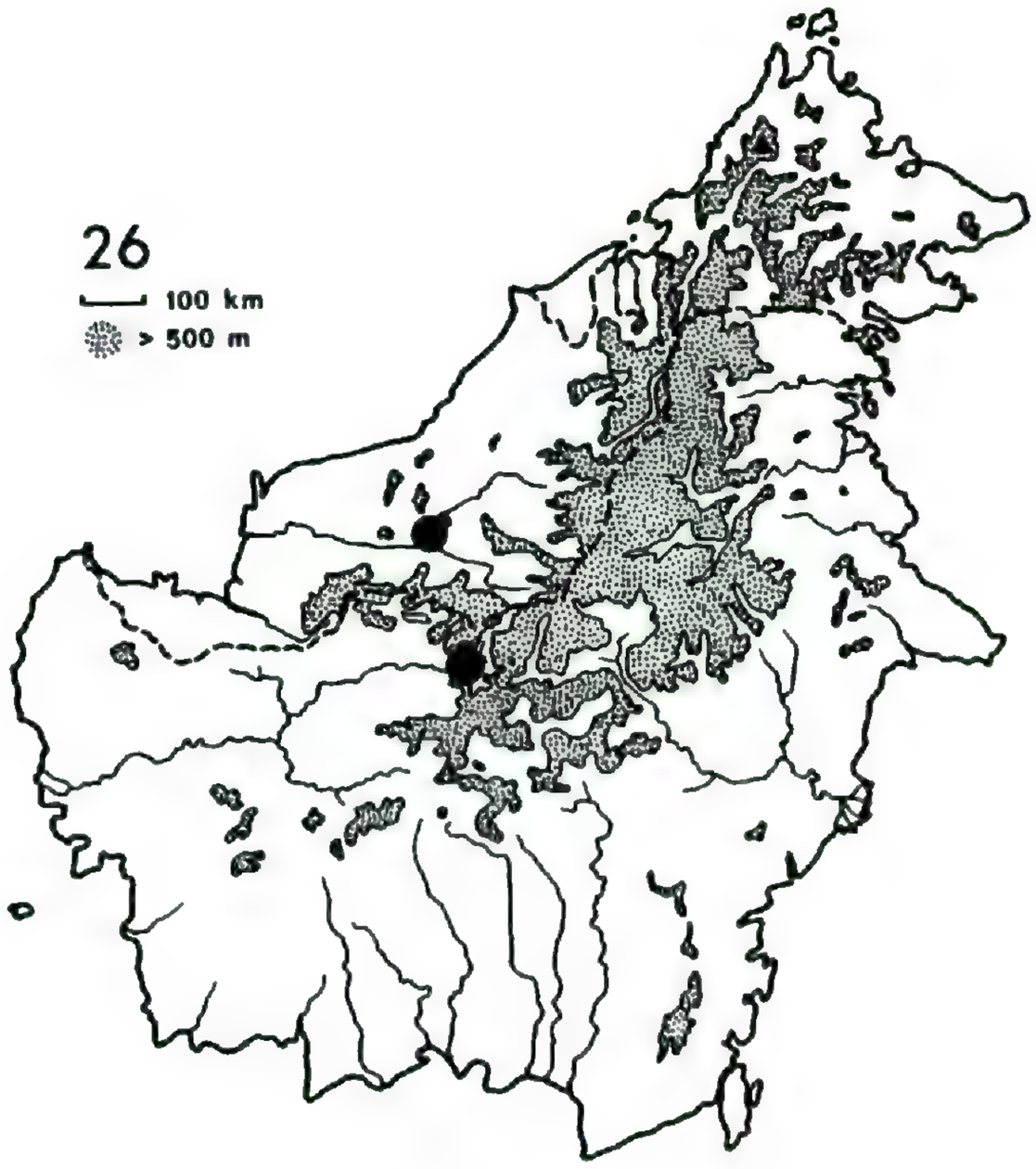


FIGURE 28. *Argostemma psychotrioides*.—A. Flowering branch.—B. Flower.—C. Anthers.—D. Style.—E. Stipule.—F. Nanophyllous leaf.—G. Hair from outer surface of the corolla. From *Burtt & Martin 4991* (E).

or glabrous; internodes 7–30 mm long. Leaves opposite, very unequal; stipules deciduous, 6–20 mm long, ovate to lanceolate, acuminate at apex; larger leaves of the anisophyllous pairs with finely pubescent or glabrous petioles 3–19 mm long; lamina 5–18 × 1–6 cm, obovate or oblanceolate to ovate or lanceolate, basally acute to attenuate with the lobes equal, marginally entire, apically acuminate or rarely acute to obtuse, herbaceous, glabrous above, glabrous to finely pubescent on the veins below; midrib and primary veins (7–15 pairs) distinct. Nanophyllous leaves deciduous, 5–13 mm long, ovate to lanceolate, acuminate. Inflorescences 3–30-flowered, umbelliform, rarely with lateral branches to corymbiform, solitary or a few together; peduncle 1–4 cm, pubescent or glabrous; bracts 0.7 cm long, ovate or lanceolate to linear; lateral branches, if present, to 3 cm, pubescent; pedicels 0.5–1.5 cm, pubescent. Flowers 5-merous; calyx





MAPS 25, 26. Distributions in Borneo.—25. *Argostemma psychotrioides.*—26. *A. variegatum.*

lobes 2–6 mm long, subspatulate or ovate to oblong, acute, reflexed and pressed against the ovary concealing it even before anthesis, pubescent to glabrous; corolla 3–5 mm long, cleft to about ½ its length, externally pubescent, internally papillose to pubescent only on the lobes; lobes ovate to triangular, recurved. Stamens 2–4 mm long, coherent; anther cells free, the apical appendages connate; anther cone ovoid to shortly ovoid, straight; filaments very short, equal, straight; sacs opening completely longitudinally; apical appendage ¼–⅓ the anther length, thick, coriaceous, papillose; connective coriaceous, distinct, generally smooth. Style 4–7 mm long, glabrous or rarely with a few hairs, with a clavate stigma, long-exserted. Fruit without furrows or ribs.

Argostemma psychotrioides is found mostly at altitudes less than 250 m, although it occurs up to 1,000 m. It grows in shady, wet places on exposed roots and pneumatophores in swampy forests and on boulders in streams. It also grows under drier conditions on limestone and at higher altitudes in mossy forests.

It is easily identified by its strongly reflexed calyx lobes which in living material are green with white margins and tips. The corolla is thin and pubescent to densely pubescent and has recurved lobes. The anther cone is low, pale yellow to creamish. Only the apical appendages are connate, and the thecae are free. The thick apical appendages and the back of the thecae are distinctly papillose to hairy, while the connectives are smooth (cf. *A. trichosanthes*). There is little variation in the characters of the flowers, but a few specimens (*Bremer 1730, 1744, 1748*) from the 7th Division have shorter calyx lobes. The shape and size of the leaves as well as the occurrence of hairs are variable and do not correlate with distribution patterns.

Additional specimens examined. BORNEO. SARAWAK: 1st Div., Kuching, 1893, *Haviland 2960* (BO, L, SAR); 1894, *Haviland s.n.* (BM, L); 1894, *Haviland & Hose s.n.* (A, GH); 1905, *Ridley 12302* (BM, K, SING); 1st Div., Setapok, 1966, *Anderson S19690* (K, L, SAR); 1st Div., Mt. Matang, 1924, *Mjöberg 216* (BO, NY, SING, UC); 2,000 ft., 1927, *native collector s.n.* (UC); 1st Div., Padawan area, Gunong Maja, 1979, *Bremer 1703* (S, SAR); 1st Div., Bukit Manok, halfway between Teng Bukap and Padawan, 1979, *Bremer 1706* (S, SAR); 1st Div., Semengoh, 1979, *Bremer 1643* (S, SAR); *Banyeng ak Nudong & Sibat ak Luang S25355* (K, L, SAR); 2nd Div., Simangang, 1955, *Brooke 10716* (BM, L); 2nd Div., Bukit Sadok, 1982, *Axelius 86, 93* (S); 2nd Div., between Entalau and Tisak, 1982, *Axelius 122* (S); 2nd Div., Bukit Sengkajang, Lanjak-Entimau, 3,100 ft., 1974, *Chai S33980* (L); 3rd Div., Kelapaan, 1954, *Brooke 8840* (BM, G, L, SING); 3rd Div., Sibu, Naman, low alt., *Sanusi Tahir 8954* (BO, K, L, SING); 3rd Div., Ulu Sungei Arip, 1965, *Sibat ak Luang S23664* (AAU, K, L, SAR); 4th Div., Ulu Muput Kanan, 1963, *Chai S19532* (L, SAR); 7th Div., Nanga Pelagos, 1938, *Daud & Tachun SFN35678* (A, G, K, SAR, SING); 7th Div., Hose Mts., above Melinau Falls, 4,000 ft., 1967, *Burtt & Martin 4991* (E); E of Bukit Sanpandai, 1980, *Burtt 12839* (E); 7th Div., Sungei Melinau, Nanga Tunoh, 450 ft., 1980, *Burtt 12666* (E); 7th Div., Ulu Balleh, Sungei Putai, 1979, *Bremer 1724* (S, SAR); junction of Sungei Tekalit and Sungei Mengiong, 1979, *Bremer 1730, 1744* (S, SAR); Sungei Mengiong, 1979, *Bremer 1748* (S, SAR); 7th Div., Sungei Bene, 1980,

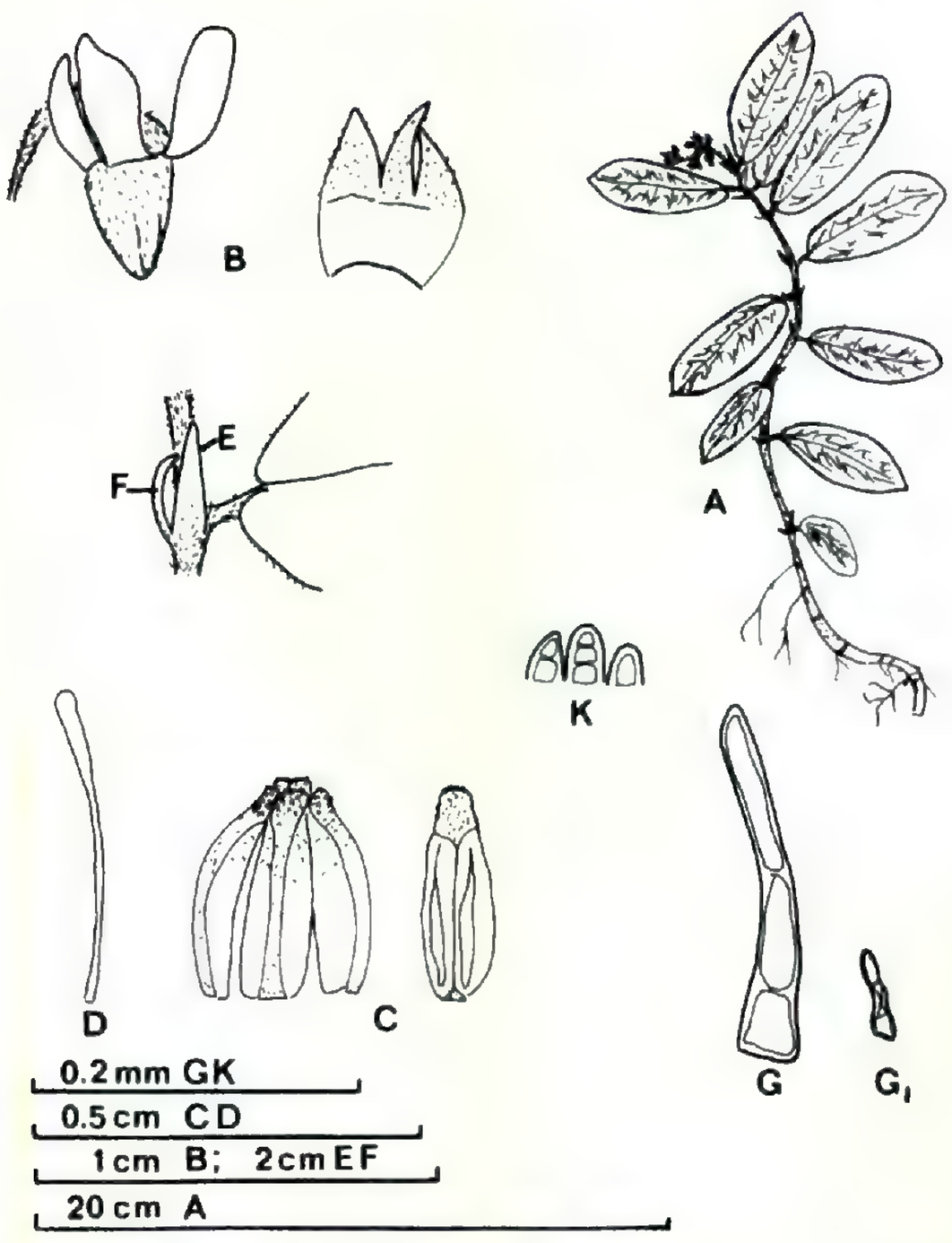


FIGURE 29. *Argostemma variegatum.*—A. Habit.—B. Flower bud and part of the corolla from the inner surface.—C. Anthers.—D. Style.—E. Stipule.—F. Nanophyllous leaf.—G. Hair from outer surface of the corolla.—G_1. Hair from inner surface of the corolla.—K. Papillae or hairs from the apical appendages. From *Winkler 1561* (HBG, NY).

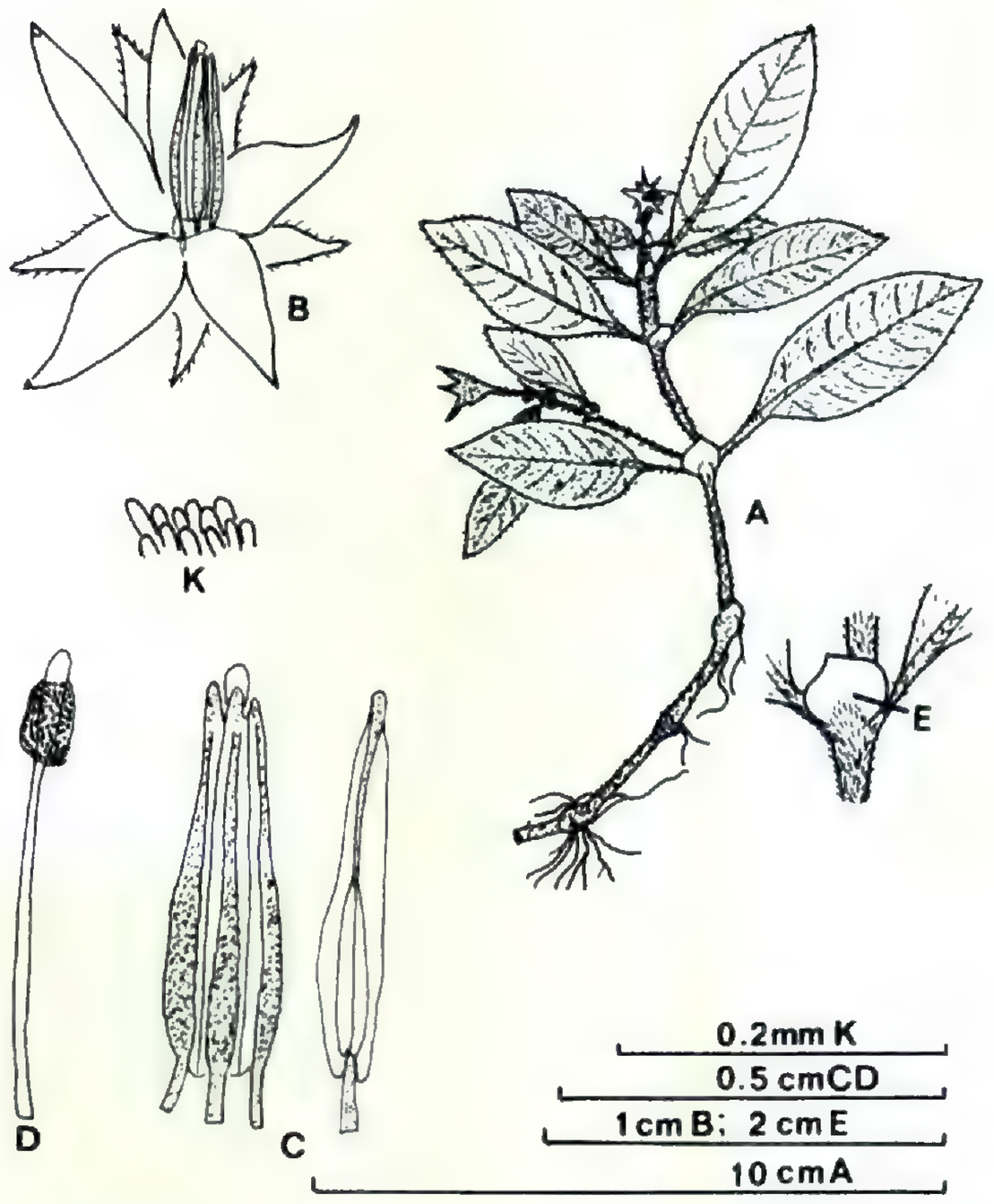


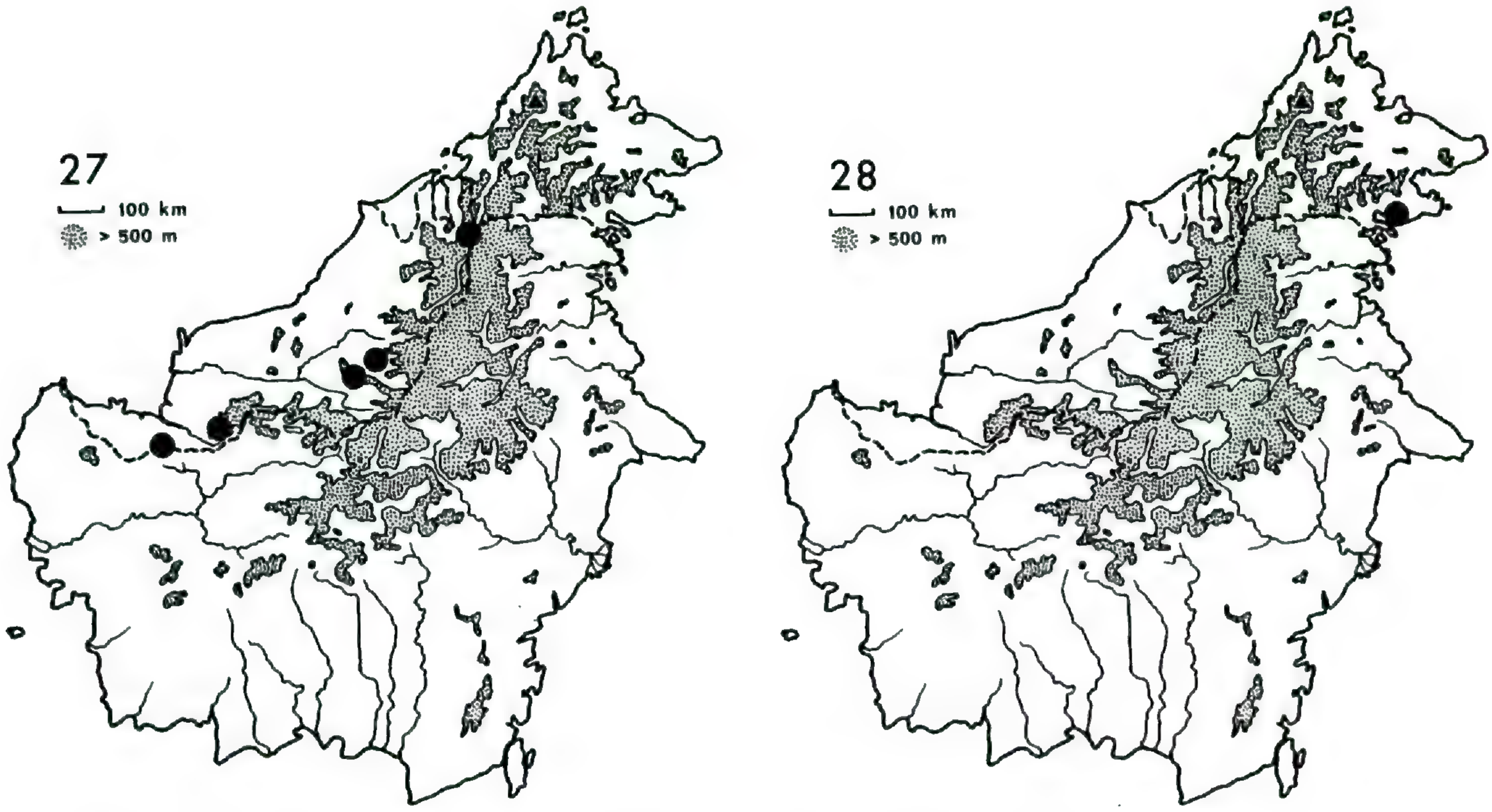
FIGURE 30. *Argostemma bryophilum.*—A. Habit.—B. Flower.—C. Anthers.—D. Style with pollen at apex.—E. Stipule.—K. Papillae from the connectives. From *Burtt 12800* (E).

Burtt 12935, 12951 (E); 7th Div., Gat, 1929, *Clemens 21738, 12740* (NY); without loc., *native collector 294*, (A, UC), *408*, (A, K, UC), *1244* (A, UC); *Lobb s.n.*, *Lowe s.n.* (K). KALIMANTAN: E Prov., Camp Malinau along Sungei Adat, 1982, *Axelius 315* (S); E Prov., C Kutai, NW of Tabang, 100–150 m, 1979, *Murata et al. 1192* (L).

26. Argostemma variegatum Merr., Mitt. Inst. Allg. Bot. Hamburg 7: 280. 1937. TYPE: West Borneo. Nanga Era, 100 m, 1925, *Winkler 1561* (holotype, HBG; isotype, NY). Figure 29.

Creeping anisophyllous herb. Stem 10–20 cm, slightly branched or unbranched, pubescent; internodes 3–17 mm long. Leaves opposite, very unequal; stipules persistent, 3–6 mm long, lanceolate, acuminate at apex; larger leaves of the anisophyllous pairs with pubescent petioles 2–5 mm long; lamina 3.5–7 × 1.4–3.4 cm, obovate to oblanceolate, basally rounded or obtuse with the lobes unequal, marginally entire or serrulate, apically obtuse or obtuse with a point, herbaceous, glabrous above, finely pubescent on the veins and margins below; midrib and primary veins (7–9 pairs) distinct. Nanophyllous leaves persistent, ca. 5 mm long, linear, petiolelike. Inflorescences ca. 7–flowered, umbelliform, solitary; peduncle 1–3 cm, pubescent or almost glabrous; bracts ca. 0.5 cm long, linear; pedicels 0.5–0.9 cm, pubescent. Flowers 5(or 6)-merous; calyx lobes 3–4 mm long, subspatulate or ovate to oblong, acute, reflexed and pressed against the ovary concealing it even before anthesis, pubescent to glabrous; corolla ca. 3 mm long, cleft to about ½, externally pubescent, internally papillose to pubescent only on the lobes; lobes ovate to triangular, recurved. Stamens 2.5–3 mm long, coherent; anther cells free, the apical appendages connate; anther cone ovoid to shortly ovoid, straight; filaments very short, equal, straight; sacs opening completely longitudinally; apical appendage ¼–⅙ the anther length, thick, coriaceous, papillose; connective coriaceous, distinct, generally smooth. Style ca. 5 mm long, glabrous, with a clavate stigma, long-exserted. Fruit without furrows or ribs.

Argostemma variegatum has been collected on steep soil banks in disturbed primary forest and in primary forest at ca. 100 m. Its habit is like that of *A. elatostemma* and *A. densifolium*, that is, creeping with anisophyllous leaves, the larger ones with unequal leaf-base lobes. The stems, petioles, and veins are distinctly pubescent. The flowers,



MAPS 27, 28. Distributions in Borneo.—27. *Argostemma bryophilum*.—28. *A. neurocalyx*.

however, are different from the above species; they are similar to those of *A. psychotrioides*. The calyx lobes are long and reflexed, the corollas are cleft to about half their length into pubescent, recurved lobes. The original collection has silvery mottled leaves while the other does not (perhaps due to drying). *Argostemma variegatum* is close to *A. psychotrioides*; the similarities to *A. elatostemma* are superficial.

Additional specimen examined. BORNEO. SARAWAK: 7th Div., Bukit Raya, 1969, *Smith S28234* (A, K, L).

27. Argostemma bryophilum Schumann in Schumann & Lauterb., Nachträge zur Flora der Deutschen Schutzgebirge in der Südsee. 393. 1905. TYPE: from Kaiser Wilhelmsland, not seen. Figure 30.

Small, creeping to erect, generally isophyllous herb. Stem 2–10 cm, unbranched or slightly branched, densely pubescent; internodes 3–20 mm. Leaves opposite, generally equal; stipules persistent, to 4 mm long, broadly ovate to cordiform, acute to obtuse at apex; petiole 3–11 mm long, pubescent; lamina 1.5–4.2 × 0.6–1.9 cm, ovate or elliptic to lanceolate, basally cuneate to attenuate with the lobes equal, marginally serrulate or entire, apically acute to acuminate or obtuse with a point, membranaceous, pubescent on both surfaces, below most prominent on the veins; midrib and primary veins (5–8 pairs) distinct. Inflorescences 1–2-flowered, solitary or a few together; peduncle 3–6 mm long, almost glabrous; bracts ca. 4 mm long, lanceolate or triangular; pedicels ca. 7 mm long, pubescent. Flowers 5-merous; calyx lobes 2–4 mm long, triangular, acuminate; corolla cleft to near the base, glabrous on both surfaces; lobes 5–7 mm long, ovate to lanceolate, acuminate, spreading. Stamens 4–5 mm long, coherent; anther cells and apical appendages connate except for the most apical part; anther cone ovoid, straight; filaments short, equal, straight; sacs of different length, opening completely longitudinally; apical appendage very short, glabrous; connective ± distinct, papillose. Style 4–5.5 mm long, glabrous, with a clavate stigma, shortly exserted. Fruit without furrows or ribs.

Argostemma bryophilum grows on wet rocks, boulders, or banks among mosses from 350 to 1,500 m.

It is the first species described in a large complex from New Guinea and the Philippines with more than ten taxa. Bakhuizen f. (pers. comm.) has treated the complex as a single species. All details of the complex are not known and so I have only accepted one variable species. This is the first report from Borneo. The collections from Borneo are all rather similar, with the exception of *Axelius 112A*, which has anisophyllous leaves. The Borneo specimens form a homogenous group and may in the future be recognized as a distinct taxon separate from the New Guinea and Philippine members of the complex. It is a small plant with pale green, thin, and hairy leaves. With one exception, all

collections have isophyllous, opposite leaves, very pubescent stems, and cordiform, glabrate stipules. The flowers are solitary, starlike and with long, bright yellow anther cones. The thecae distinguish this species from all others: the inner pollen sac of each theca is only ca. half as long as the outer one, which is almost as long as the whole anther, and there is no distinct apical appendage. The stigma is distinctly clavate with papillae covering the clavate area. In all flowering specimens (five of the seven known specimens), the stigma is totally covered by germinated pollen grains. The pollen is probably from the same flower, because the stigma is partly covered by the apical anther parts. I have not found more than a few pollen grains on the stigmas of any other species. Probably this species is autogamous.

Specimens examined. BORNEO. SARAWAK: 1st Div., Sabal, 350 m, 1979, *Bremer 1664* (S, SAR); 2nd Div., Bukit Sadok, 1982, *Axelius 112A* (S); 5th Div., Bakelalan, 4,000 ft., 1955, *Brooke 10406, 10464* (BM, L); 7th Div., Hose Mts., Bukit Salong, 1980, *Burtt 12733* (E); Bukit Sanpandai, 4,500 ft., 1980, *Burtt 12800* (E); 7th Div., Bukit Dema, 1978, *Burtt 11328* (E).

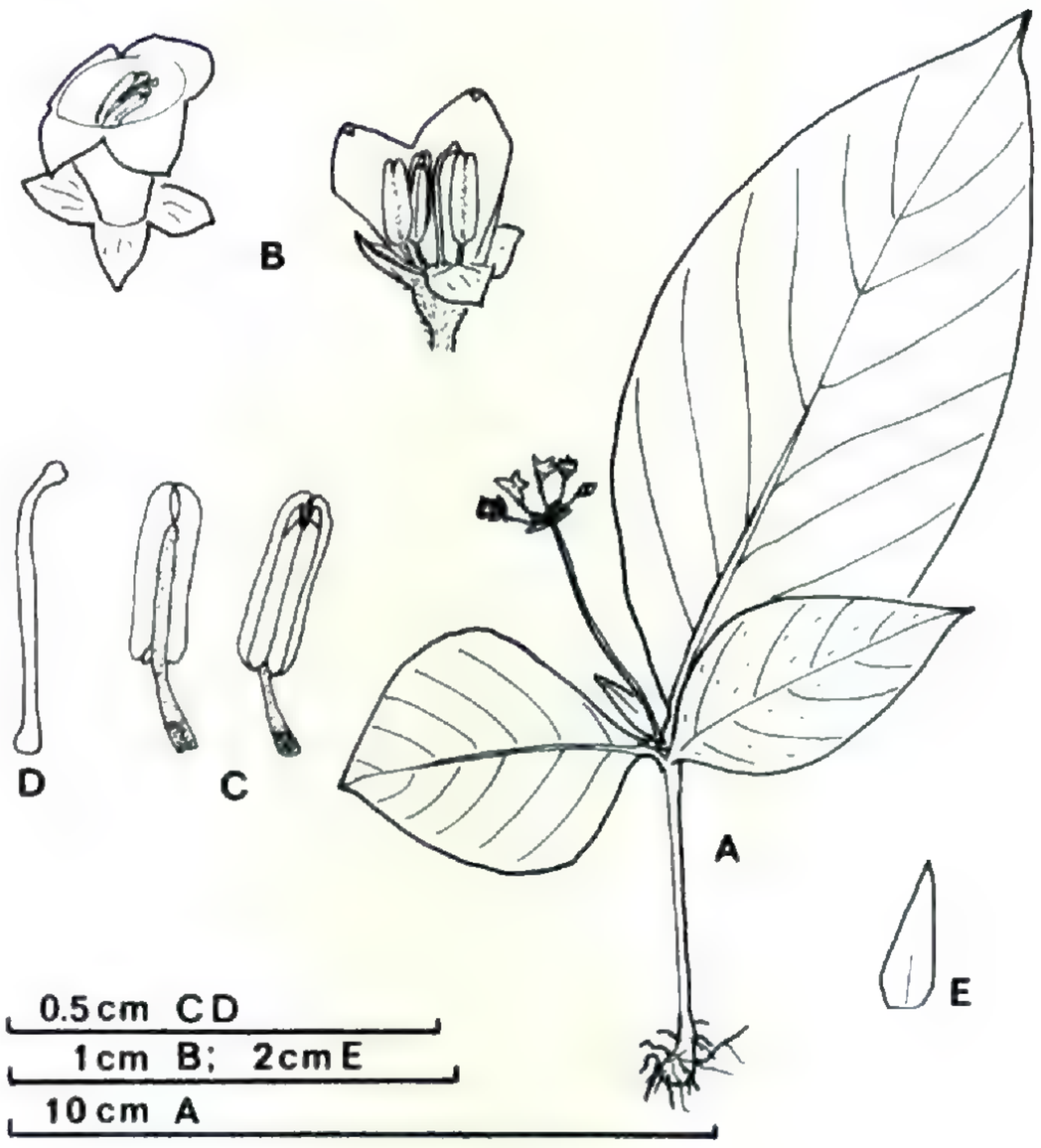


FIGURE 31. *Argostemma neurocalyx.*—A. Habit.—B. Flower.—C. Anthers.—D. Style.—E. Stipule? From *Elmer 21138* (G, SING).

28. Argostemma neurocalyx Miq., Ann. Mus. Bot. Lugd.-Bat. 4: 229. 1869. TYPE: Sumatra?: *Junghuhn s.n.* (holotype, U). Figure 31.

A. platyphyllum Merr., Univ. Calif. Publ. Bot. 15: 275. 1929. TYPE: British North Borneo: Tawao, 1922–1923, *Elmer 21138* (lectotype, K; Bakh. f. in herb., confirmed here; isolectotypes, BO, BR, G, GH, NY, S, SING, U, UC, US).

Erect anisophyllous herb with an apical rosette of 2–4 leaves. Stem 4–8 cm, unbranched, glabrous or glabrate, without distinct internodes. Leaves verticillate, compressed in an apical rosette; stipules(?) persistent, 4–9 mm long, lanceolate, acuminate at apex; petiole absent; lamina 2–15 × 12.7–7.6 cm, suborbicular or ovate to elliptic, basally obtuse or shortly attenuate and equal, marginally entire, apically acute to shortly acuminate, membranaceous, pubescent above, below with a few hairs on the veins; midrib and primary veins (7–9 pairs) distinct. Inflorescences 4–15-flowered, umbelliform, solitary or a few together; peduncle 2.3–5.5 cm, glabrous; bracts to 0.5 cm long, ovate; pedicels 0.4–0.7 cm, pubescent. Flowers 4(or 5?)-merous; calyx lobes 1–2 mm long, ovate to broadly ovate, acute, glabrous; corolla ca. 5 mm long, cleft less than ⅓ its length, glabrous on both surfaces; lobes ovate to triangular, erect. Stamens ca. 3 mm long; free, not forming a cone; filaments ca. ½ as long as the anthers, equal, straight; sacs opening by pores; without apical appendages; connective distinct, smooth. Style ca. 4 mm long, glabrous, with a capitate stigma, exserted. Fruit without furrows or ribs.

Merrill based *A. platyphyllum* on one collection by *Elmer*; no specimen is indicated. All specimens are suitable for lectotypification. Bakhuizen f. (in herb.) has selected the K specimen, and I follow his choice.

Argostemma neurocalyx was collected just once on Borneo, by Elmer, near Tawau, and was described by Merrill as *A. platyphyllum*. The protologue says "a succulent erect herb in dense forests on moss-covered basaltic rocks over which water trickles." It is not only the sole collection of the species on Borneo, it is also the only collection representing this section of the genus from Borneo. Possibly it was erroneously labeled in the herbarium by Elmer or Merrill. However, it is an easily distinguished species with two or four verticillate, slightly unequal leaves. On dry specimens, the leaves are very thin and membranaceous. It is difficult to determine from the herbarium specimens if there are stipules or just smaller leaves. The umbelliform inflorescences have long glabrous peduncles, rather large, ovate bracts, and pubescent pedicels. The flowers are tetramerous and campanulate, and the corolla lobes seem to be reflexed. The stamens are free with long filaments and connectives ending below the thecae. The pollen sacs open by pores formed by short, broad slits in the upper part of each pollen sac. The pores (slits) are placed between the sacs of each theca. As the dorsal sacs are larger

than the ventral sacs, only the pores of the dorsal ones can be seen (from the inside of the flower), and the pores of the ventral sacs are hidden by the longer dorsal sacs.

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Appendix I

Index to Collections

The species number is given within parentheses after each collection number. Only cited specimens from Borneo are listed.

Anderson 4090 (3), 4284 (13), 4349 (14), 4516 (19), 8982 (21), 9106 (21), 12581 (21), 12915 (21), 14600 (21), S4516 (14), S19690 (25), S25106 (14), S28396 (15), S28735 (13), S30826 (21), S31672 (13), S31672 (22); **Anderson & Ilias Paie** S28295 (15), S28657 (8), S28667 (18), S28881 (15); **Anderson et al.** S20288 (2); **Argent** 1308 (14); **Argent & Coppins** 1076 (14), 1081 (19), 1142 (18); **Argent & Jermy** 1038 (14); **Argent et al.** 666 (21); **Asah ak Luang** S22752 (7); **Ashton** 42 (13), 199 (14), S12132 (14), S17606 (3), S17691 (10), S18063 (13), S21238 (14), S21249 (14), S21265 (11); **Axelius** 86 (25), 112A (27), 112B (14), 122 (25), 198 (13), 217 (15), 314 (3), 315 (25); **Banyeng ak Nudong & Sibat ak Luang** S25355 (25); **Beccari** 621 (16), 150 (24), 1716 (14); **Bell** 2068 (20); **Bogle** 545 (15); **Bogle et al.** 389 (19); **Bremer** 1643 (25), 1647 (21), 1652 (1), 1662 (21), 1664 (27), 1665 (10), 1667 (18), 1668 (15), 1673 (15), 1675 (10), 1687 (10), 1688 (5), 1689 (21), 1703 (25), 1706 (25), 1707 (22), 1717 (21), 1719 (14), 1720 (15), 1722 (2), 1724 (25), 1725 (13), 1730 (25), 1742 (15), 1744 (25), 1747 (13), 1748 (25), 1752 (13); **Brooke** 1034 (14), 8502 (17), 8562 (20), 8564 (14), 8599 (20), 8670 (5), 8840 (25), 8984 (13), 9128 (13), 9131 (10), 9258 (13), 9465 (2), 9474 (17), 9487 (21), 9517 (5), 9743 (5), 9749 (15), 9770 (21), 10123 (13), 10177 (14), 10183 (3), 10283 (13), 10406 (27), 10408 (14), 10411 (11), 10448 (13), 10461 (18), 10464 (27), 10542 (17), 10716 (25), 10792 (21); **Burtt** 2655 (12), 8175 (2), 8228 (3), 8300 (21), 11274 (13), 11328 (27), 11355 (14), 11383 (13), 11401 (14), 11409 (14), 11419 (3), 11431 (14), 11443 (11), 11444 (18), 11461 (13), 11521 (1), 11565 (13), 11640 (1), 12666 (25), 12667 (10), 12709 (14), 12733(27), 12734(10), 12734(21), 12750A(18), 12750 (9), 12796 (10), 12797 (14), 12800 (27), 12817 (9), 12839 (25), 12848 (18), 12896 (13), 12908 (14), 12935 (25), 13003 (15); **Burtt & Martin** 4986 (9), 4991 (25), 5211 (18), 5216 (15), 5326 (14); **Burtt & Woods** 1959 (2), 2005 (22), 2090 (14), 2095 (14), 2150 (19), 2152 (14), 2176 (18), 2178 (19), 2182 (13), 2185 (11), 2214 (4), 2293 (14), 2366 (1), 2372 (13), 2512 (5), 2516 (14), 2518 (5), 2682 (14), 2701 (5), 2710 (15), 2761 (14), 2762 (5), 2800 (20), 2816 (1), 2845 (14); **Chai** S19532 (25), S30081 (13), S30085 (21), S33836 (13), S33980 (25), S34006 (18), S34797 (10), S36137 (15), S36485 (13), S37296 (14); **Chai et al.** S33328 (14), S37338 (1); **Chew & Corner** RSNB4618 (14); **Chew et al.** 1041 (13), 2875 (13), 1713 (18); **Clemens** 10058 (15), 10059 (13), 10981 (19), 11076 (18), 20064 (20), 20331 (20), 20910 (5), 20911 (5), 20912 (2), 21737 (10), 21738 (25), 22372 (15), 26033 (13), 26990 (13), 28179 (19), 28250 (14), 29499 (14), 29538 (13), 30650 (3), 31077 (15), 31963 (3), 32113 (18), 32578 (13), 32962 (15), 33962A (15), 33962 (15), 34110 (18), 35136 (19), 35137A (13), 35137 (15), 40049 (14), 51020 (19), 51670 (14), 223221 (14), 26926A (18), field n 6891 (14), field n 6920 (14), field n 6958

(5), field n 6973 (14), field n 7083 (5), s.n. (5), s.n. (13), s.n. (15), s.n. (18); **Collenette** 60 (14), 116 (13), 4179 (11), A77 (19), A103 (19), s.n. (12); **Cox** 957 (13); **Darnton** 568 (15); **Daud & Tachun** SFN35678 (25); **Ding Hou** 220 (13), 225 (19); **Elmer** 21138 (28); **Endert** 2952 (15), 3614 (14), 3800 (11), 3874 (14), 3916 (11), 4171 (19), 4172 (13), 4238 (14), 4327 (3); **Fedilis & Sumbing** SAN 88281 (13); **Fuchs** 21031 (13); **Gardner** 88 (14); **Geesink** 9036 (13), 9112 (14), 9113 (11), 9226 (13), 9255 (14), 9272 (11); **Gibbs** 4056 (19), 4101 (13); **Grieswold** 27 (14), 29 (13); **Hallier** 1720 (14), 2686 (15), 2779 (13), 3230 (13), B3228 (21); **Hansen** 20 (3), 187 (14); **Haviland** 684 (14), 689 (25), 1031 (10), 1325 (18), 1326 (19), 2958 (21), 2960 (25), 8475 (16), s.n. (13), s.n. (21), s.n. (25); **Haviland & Hose** 3409 (22), s.n. (25); **Hullett** 329 (13), s.n. (5); **Ilias Paie** S28445 (14), S36357 (14); **Ilias & Yeo** S38349 (1); **Jacobs** 5065 (10); **Jaheri in exp. Nieuwenhuis** 1636 (7); **James Mamit** S35046 (21); **Kanis & Kuripin** 53966 (3); **Kloss** SFN19154 (13); **Kostermans** 7437 (5), 9216 (13), 10121 (15), 10570 (13), 12845 (21), 12851 (18); **Lobb** s.n. (25); **Lowe** s.n. (25); **Madani** 90812 (13); **Martin** S38185 (18), S38848 (14); **Martin & Ismawi** S36861 (13); **Meijer** 687 (5), 2286 (3), 2343 (13); **Mjöberg** 8 (7), 82 (14), 85 (14), 88 (14), 205 (5), 206 (5), 216 (25), 218 (15), s.n. (2), s.n. (5), s.n. (13), s.n. (14), s.n. (14), s.n. (15), s.n. (20); **Motley** 1174 (2); **Moulton** 105 (14), 6695 (14), 6726 (14); **Moulton's native collectors** 365 (15); **Murata et al.** 1192 (25); **native collector** 85 (21), 294 (25), 408 (25), 1227 (17), 1232 (21), 1244 (25), 1256 (13), 1428 (13), 2403 (21), 5181 (21), D131 (24), s.n. (5), s.n. (14), s.n. (21), s.n. (25); **Nielsen** 204 (13), 368 (17) 494 (13), 538 (4), 833 (18), 838 (14); **Nooteboom** 921 (14), 922 (19), 1031 (15), 1035 (14); **Nooteboom & Aban** 1552 (13), 1593 (13); **Nooteboom & Chai** 1704 (13), 1744 (14), 1856 (14), 1935 (14), 2198 (11), 2307 (13); **Othman Ismawi** S37437 (15); **Price** 194 (19); **Purseglove** 4987 (5), 5095 (10), 5096 (17), 5129 (13), 5256 (13), 5282 (15), 5534 (10); **Purseglove & Shah** 4811 (5); **Richards** 1052 (13), 1537 (14), 1689 (18), 1711 (7), 1790 (14), 1799 (13), 2090A (3), 2101 (7), 2455 (10), 7090 (13); **Ridley** 11751 (5), 11753 (2), 12302 (25), 12303 (2), 12304 (14), 12448 (4), s.n. (4); **Sanusi Tahir** 8954 (25); **Sibat ak Luang** S23664 (25); **Sidek Kiah** 2 (13); **Sinclair** 9212 (14), 10355 (15); **Sinclair et al.** 9215 (15); **Smith** S28234 (26); **Sylvester Tong** S34346 (4), S34847 (7); **Teysmann** 11292 (21), 11921 (21); **Tong & Banyeng** S33271 (14); **van Niel** 3558 (13), 4580 (13); **Winkler** 660 (3), 767 (1), 781 (23), 791 (3), 879 (15), 897 (6), 949 (13), 950 (6), 951 (10), 1007 (15), 1282 (15), 1353 (15), 1428 (21), 1479 (18), 1561 (26), 1562 (15), 2853 (15), **Wood** SAN16695 (14).

Appendix II

Index to taxa

Accepted names are in boldface, synonyms in italics.

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STUDIES IN NEOTROPICAL PALEOBOTANY. VII. THE LOWER MIOCENE COMMUNITIES OF PANAMA—THE LA BOCA FORMATION[1]

Alan Graham[2]

ABSTRACT

Thirty-nine palynomorphs have been identified from among 54 forms recovered from the lower Miocene La Boca Formation in the Canal region of Panama. These are ascomycete cleistothecia, the dinoflagellates *Spiniferites* and *Operculodinium*, *Lycopodium*, *Selaginella*, *Cyathea*, *Pteris* (types 1 and 2), cf. *Antrophyum*, other trilete fern spores (types 1–3), monolete fern spores (types 1–5), Gramineae, Palmae (*Attalea*, *Manicaria*, and *Synechanthus* types), *Ilex*, cf. *Aguiaria*, cf. *Ceiba*, *Pseudobombax*, *Alchornea*, *Alfaroa/Engelhardia*, *Crudia*, *Utricularia*, Malpighiaceae (types 1–5), Malvaceae, *Rhizophora* (constituting 67–88% of five samples counted), Rubiaceae (types 1 and 2), and *Pelliciera*. The flora is estuarine in aspect, and consistent with three other lower Miocene assemblages (Uscari, Culebra, Cucaracha), reflects low-lying volcanic islands fringed seaward by mangroves, with freshwater fern and palm swamp marshes in the lowlands and versions of the tropical wet, tropical moist, and premontane forests on the adjacent slopes. There is no palynological evidence for communities of drier to arid aspect (including savannahs) or of high altitudes; elevations of 1,200 to 1,500 m would accommodate all taxa present in the La Boca and other fossil floras. The affinity of the flora is distinctly with Central America and areas to the north. With the exception of *Crudia*, all genera occur in the modern vegetation of Panama, and consequently the paleoclimate, in agreement with Tertiary paleotemperature curves, was similar to that prevailing today in coastal, lowland, and moderate-altitude tropical habitats in southern Central America.

The La Boca Formation is the third in a series of three stratigraphically and lithologically similar formations from the geologically complex Canal region of Panama yielding well-preserved fossil pollen and spores. The Culebra Formation is oldest (basal) and is overlain by the Cucaracha Formation. The La Boca does not anywhere lie directly on the Cucaracha, but it interfingers (viz., is contemporaneous) with the Pedro Miguel Formation, which overlies the Cucaracha elsewhere in the Canal region. Age estimates are based primarily on molluscan (Woodring, 1957–1982) and ostracod (Van den Bold, 1972, 1973) data which suggest an early Miocene age for the three formations.

The La Boca outcrops along both sides of the Panama Canal from the Pacific entrance to the Las Cascadas Reach. The sediments were deposited in an estuarine environment and include an alternating sequence of mudstones, siltstones, sandstones, lignitic shales, tuffs (waterlain volcanic ash), and limestones typical of that environmental setting. The presence of the coralliferous Emperador limestone member in the lower part of the formation and *Rhizophora*-containing lignitic shales indicate deposition in warm temperate to tropical, shallow seas and in adjacent coastal, brackish-water habitats.

Fifty-four samples were collected from two exposures of the La Boca Formation along the Las Cascadas Reach in September 1967 (latitude 9°04′N, longitude 79°40′W; ground elevation 52.7 m). Locality A (samples 1–26) was at Canal marker 1600 (1766 in the new marking system), and locality B (samples 27–54) at markers 1622 (1788), 1625 (1791), and 1627 (1793). Since that time the Canal has been widened from 90 m to 155 m, and compared with the present physiography, the 1967 samples were collected about 25 m up and 60 m out over the present Canal. The beds dipped back into the slope at a 20–25° angle so that now

[1] The author gratefully acknowledges information provided by William Elsik (Exxon Company, U.S.A.) and William Evitt (Stanford University) on the fungi and dinoflagellates. Research was supported by National Science Foundation grant BSR-8500850.

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the same lignite layers are nearly at water level. Other details of the collecting site and geology of the area are summarized in Graham et al. (1985: 495–502).

Materials and Methods

Extraction and processing techniques are described in Graham (1985). Slides are labeled according to locality, sample number, and slide number (e.g., Pan A 5-1). Of the 54 samples collected, 20 contained fair to well-preserved palynomorphs (locality A—5, 14, 16, 17, 19, 20, 21; locality B—27, 28, 29, 30, 33, 34, 35, 45, 46, 47, 50, 52, 54). Location of the specimens on the slides is by England Slide Finder coordinates (e.g., ESF C-29). The tabulations in Table 1 are based on five representative samples (14, 16, 20, 21, 50) containing diverse and well-preserved palynomorphs. All materials are deposited in the palynology collections at Kent State University.

Systematics

Thirty-nine palynomorphs have been identified from the La Boca Formation (Table 1) in addition to 15 others that cannot presently be identified (unknowns 1–15). Most of the specimens have been recovered from other Tertiary formations in the Gulf/Caribbean region and discussed in previous publications, hence the material presented here is synoptic. These formations and references are as follows: Gatuncillo (middle(?) to late Eocene, Panama; Graham, 1985); San Sebastian (middle to late Oligocene, Puerto Rico; Graham & Jarzen, 1969); Uscari (early Miocene, Costa Rica; Graham, 1987a, b); Culebra (early Miocene, Panama; Graham, 1988a), and Cucaracha (early Miocene, Panama; Graham, 1988b). Present ranges of the modern analogs within the Neotropics and ecological data are based on field observations, personal communication with specialists, and the literature, especially Croat (1978), D'Arcy (1987), Hartshorn (1983), Tryon & Tryon (1982), and Woodson & Schery (1943–1980). Terminology for vegetation types follows Holdridge (1947; Holdridge et al., 1971), used by Croat (1978) and Hartshorn (1983) for describing the plant communities of Panama and Costa Rica. In instances where the modern analogs extend into South America, their altitudinal ranges and community affiliations may differ slightly from their Central American occurrences. The data for Central America are considered first in paleocommunity and paleoenvironmental reconstruction of the La Boca flora, since communities in South America are more distant and were isolated from Central America until about 3 Ma.

FUNGI

Ascomycete cleistothecium (Fig. 1). Flattened, circular, multicellular, cells cubical, 6 × 9 μm, outer and some lateral walls of peripheral (marginal) cells thickened, center opaque (solid?), cells disrupted along outer edge, forming slitlike opening 35 μm long (attachment scar?); 124 μm.

Reproductive structures of the Plectomycetes group of ascomycete fungi are frequent in Gulf/Caribbean Tertiary deposits but never in large numbers. Although entire specimens are relatively rare, fragments are present in almost all samples. Another type with radially aligned cells and marginal spines was recovered from the lower Miocene Uscari sequence of Costa Rica (Graham, 1987a, fig. 1).

PYRROPHYTA

Spiniferites (Figs. 2, 3). These dinoflagellate cysts, as fossils referable to *Spiniferites*, are common in the Tertiary and extend back to the Early Cretaceous. They are produced by some species of the extant *Gonyaulax* group (Evitt, pers. comm., 1987).

Operculodinium centrocarpus (Fig. 4). This is also a common Tertiary form produced by the modern *Gonyaulax grindleyi* (= *Protoceratium reticulatum*) and a frequent associate of *Spiniferites* in the Miocene. According to Evitt (pers. comm., 1987), "These two cyst types are common constituents of Tertiary nearshore sediments. They occur, virtually to the exclusion of other forms, in the Miocene Monterrey Formation in California (*Spiniferites* much the more abundant), and together with a very rich associated assemblage in the Calvert Formation along the east coast. It would be entirely plausible to find them in estuarine deposits of Miocene age virtually anywhere. No examples of *Spiniferites*, which has a very distinctive and easily recognized morphology (at least at the generic level), have been found in fully freshwater sediments."

LYCOPODIACEAE

Lycopodium (Fig. 5). Amb triangular, apices rounded; trilete, laesurae straight, narrow, ca. 20–22 μm long, extending to spore margin, inner margin entire, distal surface with numerous circular punctae ca. 1 μm diam., proximal face laevigate; wall 1–1.5 μm thick; 40 μm.

These spores are similar to those of *L. reflexum*

TABLE 1. Identification and numerical representation of fossil palynomorphs from the lower Miocene La Boca Formation. Figures are percentages based on counts of 200 specimens from four samples at locality A (14, 16, 20, 21) and one sample at locality B (50). Minus sign (−) indicates specimens are present in the sample but were not encountered in counts of 200. The counts do not include clusters of 20 or more grains of *Rhizophora* found in sample 14, or *Pelliciera* in sample 16.

	Locality A				Locality B
	14	16	20	21	50
Fungi					
Ascomycete cleistothecium					−
Pyrrophyta					
Spiniferites	0.5				1
Operculodinium centrocarpus	1	0.5			
Lycopodiaceae					
Lycopodium	−	−		0.5	
Selaginellaceae					
Selaginella		1	−	−	−
Cyatheaceae					
Cyathea	−	3	1	2.5	
Pteridaceae					
Pteris type 1	−	1		−	−
Pteris type 2	1	1.5	1.5	1	2
Vittariaceae					
Cf. *Antrophyum*	−	1	1	1	2
Trilete fern spores					
Type 1	−	1	0.5		−
Type 2					−
Type 3				−	
Monolete fern spores					
Type 1		0.5	1.5	1	
Type 2	−	1		1.5	−
Type 3		1.5	−	1.5	2.5
Type 4	1	1.5	1.5	−	−
Type 5	1	1.5	1.5		−
Gramineae	−	−			
Palmae					
Attalea type	−	0.5	0.5	1.5	
Maricaria type	1.5	−	1	−	1
Synechanthus type	−	1	1		−
Aquifoliaceae					
Ilex	−	−		−	
Bombacaceae					
Cf. *Aguiaria*		−			
Cf. *Ceiba*		−			
Pseudobombax			−		
Euphorbiaceae					
Alchornea		0.5	−	−	−
Juglandaceae					
Alfaroa/Engelhardia	1	0.5	1	−	2.5

TABLE 1. Continued.

	Locality A				Locality B
	14	16	20	21	50
Leguminosae—Caesalpinioideae					
Crudia	–	2	1	1	1
Lentibulariaceae					
Utricularia	–				
Malpighiaceae					
Type 1		0.5		–	
Type 2	–				1
Type 3				–	–
Type 4	–	–			
Type 5		0.5			
Malvaceae				–	
Rhizophoraceae					
Rhizophora	88	67	76	77.5	74
Rubiaceae					
Type 1	–	1	0.5	–	1
Type 2		1	0.5	–	–
Theaceae					
Pelliciera	2	3	2.5	1	2
Unknowns					
Type 1			–		
Type 2					–
Type 3	–	1	0.5		
Type 4	–				
Type 5	0.5	0.5	0.5		–
Type 6	0.5		–		1
Type 7		–			
Type 8					–
Type 9		–			
Type 10	–	0.5		0.5	
Type 11					–
Type 12				–	
Type 13		0.5	0.5		1
Type 14	–	0.5	–	0.5	
Type 15	0.5	–	1	1	1.5
Other unknowns	1.5	4.5	5	8	6.5

Lam. and *L. linifolium* L. presently occurring in moist shaded habitats in Panama. They have been recovered from the Culebra, Uscari, and Paraje Solo formations, although the Uscari specimens have thicker walls (3–4 μm vs. 1–1.5 μm).

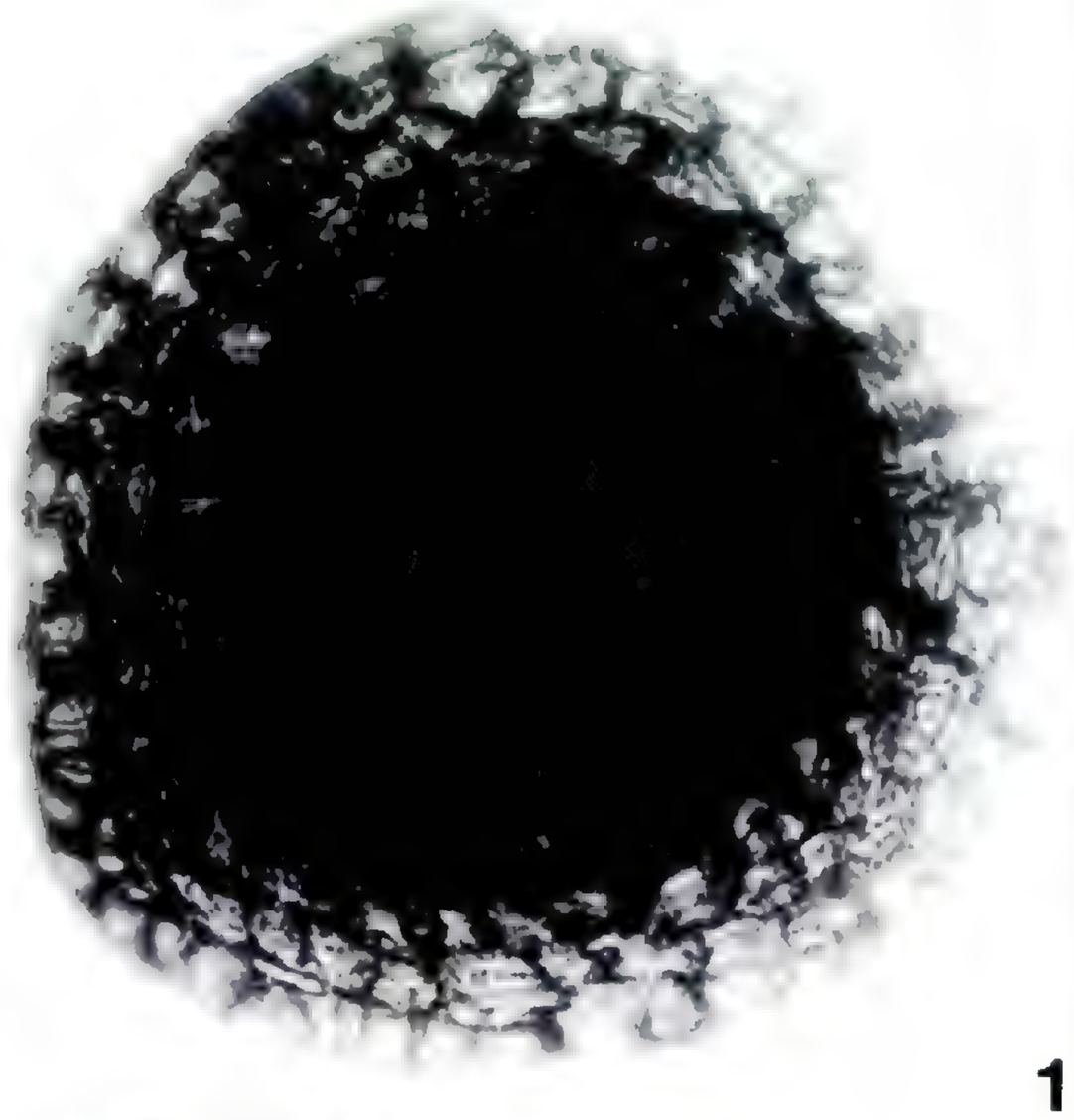
SELAGINELLACEAE

Selaginella (Fig. 6). Spherical, amb circular to oval-triangular; trilete, laesurae frequently obscured by dense sculpture, arms variously developed and spores often appearing monolete, straight, narrow, ca. 20–24 μm long, extending nearly to spore margin; echinate, echinae short (ca. 2–3 μm), occasionally curved, dense, bases broad; wall ca. 2 μm thick (excluding echinae); 30–32 μm.

Selaginella is widespread in moist, shaded habitats in the Neotropics. The spores occur in low numbers in the Gatuncillo, San Sebastian, Uscari, Culebra, Cucaracha, and Paraje Solo formations.

CYATHEACEAE

Cyathea (Figs. 10, 13). Amb oval-triangular, apices rounded; trilete, laesurae straight, narrow, 19–21 μm long, extending to or nearly to spore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2

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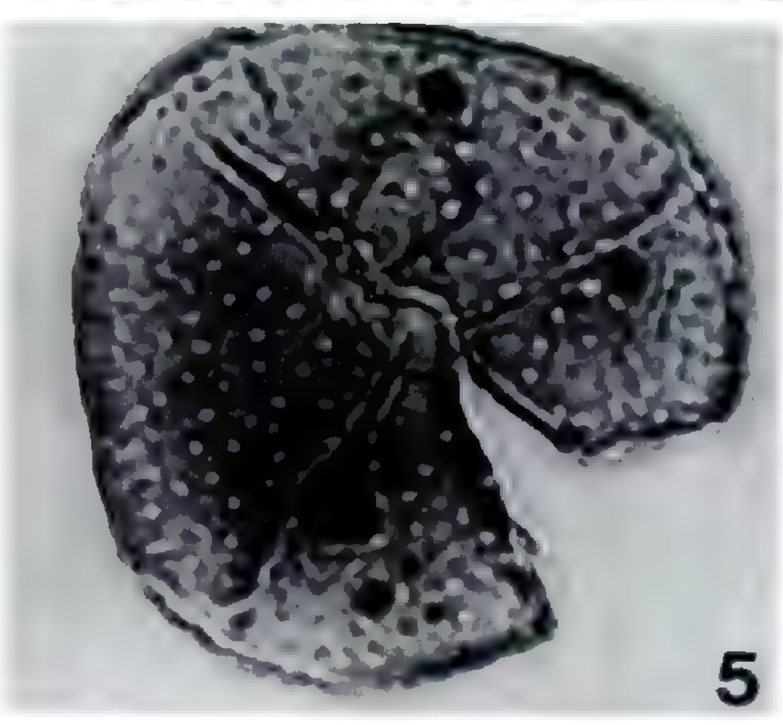
4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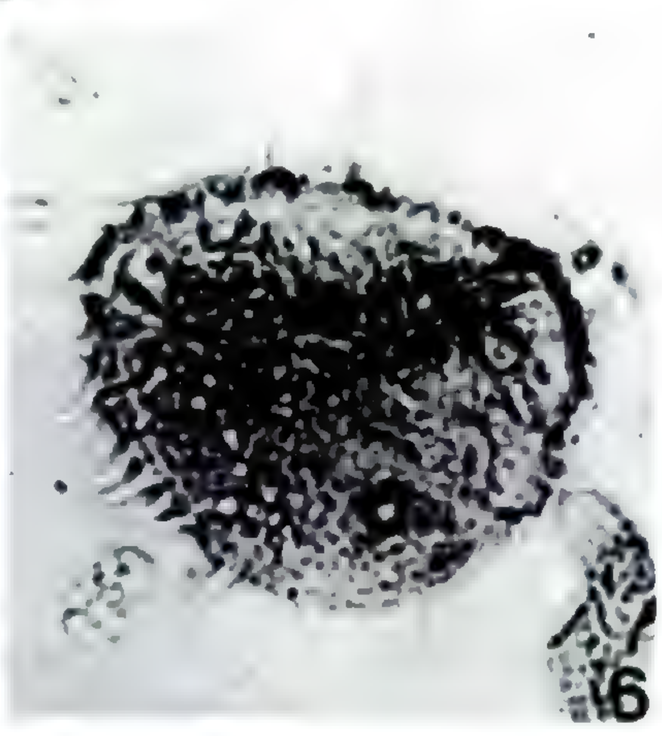
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FIGURES 1–7. Fossil spores from the La Boca Formation, Panama.—1. Ascomycete cleistothecium, Pan B 27-1, ESF C-29, 3–4.—2, 3. *Spiniferites* sp., Pan A 14-1a, ESF R-46, 1–3.—4. *Operculodinium centrocarpus*, Pan A

margin, inner margin entire, bordered by lip 2–3 μm wide with punctae 1 μm diam.; distal surface finely punctate, proximal surface more laevigate near laesurae; wall 1.5–2 μm thick; 32–36 μm.

Tryon & Tryon (1982: 204) noted that the classification of tree ferns differs among various authors and that the name *Cyathea* has been used to include nearly all members of the family. The labels on reference slides used for identification often reflect this confusion, especially between *Cyathea* and *Alsophila*. A further complication is that the lip surrounding the laesurae is difficult to observe on some fossil specimens because of preservation and/or orientation. According to recent illustrations by Gastony & Tryon (1976) and Tryon & Tryon (1982), trilete, micropunctate forms with a lip often bordered by punctae are referred to *Cyathea*, while forms with a laevigate surface beneath the perine belong to *Alsophila*. Laevigate spores of similar size and morphology lacking the lip and bordering punctae are produced by several extant genera (e.g., species of *Adiantum*). Following this classification, *Cyathea* spores are known from the Culebra, Cucaracha, La Boca, and Paraje Solo formations (as *Alsophila* in the latter; Graham, 1976, figs. 16–18). *Alsophila* is known from the Gatuncillo Formation (Graham, 1985, fig. 10, as trilete fern spore type 1) and from the Paraje Solo Formation (Graham, 1976, fig. 19, as *Cyathea*).

In Central America *Cyathea* grows primarily in low rain forests, montane forests, and cloud forests, usually between 1,500 and 2,000 m.

PTERIDACEAE

Pteris. *Pteris* is a genus of about 250 species, with some 55 occurring in the Neotropics from northern Mexico (Nuevo León) and Florida to Argentina and Chile (Tryon & Tryon, 1982: 334). It usually grows at altitudes below 2,000 m in wet, cloud, or gallery forests. Spores are frequent but not abundant in the Gatuncillo, San Sebastian, Uscari, Culebra, Cucaracha, and Paraje Solo formations.

Type 1 (Figs. 8, 9). Amb oval-triangular, apices rounded, margin entire to slightly undulating; trilete, laesurae straight, narrow, inner margin entire, 23–25 μm long, extending to spore margin; wall with coarse irregular verrucae on distal surface, proximal surface more laevigate, hyaline marginal flange 12–15 μm wide; 62–68 μm.

Type 2 (Figs. 11, 12). Smaller (40–42 μm), the marginal flange narrower (4–5 μm wide), and the verrucae smaller and more numerous.

VITTARIACEAE

Cf. Antrophyum (Fig. 14). Amb triangular, apices rounded; trilete, laesurae relatively small in relation to spore diam., straight, narrow, 12–16 μm long, extending ca. ⅔ distance to spore margin, inner margin entire; laevigate; wall ca. 1.5 μm thick; 50–52 μm.

Antrophyum is represented by about 10 species in the Neotropics, growing in cloud and rain forests usually at elevations between 100 and 1,500 m from Mexico (Hidalgo) through Central America and the Antilles to northern Argentina and southeastern Brazil (Tryon & Tryon, 1982: 360). The spores are similar to those of *Acrostichum aureum* L. (cf. Tryon & Tryon, 1982, figs. 49.10, 12 and 51.8), a species expected in the La Boca and other estuarine formations because it grows in brackish mangrove swamps. The spores of *A. aureum* in our reference material (nine collections) have a granular, scabrate sculpture, while those of *Antrophyum* are more laevigate. The distinction is difficult among fossil specimens, and it is possible that both genera are represented in Gulf/Caribbean Tertiary deposits. Since the fossils are laevigate, however, they are referred to cf. *Antrophyum*. Similar spores are known from the Gatuncillo, San Sebastian (not figured in Graham & Jarzen, 1969), Culebra, Cucaracha, and Paraje Solo (as an unknown in Graham, 1976, fig. 227) formations.

OTHER TRILETE FERN SPORES

Several trilete fern spores were recovered for which biological affinities could not be determined. Three of the more distinctive ones are described below.

Type 1 (Fig. 7). Amb oval-triangular, apices rounded, margin entire; trilete, laesurae straight, narrow, inner margin entire, 12 μm long, extending ca. ¾ distance to spore margin; laevigate; wall 1.5 μm thick; 29–32 μm.

These spores are similar to those of several ferns, including *Adiantum*, and cannot be referred to any

←

16-1, ESF L-33, 1–3.—5. *Lycopodium*, Pan A 21-1, ESF F-11, 3.—6. *Selaginella*, Pan A 16-3, ESF P-40, 3.—7. Trilete fern spore type 1, Pan A 16-2, ESF X-41, 1.

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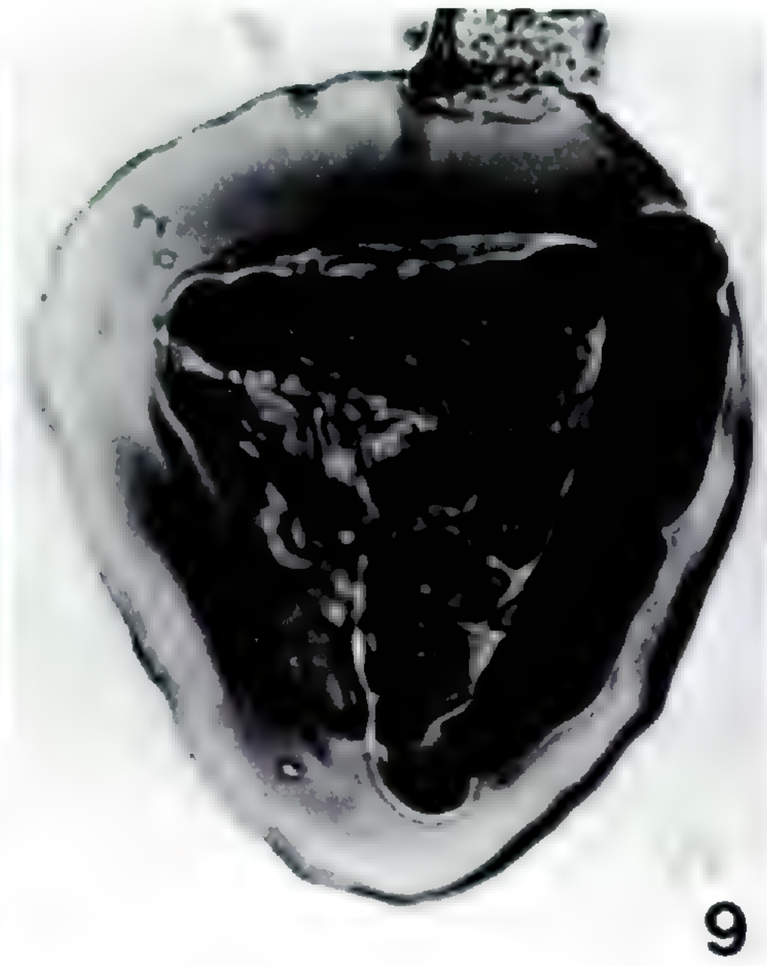
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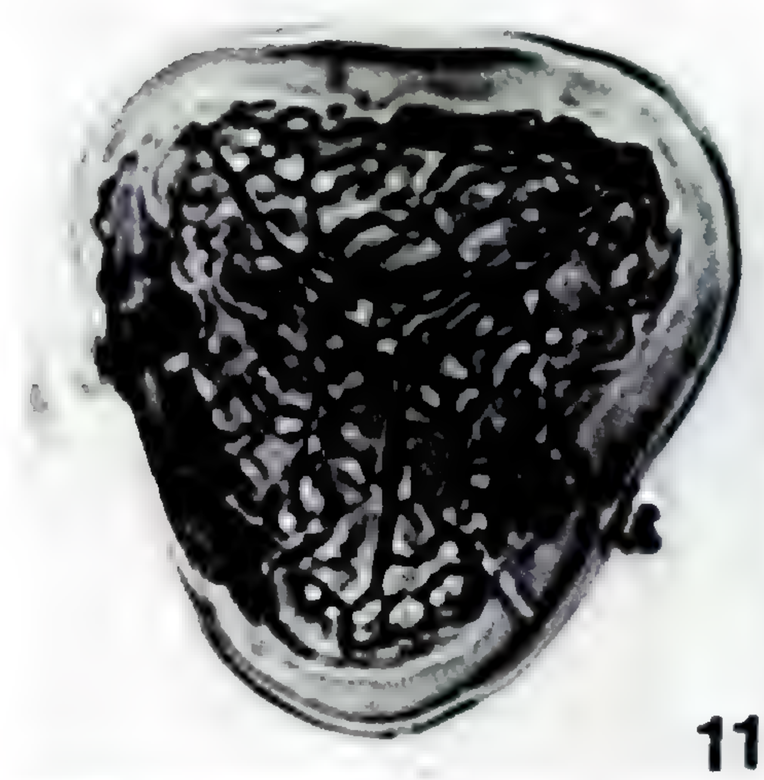
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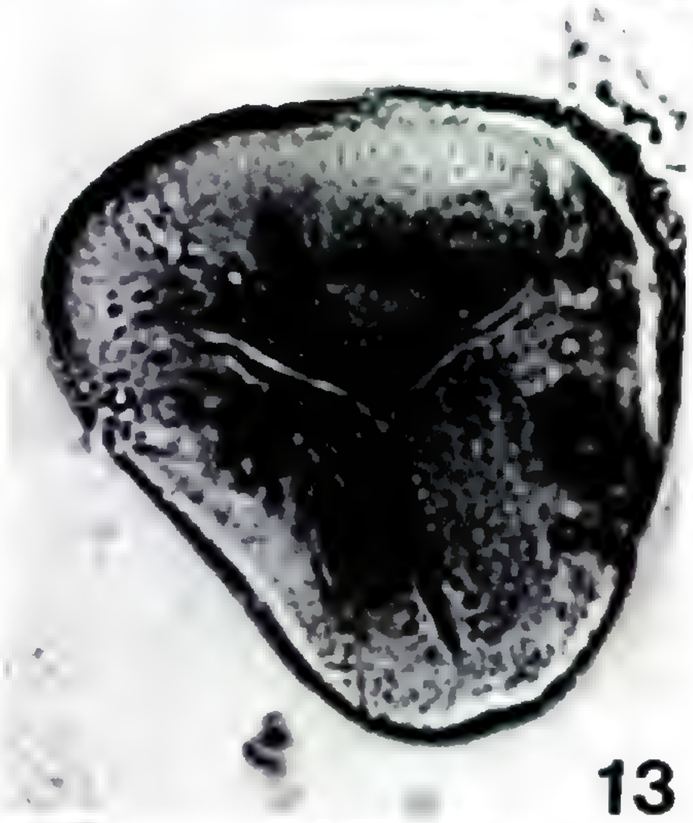
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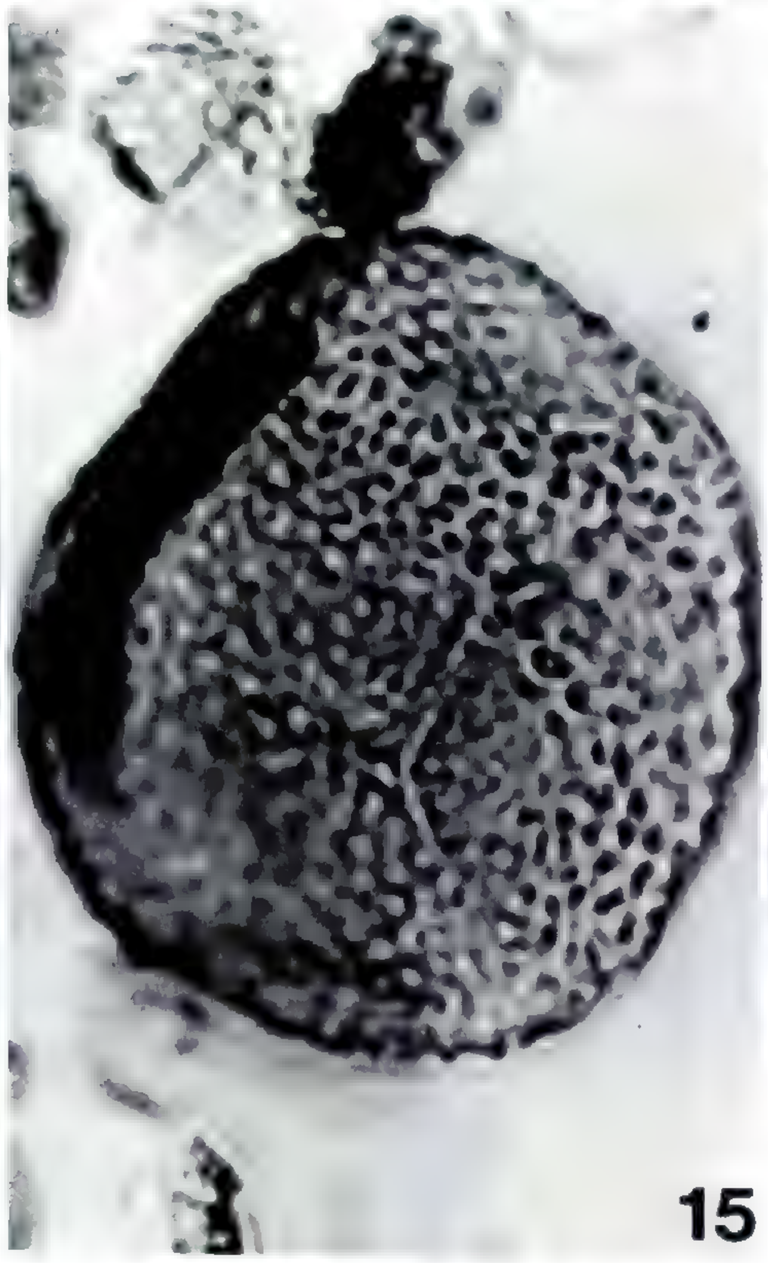
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FIGURES 8–17. Fossil spores from the La Boca Formation, Panama.—8, 9. *Pteris* type 1, Pan A 16-1, ESF S-35, 1.—10, 13. *Cyathea*, Pan A 16-1, ESF X-49; Pan A 16-2, ESF L-34.—11, 12. *Pteris* type 2, Pan A 16-2, ESF K-34.—14. Cf. *Antrophyum*, Pan B 50-2, ESF N-14, 2.—15. Trilete fern spore type 2, Pan B 30-3, ESF Q-46, 1–2.—16, 17. Trilete fern spore type 3, Pan A 21-1, ESF W-11, 1–3.

one genus. They are also known from the Uscari sequence of Costa Rica (Graham, 1987a, fig. 30).

Type 2 (Fig. 15). Amb oval-triangular to circular; trilete, laesurae straight, narrow, 17–20 μm long, extending ca. ¾ distance to spore margin, inner margin entire; finely reticulate; wall 1.5 μm thick; 45–48 μm.

Type 3 (Figs. 16, 17). Amb triangular, trilete, laesurae straight, narrow, 12–14 μm long, extending to or nearly to spore margin, prominent lip (partially folds?), inner margin entire; distal surface divided into low, irregular, verrucaelike segments by short, sinuous furrows, proximal surface more laevigate; wall 2–3 μm thick; 31–33 μm.

MONOLETE FERN SPORES

Reniform, monolete fern spores are common in all Tertiary formations studied for the Gulf/Caribbean region. They are produced by members of the Blechnaceae, Polypodiaceae, and Pteridaceae and range from Paleozoic to Recent. Five types illustrate the range in sculpture and size. Type 1 (Fig. 18; 45 × 32 μm) is laevigate; type 2 (Fig. 19; 70 × 46 μm) is finely verrucate; type 3 (Fig. 20; 69 × 51 μm) has numerous, small, densely arranged verrucae; type 4 (Fig. 21; 42 × 36 μm) is coarsely verrucate; and type 5 (Fig. 22; 54 × 36 μm) has prominent, widely scattered, peglike verrucae.

GRAMINEAE

Spherical, amb circular; monoporate, pore circular, 2 μm diam., inner margin entire, annulus ca. 2 μm wide, outer margin entire; tectate, wall ca. 2 μm thick; psilate to faintly scabrate; ca. 30 μm (folded) (Fig. 23).

The Gramineae are stenopalynous, and the specimens cannot be referred to any single genus. Grass pollen continues to be rare or absent in Gulf/Caribbean Tertiary deposits studied to date, with only a few grains previously reported from the Culebra and Paraje Solo formations. Specimens are known in the stratigraphic literature as *Monoporites annulatus* and range from the Paleocene (Brazil) to Recent (Muller, 1981, 1984).

PALMAE

Although several surveys of modern palm pollen are available (e.g., Ferguson, 1986; Thanikaimoni, 1970), it is still difficult to identify Gulf/Caribbean Tertiary specimens. The palms were a prominent component of the vegetation, and three types are recognized for the La Boca Formation.

Attalea type (Fig. 24). Wedge-shaped, with greatest diam. near pole; amb ca. rectangular; monocolpate, colpus straight, narrow, 19–22 μm long, inner margin entire to minutely dentate; scabrate; tectate, wall ca. 1.5 μm thick; 43–47 × 25–29 μm.

Attalea is a genus of about 40 species occurring in South America, the West Indies, and the Old World tropics, with one species (*A. allenii* H. Moore) listed for Panama (D'Arcy, 1987), where it grows at elevations up to ca. 1,000 m.

Manicaria type (Figs. 25–27). Prolate, with greatest diam. at or near equator; monocolpate, colpus straight to slightly sinuous, narrow, 30–42 μm long, extending nearly entire length of grain, inner margin entire; finely reticulate (diam. of lumen 1 μm or slightly less); tectate-perforate, wall ca. 1 μm thick; 36–48 × 21–30 μm.

Manicaria is a tree up to 10 m tall, with three species in the Antilles, Central America, and South America (fide Bailey, 1943), where it often occurs in dense groves in wet places. Similar pollen is known from the Gatuncillo and Culebra formations.

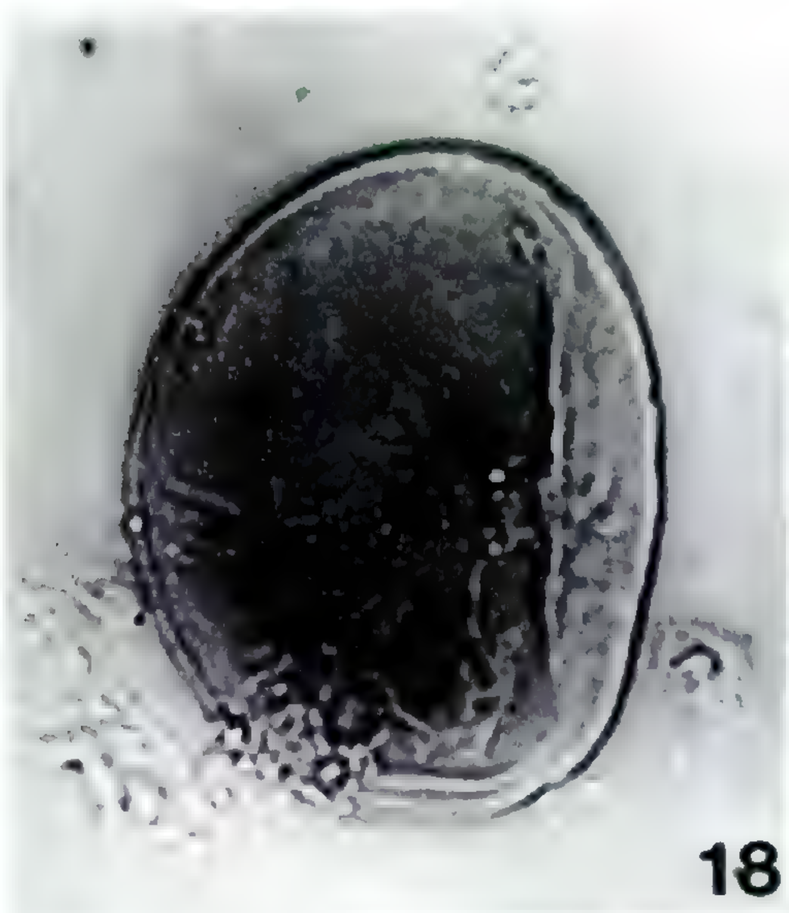
Synechanthus type (Figs. 28, 29). Prolate; monocolpate, colpus straight, narrow, 30–42 μm long, extending entire length of grain, inner margin entire; microreticulate; tectate-perforate, wall 1.5–2 μm thick; 36–48 × 30–38 μm.

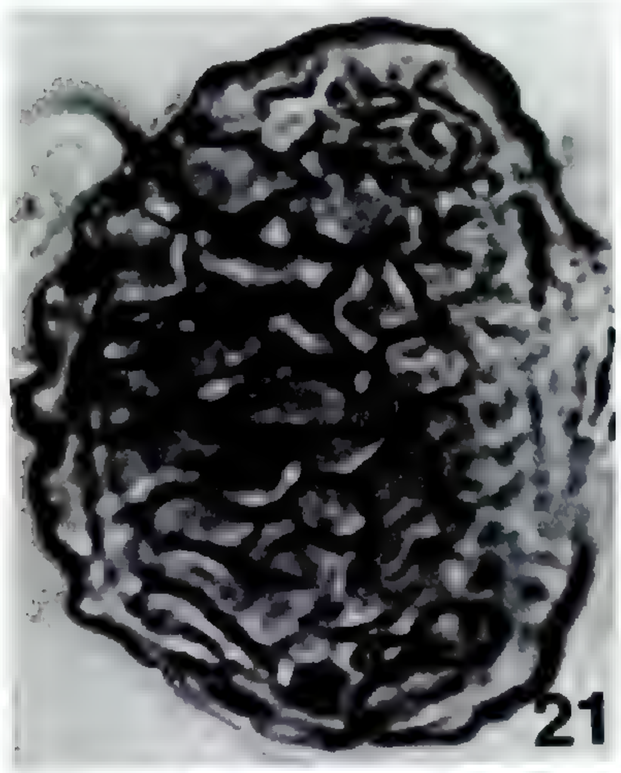
Synechanthus grows in Panama at low elevations in the tropical moist, premontane wet, and premontane rain forests (Croat, 1978: 178). Similar pollen occurs in the Culebra Formation.

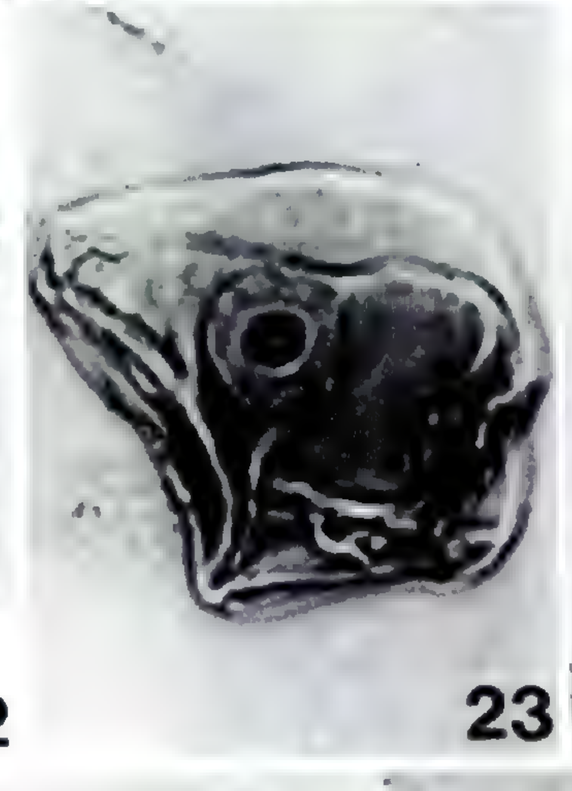
AQUIFOLIACEAE

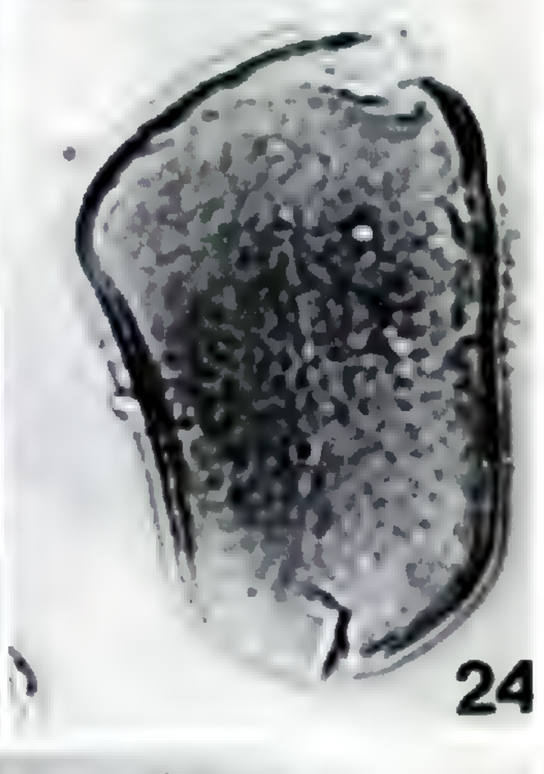
Ilex (Fig. 31). Oblate-spheroidal, amb oval to circular, tricolporoidate, colpi straight, 18 μm long, equatorially arranged, meridionally elongated, equidistant, inner margin diffuse, pores obscure, diam. ca. 2–3 μm, circular, situated at midpoint of colpus; intectate, clavate, wall 3 μm thick; 27 × 18 μm.

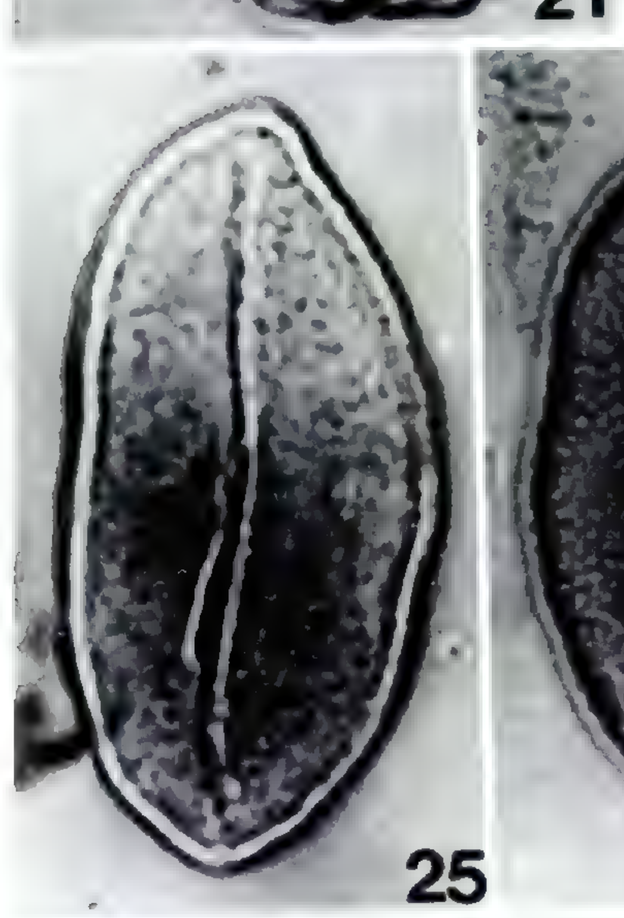
In Central America *Ilex* commonly grows at mid altitudes in moist to slightly drier habitats. It is a frequent component of Gulf/Caribbean Tertiary microfossil floras in low percentages and has been recovered from the Gatuncillo, San Sebastian, Uscari, Culebra, Cucaracha, and Paraje Solo formations.

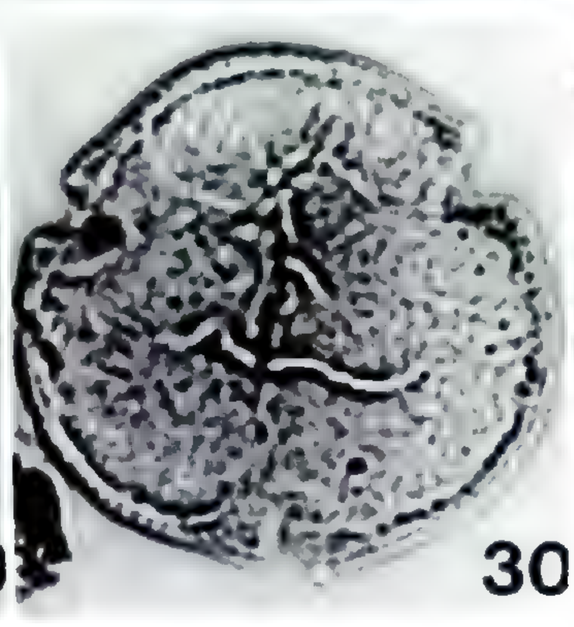


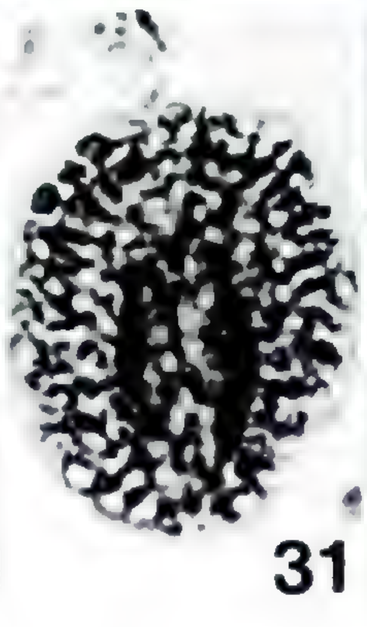


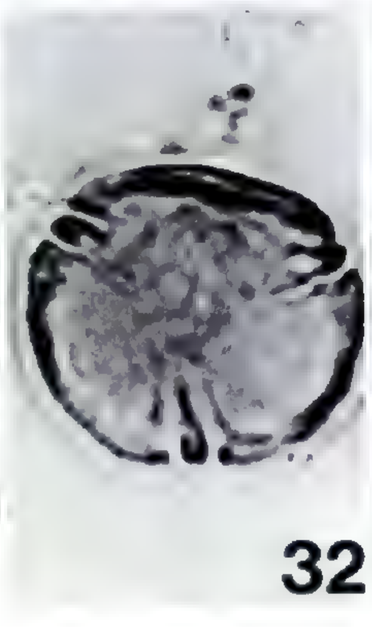












FIGURES 18–33. Fossil spores and pollen from the La Boca Formation, Panama.—18. Monolete fern spore type 1, Pan A 16-1, ESF D-32, 1–3.—19. Monolete fern spore type 2, Pan A 16-1, ESF T-45, 3.—20. Monolete fern spore type 3, Pan A 16-3, ESF J-43, 3–4.—21. Monolete fern spore type 4, Pan A 14-1a, ESF M-48, 3–4.—22. Monolete fern spore type 5, Pan B 50-2, ESF V-23, 1–2.—23. Gramineae, Pan A 14-1a, ESF W-35, 1.—24.

BOMBACACEAE

The pollen of several Bombacaceae are distinct (Tsukada, 1964; Nilsson & Robyns, 1986), but other generalized types cannot be referred to any one genus (see listings in Muller, 1981: 46–48). There is also some overlap with the closely related families Sterculiaceae and Tiliaceae, and in fossil deposits types are recovered that do not match exactly any extant members of the complex (Graham, 1976, figs. 248–255). It is possible that some unidentified pollen represents extant species not yet collected or extinct taxa from early speciation after introduction into the Caribbean region. Further studies are needed on the pollen morphology of modern forms, including newly described taxa, and a complete assessment should be made of fossil types.

Bombacaceae are prominent members of neotropical forests, and the pollen is frequent but not abundant in Tertiary sediments. Muller (1981: 46–48) listed the oldest occurrence of this family as Maestrichtian (uppermost Cretaceous) from the southeastern United States and cited other records supporting Wolfe's (1975) suggestion that the family originated in eastern North America and subsequently spread to South America and Africa where it diversified. In the Caribbean region it first appears in the Paleocene of northern South America (*Bombacacidites annae* = *Bombax ceiba* type; Germeraad et al., 1968: 277), and in our material, pollen of the family occurs in the San Sebastian Formation and Uscari sequence.

Cf. Aguiaria (Fig. 30; cf. modern pollen illustrated by Nilsson & Robyns, 1986, fig. 7f, g). Oblate, amb circular; tricolpate, colpi short (8–10 μm apex to equator), equatorially arranged, meridionally elongated, equidistant, inner margin minutely dentate, bordered by narrow margo ca. 1.5–2 μm wide; finely reticulate; tectate-perforate, wall ca. 2 μm thick; 30–34 μm.

Cf. Ceiba (Fig. 34; cf. modern pollen illustrated by Nilsson & Robyns, 1986, fig. 11I). Oblate, amb circular; tricolpate, colpi short (13–15 μm apex to equator), equatorially arranged, meridionally elongated, equidistant, inner margin entire to minutely dentate, bordered by narrow margo ca. 2–3 μm wide; reticulate, muri smooth, slightly sinuous, narrow (ca. 0.5–1 μm), lumina polygonal, 4–5 μm diam. at poles, smaller toward equator; tectate-perforate, wall ca. 1.5 μm thick; 56–60 μm.

Pseudobombax (Fig. 35; cf. modern pollen illustrated by Nilsson & Robyns, 1986, fig. 6I). Oblate, amb triangular, sides slightly concave, apices rounded; tricolpate, colpi short (8–10 μm apex to equator), equatorially arranged, meridionally elongated, equidistant, inner margin entire, bordered by faint narrow margo ca. 1 μm wide; reticulate at poles, muri smooth, straight to occasionally curved, narrow (ca. 1 μm), lumina polygonal, ca. 3 μm diam., becoming minutely reticulate around apices; tectate-perforate, wall 1.5–2 μm thick; 54–56 μm.

Pseudobombax is a tree to 25 m tall distributed from Nicaragua to Brazil and Peru. In Panama it typically occurs at lower elevations in the tropical moist forest but is also found in the premontane moist, tropical wet, and locally from the tropical dry forest (Croat, 1978: 591).

EUPHORBIACEAE

Alchornea (Fig. 32). Oblate, amb circular; tricolpate, colpi straight, 6–8 μm long (apex to equator), equatorially arranged, meridionally elongated, equidistant, extending within 6–7 μm of pole, inner margin entire, operculum distinct; psilate to faintly scabrate; tectate, wall 1.5 μm thick; 18–20 μm.

Pollen of *Alchornea* is frequent in low numbers in Gulf/Caribbean Tertiary deposits. It ranges from the lower and middle Eocene (Colombia; González Guzmán, 1967) to Recent (Muller, 1981). Its ecology and distribution have been summarized by Graham (1987a) based on Croat (1978) and Webster & Burch (1967). In Central America *Alchornea* grows in the tropical moist, premontane wet, and premontane rain forest typically at elevations between 300 and 2,000 m.

JUGLANDACEAE

Alfaroa/Engelhardia (Fig. 33). Oblate, amb oval-triangular; triporate, pores circular, ca. 2 μm diam., inner margin entire, equatorially arranged, equidistant; psilate; tectate, wall 1.5–2 μm thick; 20–25 μm.

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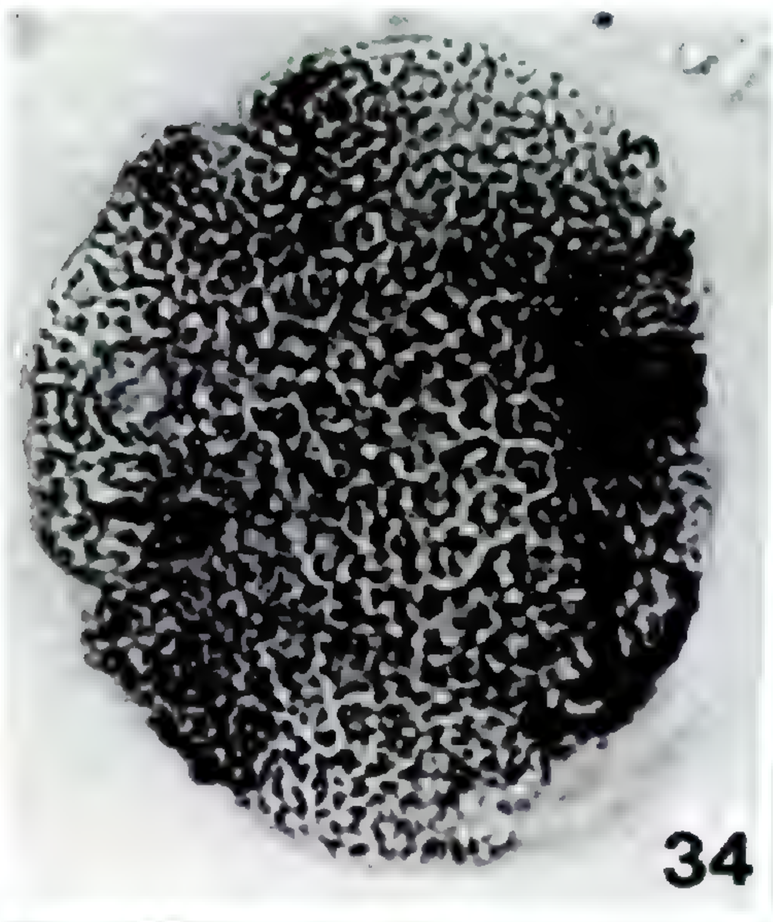
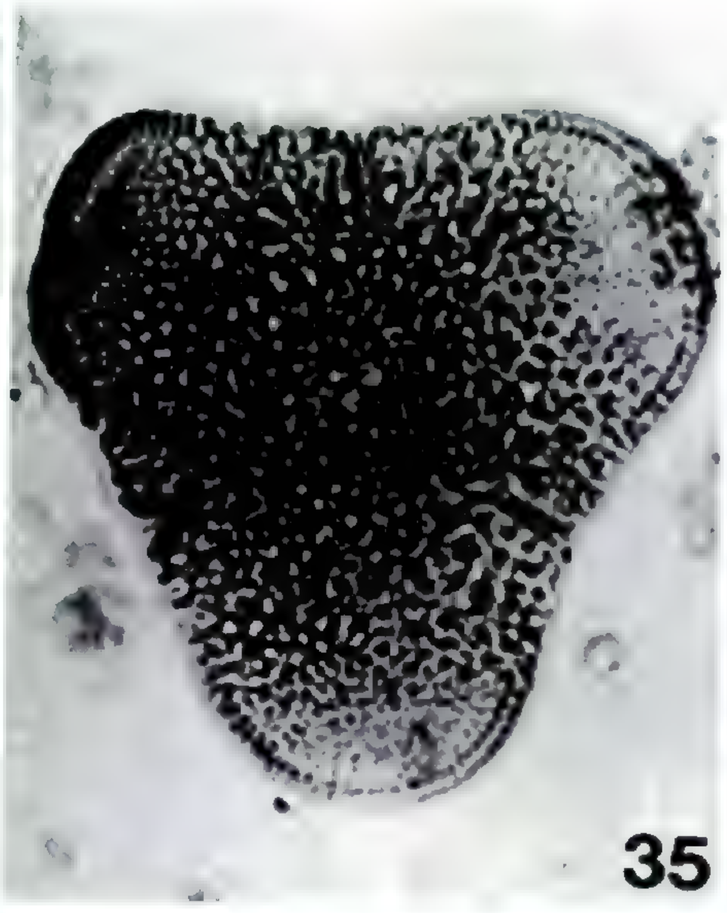
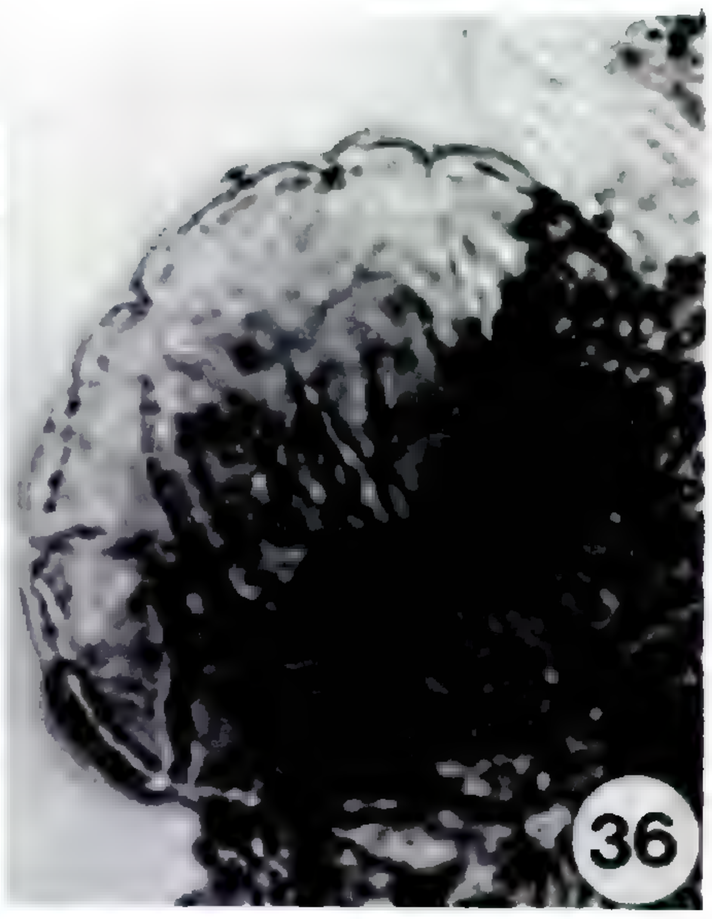
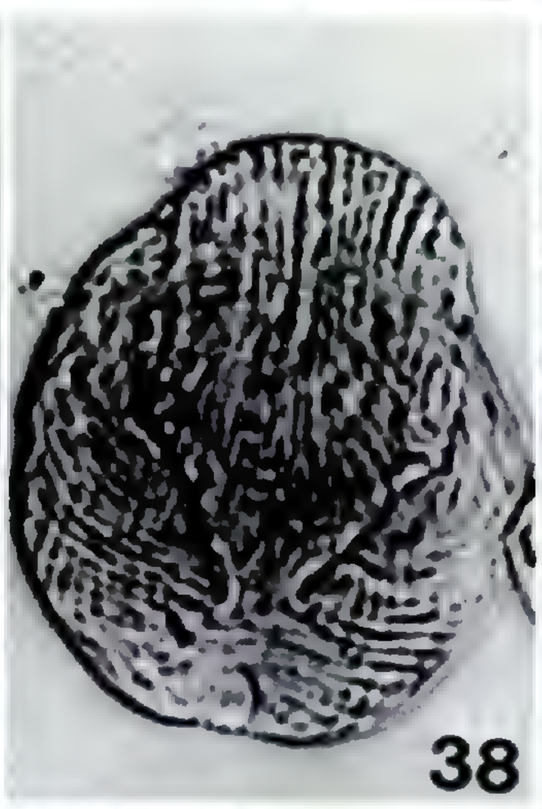
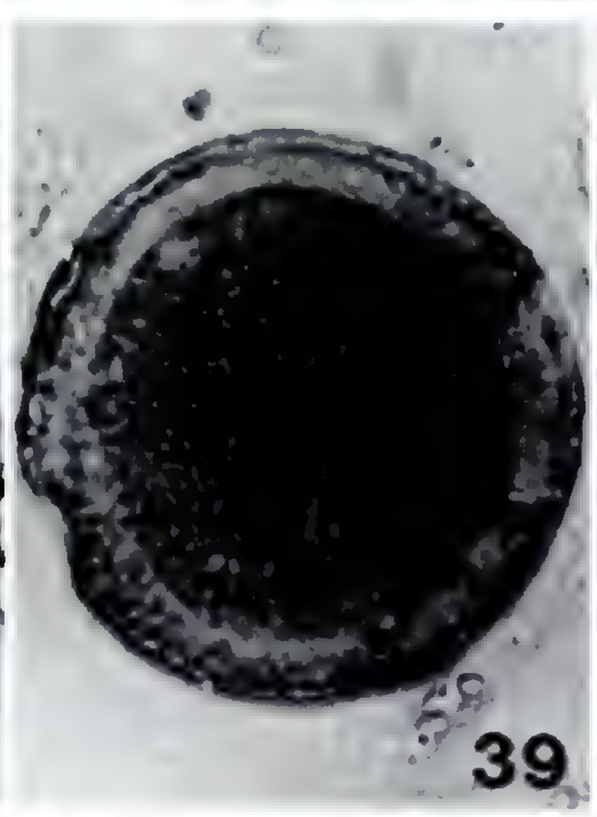
Attalea type, Pan A 16-2, ESF U-38, 2.—25–27. *Manicaria* type, Pan A 14-1a, ESF U-34, 1–3; Pan A 20-2, ESF Y-22, 2–4; Pan A 20-2, ESF G-19, 4.—28, 29. *Synechanthus* type, Pan A 16-1, ESF D-44, 1–3; Pan A 16-1, ESF L-46, 1–3.—30. Cf. *Aguiaria*, Pan A 16-2, ESF D-42.—31. *Ilex*, Pan A 16-3, ESF K-46.—32. *Alchornea*, Pan A 16-3, ESF E-33, 2.—33. *Engelhardia*, Pan A 20-2, ESF T-43, 4.

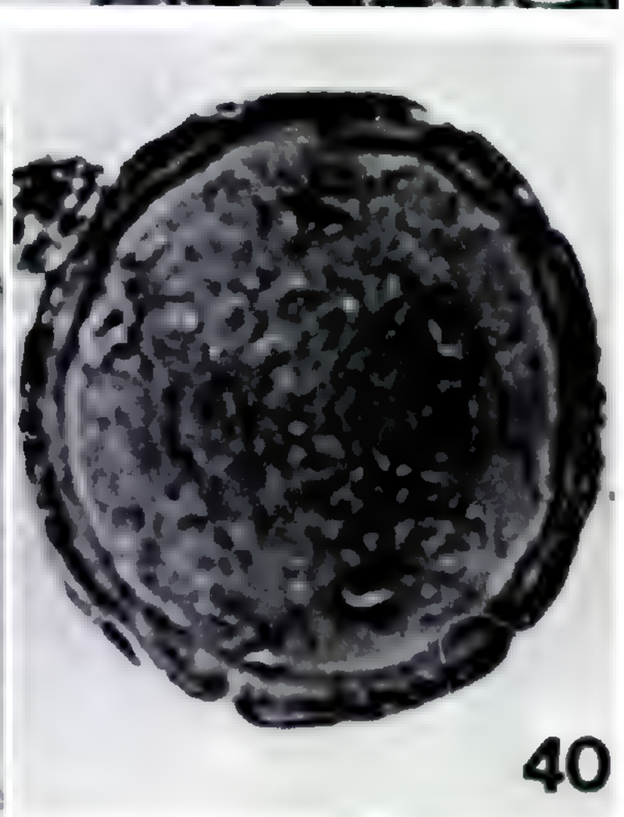


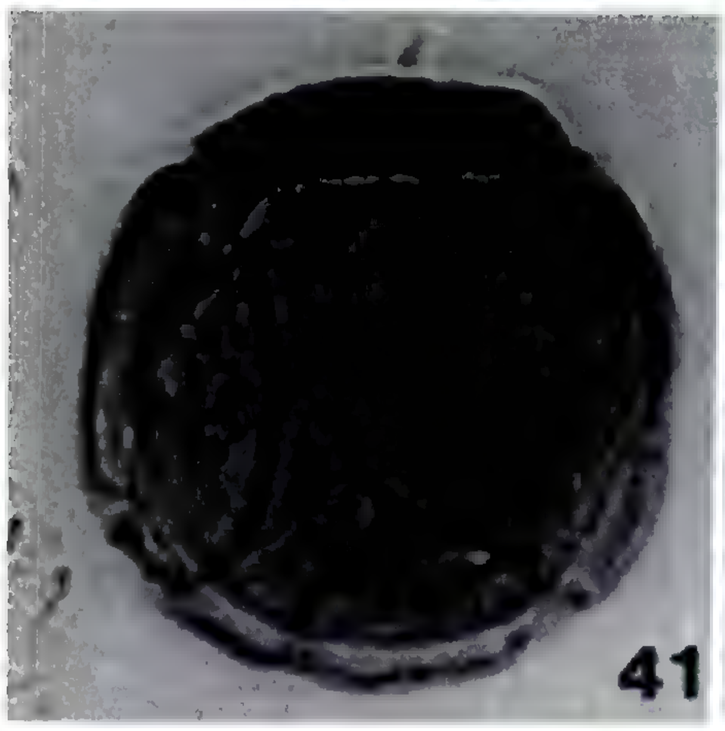


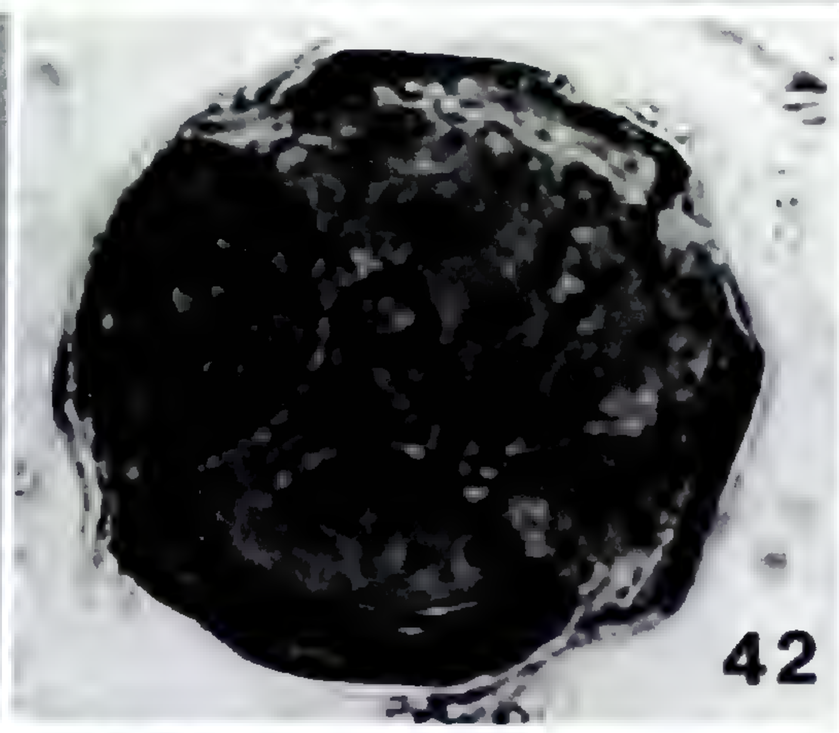


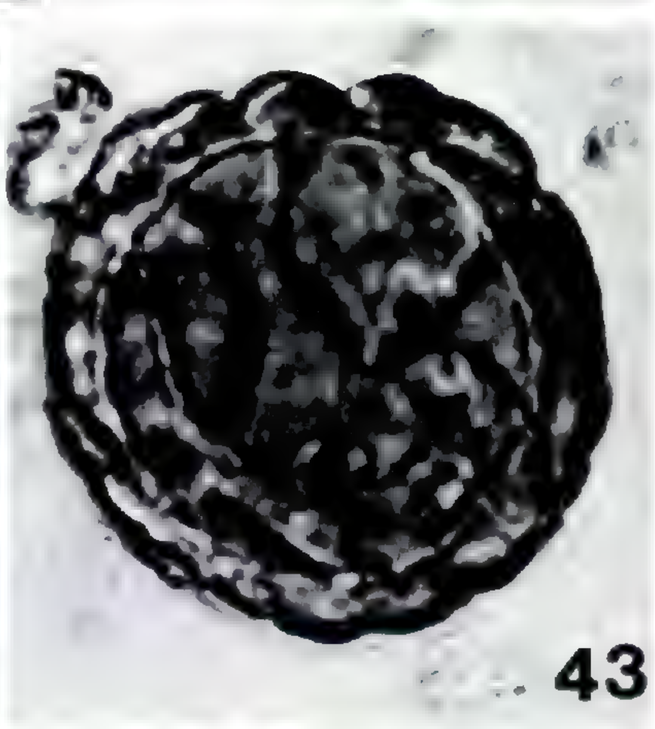


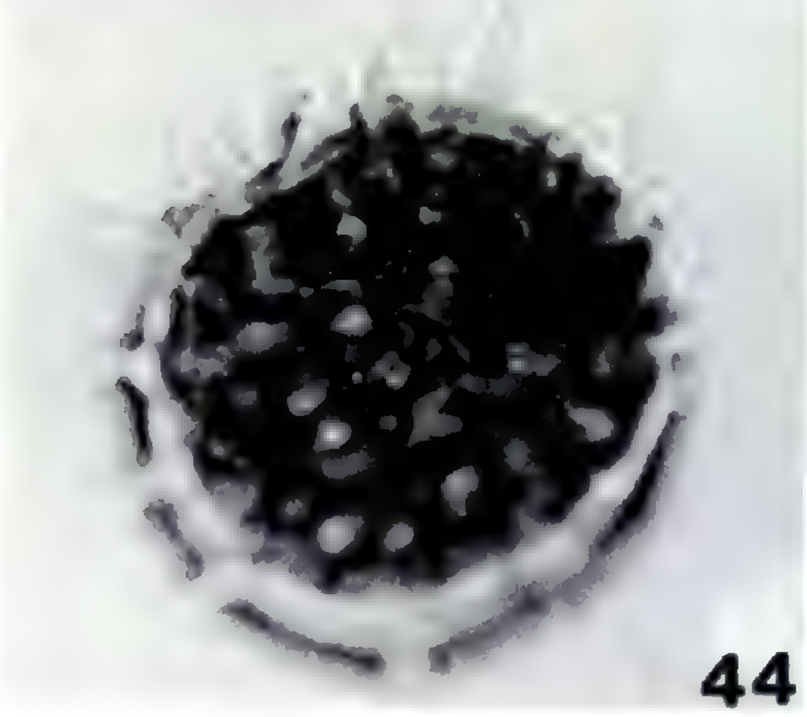


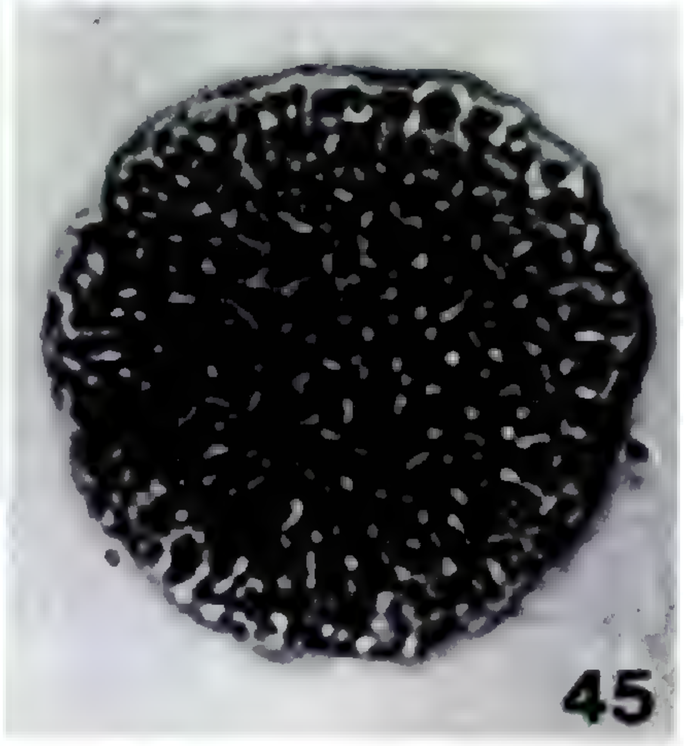


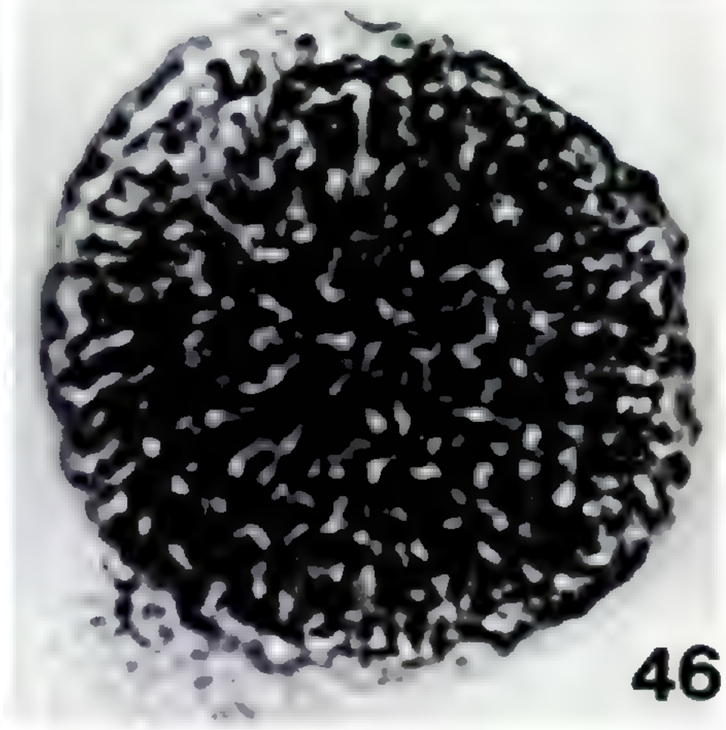












FIGURES 34–46. Fossil pollen from the La Boca Formation, Panama.—34. Cf. *Ceiba*, Pan A 16-2, ESF O-31, 2–4.—35. *Pseudobombax*, Pan A 20-2, ESF N-36, 3–4.—36. *Utricularia*, Pan A 14-1a, ESF V-32.—37, 38. *Crudia*, Pan A 16-3, ESF X-31; Pan A 16-1, ESF X-47, 1–3.—39. Malpighiaceae type 1, Pan A 16-3, ESF W-39, 2.—40. Malpighiaceae type 2, Pan B 50-2, ESF L-36, 1–2.—41. Malpighiaceae type 3, Pan B 50-2, ESF

These trees are distributed from Mexico through Central America, usually associated with lower- to mid-altitude temperate forests. Pollen occurs in the Gatuncillo, San Sebastian, Cucaracha, and Paraje Solo formations.

LEGUMINOSAE—CAESALPINIOIDEAE

Crudia (Fig. 37, 38). Prolate; tricolporoidate, colpi narrow, straight, 25 μm long, extending nearly entire length of grain, equatorially arranged, meridionally elongated, equidistant, pore area faint, circular, situated at midpoint of colpus; distinctly and coarsely striate, striae generally oriented parallel to long axis of grain, surface psilate, margins entire, occasionally appearing beaded from underlying pores in foot layer/endexine; tectate but with occasional separation between sculpture elements, wall 1.5 μm thick; 42–48 × 30–32 μm.

Crudia is a South American, mainly Amazonian, riverine tree of low altitudes (Cowan & Polhill, 1981: 131). Pollen ranges from the Eocene in northern South America (as *Striatocolpites catumbus*) and from the Paleocene in Africa (Muller, 1981). It occurs in Central America in the Gatuncillo and Cucaracha formations. Modern pollen has been studied by Graham & Barker (1981).

LENTIBULARIACEAE

Utricularia (Fig. 36). Oblate, amb circular; stephanocolpate, colpi 12–16, equatorially arranged, meridionally elongated, equidistant, 15–18 μm long, extending within 8–10 μm of pole, inner margin entire; psilate to faintly scabrate; tectate, wall 2 μm thick; 34–36 μm.

Utricularia is an annual or stoloniferous perennial, insectivorous, aquatic herb growing along the margins of freshwater lakes and rivers, swamps, and marshes from Florida to Mexico and south through the Antilles, Central America, and South America. It is represented by about 12 species in Panama (Taylor, 1976). Pollen also occurs in the Paraje Solo Formation.

MALPIGHIACEAE

Representation of the Malpighiaceae in the Gulf/Caribbean Tertiary is analogous to the Bombacaceae, wherein several types are present but many do not match exactly modern reference material or species illustrated in the literature. Generally similar modern forms include *Banisteria*, *Banisteriopsis*, *Bunchosia*, *Hiraea*, *Malpighia*, and *Mascagnia*; but since the specimens are slightly different, they are referred to types 1–5.

Type 1 (Fig. 39). Spherical, amb circular; periporate, pores circular, 3–4 μm diam., inner margin entire; scabrate; tectate, wall 5–6 μm thick; 42 μm.

The distinguishing features of this grain are the very thick wall and the absence of colpi connecting the pores.

Type 2 (Fig. 40). Spherical, amb circular; periporate, pores circular, 3 μm diam., inner margin entire, faint colpi with diffuse, granular margins connecting the pores; scabrate; tectate, wall 2 μm thick; 35 μm.

These specimens have moderately thick walls and faint connecting colpi.

Type 3 (Fig. 41). Spherical, amb circular; periporate, pores circular, 1.5–2 μm diam., inner margin entire, colpi with diffuse, granular margins connecting the pores; scabrate, some scabrae pointed; tectate, wall 2 μm thick; 36 μm.

The distinguishing features of type 3 are the moderately thick wall, distinct colpi, and some scabrae with pointed apices.

Type 4 (Fig. 42). Spherical, amb circular; periporate, pores circular, 3–4 μm diam., inner margin entire, colpi with diffuse granular margins connecting the pores; scabrate; tectate, wall 5 μm thick; 45 μm.

These specimens differ from the thick-walled type 1 by having distinct colpi.

Type 5 (Fig. 43). Spherical, amb circular; periporate, pores circular, 1.5 μm diam., colpi with diffuse granular margins connecting the pores, colpi and pores numerous, giving scalloped appearance to outer margin of grain; psilate; tectate, wall 5–6 μm thick; 37 μm.

These thick-walled specimens have numerous pores and colpi, and they are psilate.

MALVACEAE

Spherical, amb circular; apertures obscure, periporate(?), pores circular, small (ca. 1.5 μm), evenly

←

E-27, 2–4.—42. Malpighiaceae type 4, Pan A 16-3, ESF P-43, 2–4.—43. Malpighiaceae type 5, Pan A 16-3, ESF O-43, 1.—44. Malvaceae, Pan A 21-1, ESF R-21, 2–4.—45. Rubiaceae type 1, Pan A 20-2, ESF W-20, 1–2.—46. Rubiaceae type 2, Pan A 20-2, ESF L-31, 1.

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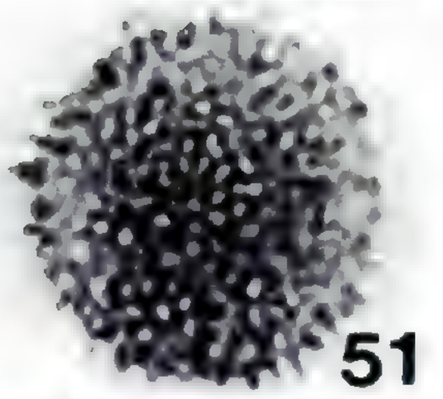

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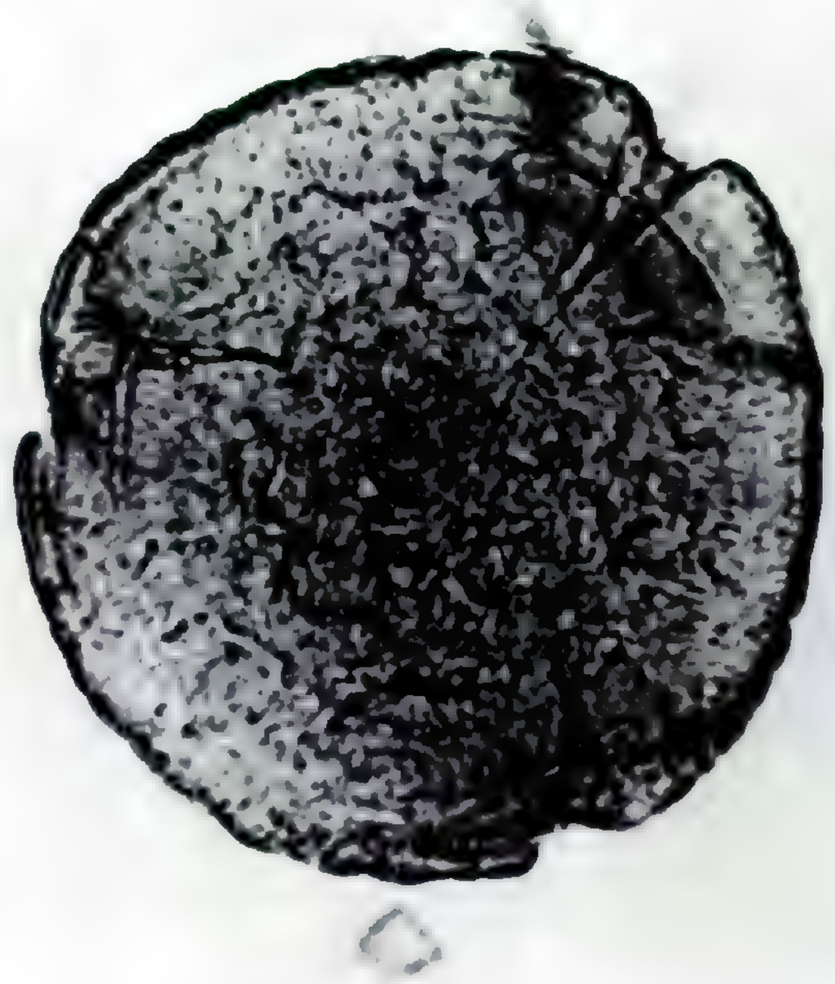

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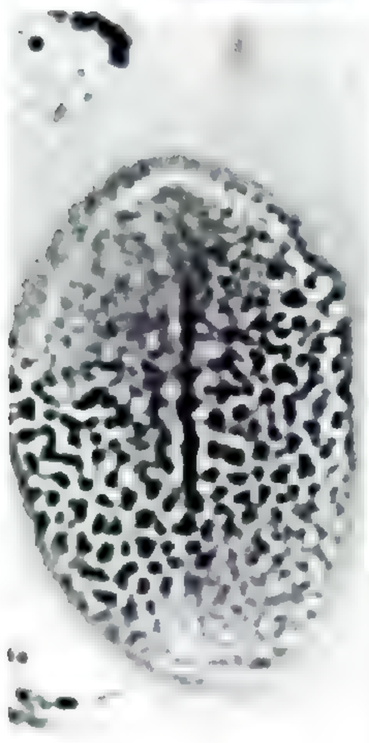

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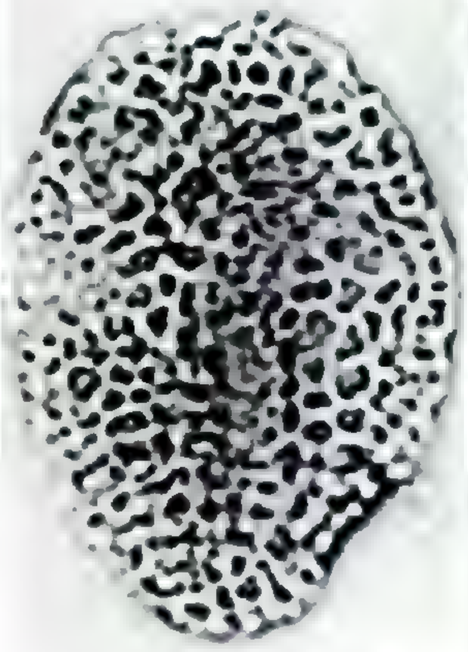

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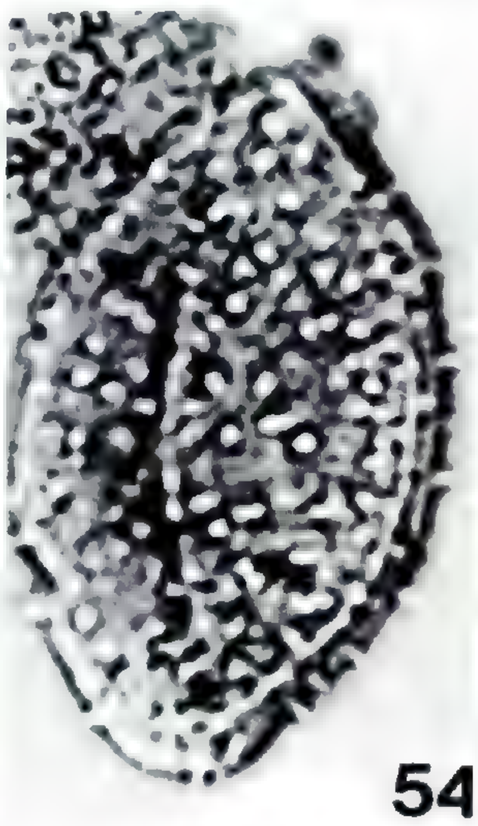

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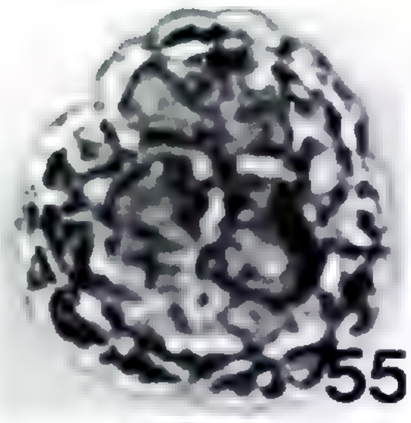

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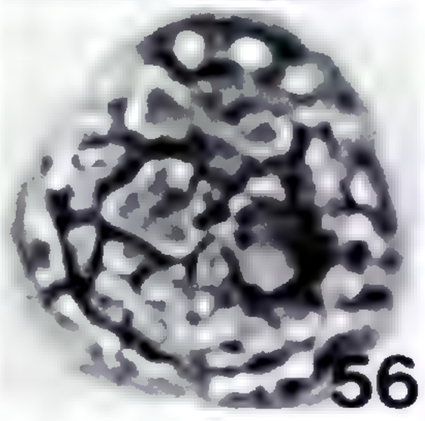

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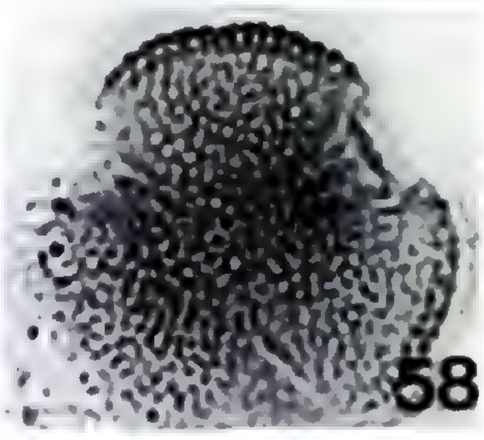

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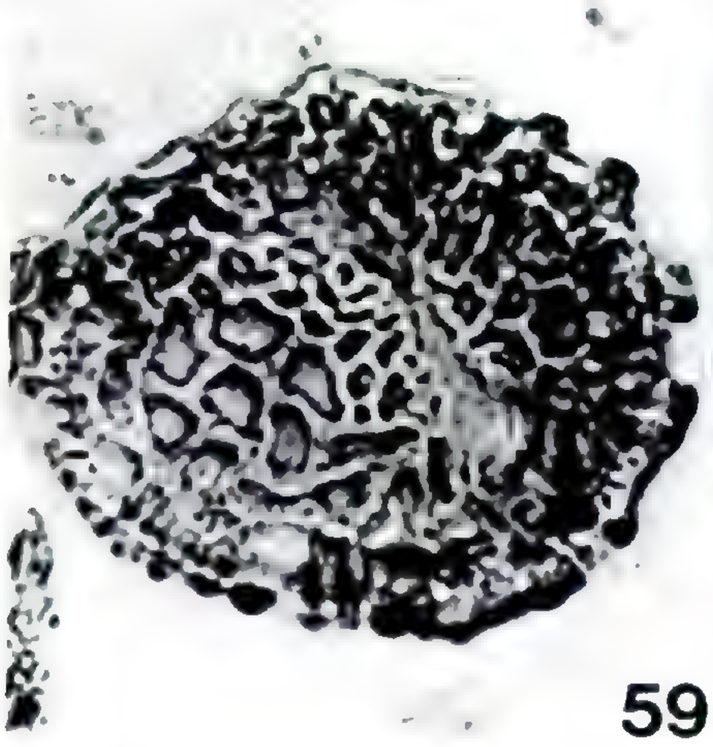

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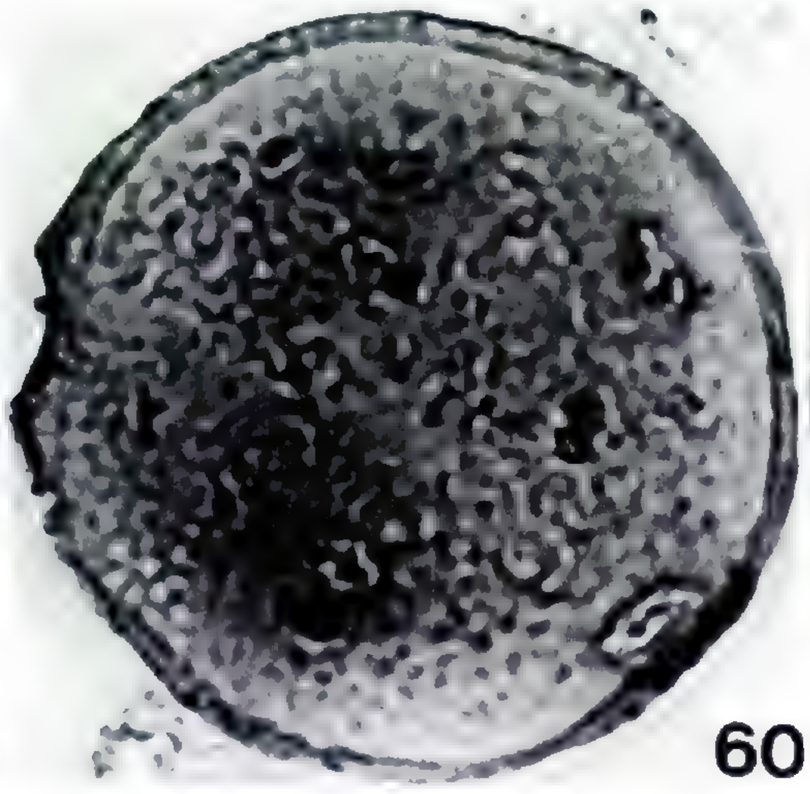

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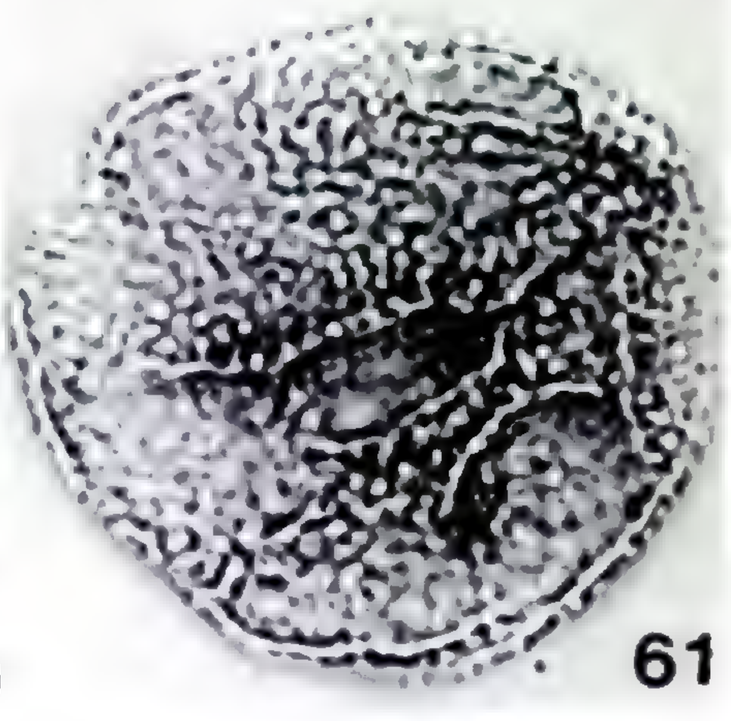

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FIGURES 47–61. Fossil pollen from the La Boca Formation, Panama.—47. *Rhizophora*, Pan B-50, 2, ESF X-33, 2.—48, 49. *Pelliciera*, Pan A 5-2, ESF N-39, 1–2; Pan A 16-3, ESF V-44, 3–4.—50. Unknown 1, Pan A 20-2, ESF E-26.—51. Unknown 2, Pan B 50-2, ESF N-11, 4.—52. Unknown 3, Pan A 16-2, ESF 32, 3–4.—53. Unknown 4, Pan A 14-1a, ESF N-45, 1–3.—54. Unknown 5, Pan A 16-2, ESF T-28, 2.—55, 56. Unknown 6, Pan A 14-1a, ESF Q-30.—57. Unknown 10, Pan A 14-1a, ESF G-29, 2–4.—58. Unknown 11, Pan B 50-2, ESF V-13, 3–4.—59. Unknown 7, Pan A 16-3, ESF Q-47, 2.—60. Unknown 8, Pan B 50-2, ESF F-33, 2.—61. Unknown 9, Pan A 16-1, ESF G-45.

distributed, inner margins entire; echinate, echinae hyaline, straight, broad at the base, densely arranged, 5 μm long, decreasing to 2–3 μm on portions of the exine; psilate; tectate, wall 1.5–2 μm thick; 30 μm (Fig. 44).

This unusual specimen may be an aberrant form and cannot be identified to genus. The Malvaceae are represented in the Caribbean Tertiary by *Hampea/Hibiscus* (probably *Hibiscus tiliaceus* L.) in the Culebra Formation and are frequent in the Tertiary of northern South America (as *Echiperiporites estelae*, late Eocene to Recent).

RHIZOPHORACEAE

Rhizophora (Fig. 47). Prolate to prolate-spheroidal; tricolporate, colpi straight, 14–16 μm, equatorially arranged, meridionally elongated, equidistant, inner margin entire, costae colpi ca. 2–3 μm wide, pores elongated equatorially (colpi transversalis), 1 × 4 μm, constricted at midpoint of colpus; finely reticulate; tectate-perforate, wall 2–3 μm thick; 16–20 × 14–18 μm.

Pollen of *Rhizophora* has been recovered from the Gatuncillo, San Sebastian, Uscari, Culebra, Cucaracha, and Paraje Solo formations and comprises 90% or more of some samples. Its fossil record has been discussed by Langenheim et al. (1967), Leopold (1969), and Muller & Caratini (1977), and its occurrence in the Gulf/Caribbean Tertiary was summarized by Graham (1985: 519, 1987a). *Rhizophora* is indicative of coastal, brackish-water conditions in tropical to subtropical regions. It is known in the stratigraphic literature as *Zonocostites ramonae* and ranges from the late Eocene to Recent. In older Tertiary deposits in Latin America it is replaced by its presumed ecological equivalent *Brevitricolpites* of unknown biological affinity.

RUBIACEAE

The Rubiaceae are represented in the La Boca Formation by two similar pollen types typical of several extant genera. These tricolpate, densely sculptured forms are produced by *Anisomeris*, *Chomelia*, *Guettarda*, *Terebraria*, and others.

Type 1 (Fig. 45). Oblate to oblate-spheroidal, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, short (4–5 μm apex to equator), often obscured by dense sculpture; reticulate, muri 1.5 μm wide, smooth, straight to occasionally curved or slightly sinuous, lumina 2–3 μm diam.; tectate-perforate, wall 2 μm thick; 26–36 μm.

Type 2 (Fig. 46). Similar to type 1 but is slightly larger (42–46 μm), and the muri are thicker (ca. 2–2.5 μm).

THEACEAE

Pelliciera (Figs. 48, 49). Oblate, amb circular; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, 20–26 μm, tapering to acute apex, inner margin entire, pore circular, 3–4 μm diam., situated at midpoint of colpus, inner margin entire; sculpture variable from finely to coarsely verrucate; tectate, wall 4 μm diam.; size variable, 40–60 μm.

Pelliciera is a small mangrove tree of lowland coastal areas from Costa Rica to northwest Colombia and Ecuador. In the Tertiary, however, it was widespread in the Gulf/Caribbean and is known from the lower middle Eocene Yellow Limestone Group of Jamaica, the middle(?) to late Eocene Gatuncillo Formation of Panama, the middle to late Oligocene San Sebastian Formation of Puerto Rico, the Oligo-Miocene Simojovel Group of Mexico, and from several localities in northern South America. Several anther-size clusters or fragments (Fig. 49) were recovered, indicating the plants grew in the immediate vicinity of the depositional basin. The presence of *Pelliciera* pollen in the La Boca Formation is one of the principal differences between that unit and the Culebra and Cucaracha formations. In the stratigraphic record it is known as *Psilatricolporites crassus* and ranges from the Eocene to Recent. Other details of the ecology and geologic record of *Pelliciera* have been summarized by Graham (1977).

UNKNOWNS

A number of specimens were recovered that could not be identified. Some of the more distinctive and/or abundant ones are illustrated and briefly described below.

Unknown 1 (Fig. 50). Spherical, amb circular; apertures obscure (nonaperturate?); echinate, echinae straight to slightly curved, dense, 2–3 μm long; wall 1.5 μm thick; 16 μm.

Unknown 2 (Fig. 51). This type is similar to unknown 1 but is slightly larger (22 μm), and the spines are shorter (1 μm) and blunt.

Unknown 3 (Fig. 52). Prolate, amb oval; monocolpate, colpus straight, 22 μm long, inner margin minutely dentate; reticulate, muri straight, smooth, 1.5 μm wide, lumina 1–1.5 μm diam., reticulum

becoming finer toward poles; tectate-perforate, wall 2 μm thick; 36 × 27 μm.

These monocot pollen grains may be palms but no exact match has been found.

Unknown 4 (Fig. 53). Prolate, amb oval; monocolpate, colpi straight, 28 μm long; reticulate, reticulum deep (columellae 3 μm long), muri straight, smooth, 1 μm wide, lumina 2 μm diam.; tectate-perforate, wall 3–4 μm thick; 40 × 30 μm.

Unknown 5 (Fig. 54). Prolate, amb oval; monocolpate, colpus 42 μm long, extending entire length of grain, inner margin entire; echinate, echinae straight, 1.5 μm long, moderately dense; tectate, wall 1–1.5 μm thick; 45 × 24 μm.

Unknown 6 (Figs. 55, 56). Oblate-spheroidal, amb circular; tricolpate, colpi often obscured by coarse sculpture elements, short (5–6 μm long), equatorially arranged, meridionally elongated, equidistant; coarsely verrucate; tectate, wall 3 μm thick; 22–26 μm. Similar specimens occur in the Paraje Solo Formation.

Unknown 7 (Fig. 59). Oblate-spheroidal, amb circular; tricolpate, colpi straight, 15 μm long, inner margin lobate; reticulate, muri straight, smooth, 2 μm wide, lumina polygonal, 4 μm diam., becoming finer toward colpi forming a margo, reticulum deep (columellae 5 μm long); tectate-perforate, wall 6 μm thick; 45 μm.

Unknown 8 (Fig. 60). Spherical, amb circular; periporate, pores circular, 3 μm diam., widely spaced, inner margin entire; scabrate; tectate, wall 2 μm thick; 43 μm.

Unknown 9 (Fig. 61). Oblate, amb oval-triangular; tricolpate, colpi short (4 μm apex to equator), equatorially arranged, meridionally elongated, equidistant, inner margin minutely dentate; echinate, echinae short (0.5 μm), moderately dense, bases forming subreticulum; tectate, wall 1 μm thick; 40 μm.

Unknown 10 (Fig. 57). Oblate-spheroidal, amb circular; stephanocolpate, colpi 6, straight, equatorially arranged, meridionally elongated, equidistant, inner margin entire; scabrate; tectate, wall 1 μm thick; 16–21 μm.

Similar specimens occur in the Culebra Formation.

Unknown 11 (Fig. 58). Oblate-spheroidal, amb circular; tricolpate, colpi straight, tapering to acute apex, 6–8 μm long, inner margin entire to minutely dentate, equatorially arranged, meridionally elongated, equidistant; finely reticulate; tectate-perforate, wall 2 μm thick; 27 μm.

Unknown 12 (Fig. 62). Prolate, amb oval; tricolporate, colpi straight, 45 μm long, equatorially arranged, meridionally elongated, equidistant, bordered by costae colpi 4–5 μm wide, inner margin entire, pores large, oval, 5 × 16 μm, situated at midpoint of colpus, inner margin entire; reticulate; tectate-perforate, columellae relatively coarse and clearly evident in median optical section, wall 2.5–3 μm thick; 58 × 36 μm.

Unknowns 12–15 are similar to pollen of several Anacardiaceae and Euphorbiaceae but cannot be referred to any one modern genus.

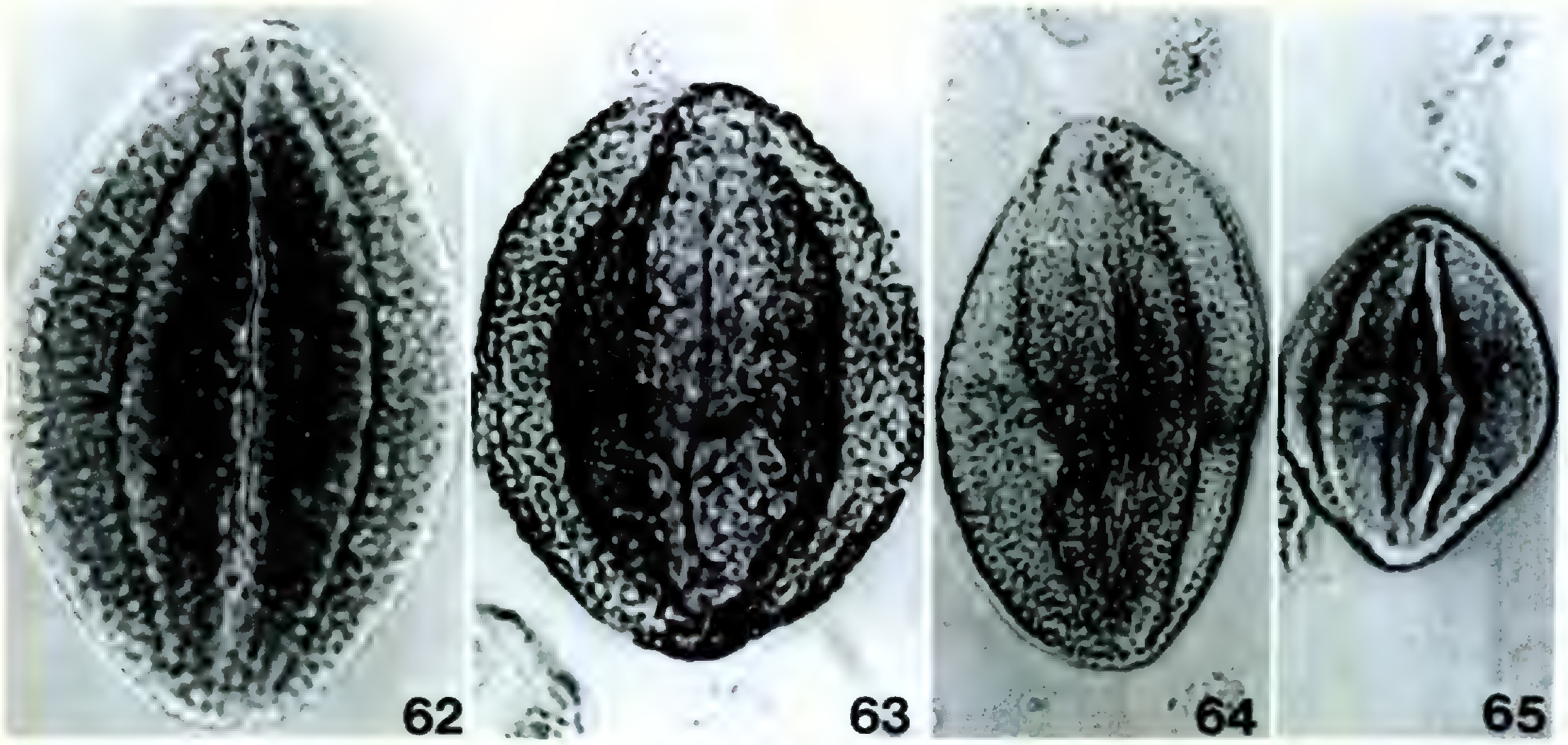
Unknown 13 (Fig. 63). This type is similar to unknown 12, but the columellae are shorter and finer; consequently, the wall is thinner (1.5–2 μm) and the reticulum finer.

Unknown 14 (Fig. 64). This type has an even thinner wall (1–1.5 μm), a finer reticulum, narrower costae colpi, and smaller and slitlike pores (2 × 4 μm).

Unknown 15 (Fig. 65). This type is similar to unknown 14 but is smaller (27–32 × 18–21 μm).

Paleocommunities and Paleoenvironments

Results of the La Boca study are of interest in demonstrating an internal consistency in paleocommunities, climates, and physiography among four fossil floras in two countries of Central America, as well as consistency with independent plate tectonic and paleotemperature data. The lower Miocene Uscari (Costa Rica), Culebra, Cucaracha, and La Boca (Panama) floras preserve elements of a mangrove swamp (*Pelliciera*, *Rhizophora*) fringing the volcanic islands constituting the isthmian region during most of the Tertiary. Freshwater marshes and swamps (palms, ferns, *Utricularia*) occupied lowland areas behind the mangrove zone. On the adjacent slopes were versions of the tropical wet, tropical moist, and premontane forests (*Lycopodium*, *Selaginella*, *Cyathea*, *Pteris*, *Ilex*, *Pseudobombax*, *Alchornea*, and *Crudia*, with *Alfaroa*/*Engelhardia* likely occupying distant, moderate highlands in the region). All available paleobotanical data are consistent in showing little evidence of dry (including savannah) habitats. Grass pollen continues to be poorly represented (maximum of 1% in one sample from the Culebra Formation; less than 0.5% in two samples from the La Boca) to absent (Uscaria, Cucaracha formations). If savannahs existed, as suggested by the



FIGURES 62–65. Fossil pollen from the La Boca Formation, Panama.—62. Unknown 12, Pan A 21-1, ESF X-14, 3.—63. Unknown 13, Pan A 16-1, ESF Q-44, 1–3.—64. Unknown 14, Pan A 16-3, ESF W-33, 4.—65. Unknown 15, Pan A 16-2, ESF W-36, 2–4.

grazing and browsing components of the Tertiary faunas, they were probably short-lived and developed locally as recovery vegetation in response to volcanic activity documented for central Panama in the form of extensive ash, tuff, and basalt deposits (see further discussion in Graham, 1988b). The affinities of the La Boca flora are clearly with Central America and areas to the north, reflecting the establishment of a land connection between Central America and South America only about 3 Ma.

The lack of any paleobotanical evidence for significant highlands is in agreement with plate tectonic models suggesting that elevation of the early volcanic islands and peninsulas gradually increased during the latter part of the Cenozoic, and that the highest elevations (3,475 m in the western mountains of Panama; 3,820 m, Cerro Chirripo, Costa Rica) are of recent origin. Altitudes up to about 1,200–1,500 m would accommodate all elements in the four lower Miocene floras known from southern Central America. No pollen was being blown, washed, or transported into the depositional basin to suggest dry vegetation or high altitudes in the Gatuncillo, Uscari, Culebra, Cucaracha, or La Boca formations of Costa Rica and Panama. Muller (1959) demonstrated that pollen from a variety of inland and upland communities is transported by rivers and deposited in coastal basins. Palynological data from Puerto Rico and southern Mexico further show that many of these habitats, represented by both wind- and insect-pollinated elements, are included in the microfossil record if such habitats exist in the region.

All taxa identified from the La Boca Formation except *Crudia* occur in the modern vegetation of Panama. Consequently the paleoenvironment must have been similar to the tropical conditions presently prevailing in coastal, lowland, and moderate-altitude habitats in southern Central America. This is consistent with paleotemperature curves (Savin, 1977; Savin & Douglas, 1985; Savin et al., 1975) that show the Uscari, Culebra, Cucaracha, and La Boca floras were deposited during a relatively warm interval just before the significant temperature drop in middle and late Miocene times.

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A REVISION OF MESOAMERICAN *PSYCHOTRIA* SUBGENUS *PSYCHOTRIA* (RUBIACEAE), PART I: INTRODUCTION AND SPECIES 1–16[1]

Clement W. Hamilton[2]

Abstract

Psychotria subgenus *Psychotria* (Rubiaceae) comprises 61 species and eight varieties of understory shrubs and small trees in Mexico and Central America. The subgenus is most diverse in Panama (40 species) and Costa Rica (32 species), with a secondary center of diversity in southern Mexico (26 species) and Guatemala (26 species). Endemism is also greatest in Panama (15 species). Species-rich regions in Costa Rica and Panama are especially recommended for conservation efforts. The 61 species are grouped into eight species-groups; several groups and species complexes contain one wide-ranging species and several species with much smaller ranges. Only one species-rich group, the *P. calophylla* group, lacks a continuously wide-ranging member.

Psychotria is a pantropical and subtropical genus of mostly shrubs but also small trees, herbs, and even epiphytes. I presently estimate the number of species to be 1,650, making it the largest genus in the Rubiaceae; this includes 700 species in the Neotropics (my estimate), 250 in Africa (Petit, 1964, 1966), and 700 in Asia and Oceania (Sohmer, pers. comm.).

The present state of its infrageneric taxonomy reflects the lack of understanding of the genus as a whole; all that can be said with some certainty is that subg. *Psychotria* occurs in all three tropical regions and that each region has one or more groups distinguishable from subg. *Psychotria*. In the Neotropics, the other group is subg. *Heteropsychotria* Steyermark (1972); in Africa, it is subg. *Tetramerae* (Hiern) Petit (1964, 1966); and in Asia and Oceania, the situation is much more complex (Sohmer, 1977).

The infrageneric uncertainty extends to delimitations of *Psychotria* and related genera; the neotropical genera *Mapouria*, *Cephaëlis*, *Uragoga*, *Naletonia*, *Nonatelia*, and *Notopleura* have been variously merged with or separated from *Psychotria*. Most of these genera, if included in *Psychotria*, fall within subg. *Heteropsychotria* and are therefore not relevant here. *Mapouria*, named by Aublet in 1775, is more critical. The principal use of that generic name was by Mueller-Argoviensis (1876, 1881), who in his Rubiaceae treatment for *Flora Brasiliensis* distinguished between *Mapouria* and *Psychotria*; the former corresponded to what is properly considered *Psychotria* subg. *Psychotria*, while the latter encompassed Steyer-

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mark's *Psychotria* subg. *Heteropsychotria*, including *Cephaëlis*. The discovery by Petit (1964), reaffirmed by Steyermark (1972), that the type species of *Psychotria*, *P. asiatica* L., falls well within the *Mapouria* generic concept makes that genus obsolete.

Members of *Psychotria* subg. *Psychotria* are distinguished easily from all others in the genus. Three characters serve to enable recognition of the subgenus: (1) the leaves are dry red-brown or sometimes dull green, as opposed to bright green; (2) the stipules are usually sheathing and caducous, leaving a small, usually pale ridge often with a fringe of red-brown hairs, as opposed to only slightly sheathing and conspicuously persistent; and (3) the seeds, hemispherical in cross section, have two longitudinal furrows on the flat ventral surface and usually four or five (or sometimes an irregular number of) longitudinal furrows on the rounded dorsal surface. *Psychotria* subg. *Heteropsychotria* has a variety of seed cross sections, none of which can be confused with those of subg. *Psychotria*. Additional characters of whole-plant architecture show differentiation between the two neotropical subgenera (Hamilton, 1985), as does mature fruit color, which is almost always red in subg. *Psychotria* and usually blue in subg. *Heteropsychotria*. The naturalness and monophyletic (or at least "convex"; see Meacham & Duncan, 1987) nature of subg. *Psychotria* is not in doubt.

In the Neotropics, *Psychotria* subg. *Psychotria* consists of ca. 200 species. It accounts for the vast majority of *Psychotria* species in the West Indies, just under half in Mesoamerica, and perhaps a third in South America, where subg. *Heteropsychotria* is most diverse. *Psychotria* subg. *Psychotria* in Mesoamerica, the subject of this treatment, includes 61 species, 15 of which are recently named (Hamilton, 1988), and eight varieties. I have sorted the species into eight species-groups; their recognition as sections awaits study of the subgenus throughout tropical America.

Systematic understanding of species-rich tropical taxa such as *Psychotria*, *Miconia*, *Piper*, *Bactris*, *Heliconia*, and *Anthurium* is the critical first step toward understanding geographical patterns of diversity and processes of diversification in the tropics. *Psychotria* subg. *Psychotria* appears to be a good index taxon for describing species diversity in tropical angiosperms as a whole (see Biogeography) and therefore provides a diversity data set of use to conservation planners and natural resource organizations. From an ecological and evolutionary standpoint, one hopes that results of the study of *Psychotria* can be extrapolated to other diversified tropical taxa.

Morphology and Terminology

In this section, characters and character states are explained and illustrated only as necessary in order to eliminate any ambiguity regarding their use in descriptions and discussions.

HABIT

Habit states, e.g., "shrub" versus "tree," are distinguished primarily by size, not by architecture or shape. Even 1-meter shrubs in this subgenus are usually treelike in having a main trunk and lateral branch complexes. Architecture of Panamanian species of *Psychotria* (both subgenera) has been studied (Hamilton, 1985); three basic types of branching event were found, differentiated by the number and orientation of new shoots to which the terminal node gives rise each growing season. In Type 1 branching, at the terminal node one lateral meristem gives rise to a relay axis that elongates the main axis by sympodial substitution. In Type 2 branching, two (or more) relay axes arise at the terminal node and remain equal, neither new axis assuming the same orientation as the axis that preceded it. Type 3 branching resembles Type 2 except that one of the new relay axes assumes the same orientation as the parent axis. Most species of subg. *Psychotria* shows Type 3 branching in both the vertical and lateral directions; this serves as an additional field character for recognizing members of the subgenus. Two exceptions within the subgenus—*P. limonensis* and *P. tenuifolia*—show Type 1 and Type 2 branching, confirming their taxonomic affiliation based on other characteristics (see Infrasubgeneric Relationships). Architecture has not been included in the descriptions because it has not yet been studied thoroughly for most species in the field.

STIPULES

Stipules can provide valuable information as to interspecific relationships but prove almost worthless as a source of key characters, since in this subgenus they are usually caducous, or deciduous. The two stipules on opposite sides of a node are frequently united to some degree into a sheath. As the young stem grows, mechanical pressure forces the stipules to sever their basal connections to the stem and subsequently to fall off (Fig. 1). Thus most herbarium specimens have no stipules re-

maining. The stipule scar consists of a ridge, usually pale in contrast to the stem, often with a dense fringe of minute red-brown hairs; the hairs often fall off shortly after the stipule. Exceptions to the above are found in the *costivenia* group, in which stipules are robust and not sheathing and thus are often found persisting several nodes from the terminus, and in the *calophylla* group, in which the herbaceous and suffruticose species do not grow sufficiently to force the stipules to break free.

Stipule shape and size vary considerably, with the general shape, apex, pubescence, and color differentiation providing critical distinctions between species and species groups (Fig. 2). Taxa descriptions include the stipule length along the stem followed by the maximum width.

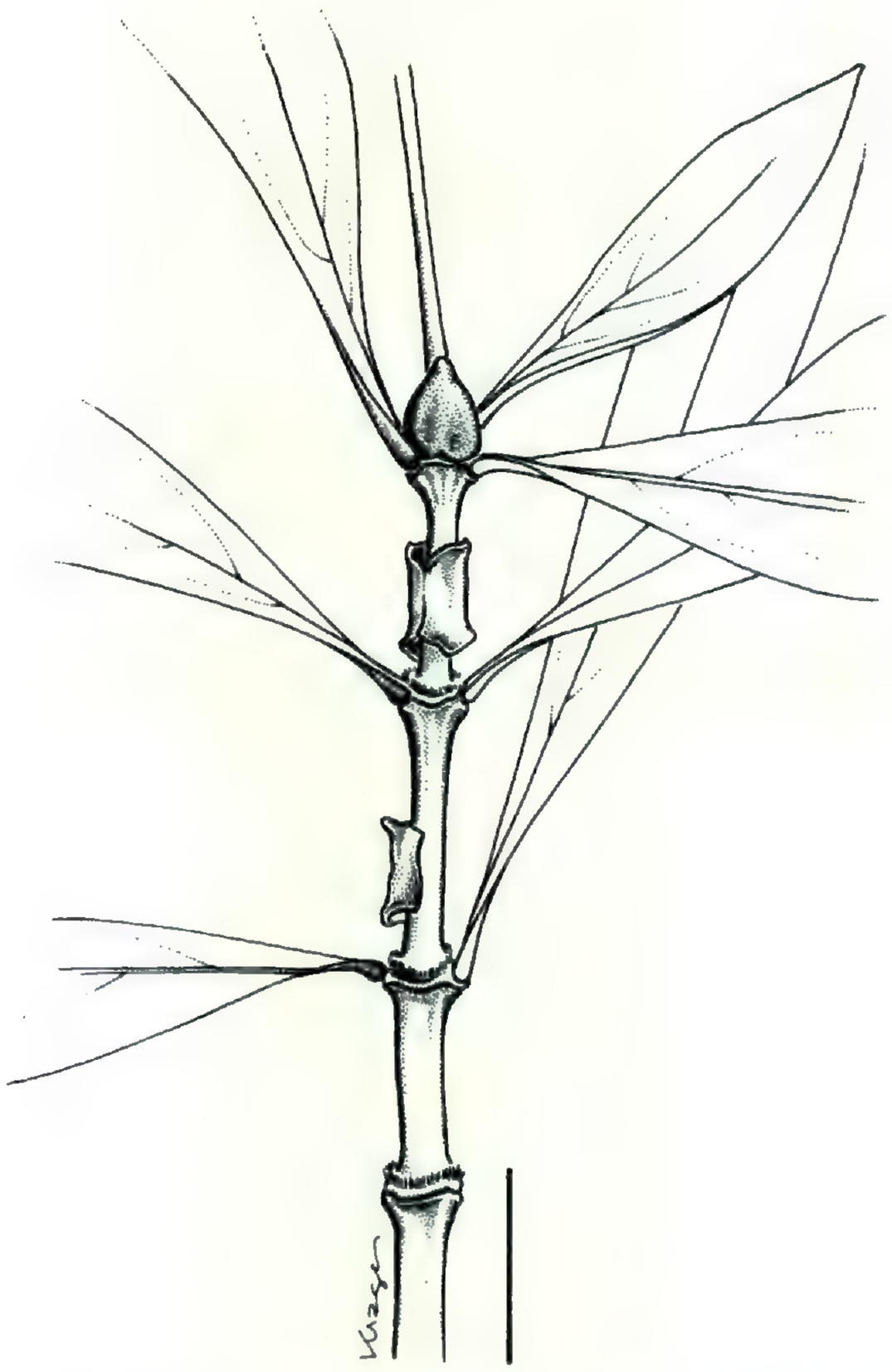


FIGURE 1. Caducous stipules being forced to fall from a branch of *Psychotria carthagenensis*. Only the terminal node has stipules firmly attached; at the node below, the sheath has broken free at the base and slid up the stem; at the next node the sheath has broken and one stipule has fallen. Note the ridge and minute fringe of hairs at the node where the stipule base has broken free. (*Knapp 4942.*) Scale bar = 1 cm.

LEAVES

Leaf characters are used extensively in this treatment in keys and as recognition characters. A single leaf, if examined critically, can suffice to identify most species in Mesoamerica. Most character states are unambiguous; descriptive terminology is from Hickey (1979). Blade measurements are the length followed by the width at the widest point. Venation character states are observed on the undersides of the leaf blades.

Secondary vein divergence is the angle formed at the junction of a secondary vein and the midvein, measured on the distal (on the leaf) side of the secondary vein. Most species have curved secondary veins, so the tangent at the base of the secondary vein was estimated and used. Angles were measured in the middle third of the leaf blade, as they often become more acute towards the base and towards the apex.

The character of secondary venation is considered to have basically three states: eucamptodromous, brochidodromous, and brochidodromous with a distinct collector vein (Fig. 3). In eucamptodromous venation, the secondary veins near the margins do not connect one to another in robust secondary arches or via a collector vein; they instead become less robust and distinct towards the margin and are often connected by a series of arches of tertiary veins (Fig. 3a). If just one connecting arch maintains the robustness of a secondary vein, the venation is said to be brochidodromous (Fig. 3b); consequently, the distinction between eucamptodromous and brochidodromous is one of degree, and many species show both states. (It may be assumed, unless stated otherwise, that the secondary arches are near the blade margin.) Much more distinct and easily differentiated—enough so to serve in the first couplet in the species-identification key—is the third state, brochidodromous with collector vein, in which there is a distinct collector vein running straight or slightly undulating near and parallel with the margin (Fig. 3c). (Note that, in keys and descriptions, the second state, "brochidodromous," should be assumed not to include a distinct collector vein unless it is otherwise stated.)

The arc shape of the secondary veins is also described, the states being: a) straight, b) constantly arcuate, and c) straight near midvein then arcuate near margin.

The axils of the secondary veins often have tufts of hairs or domatia or sometimes both. The origin and function of domatia is little understood, but the minute holes found in domatia of mature leaves suggest that early instars of some insects may inhabit the cavities (Fig. 4).

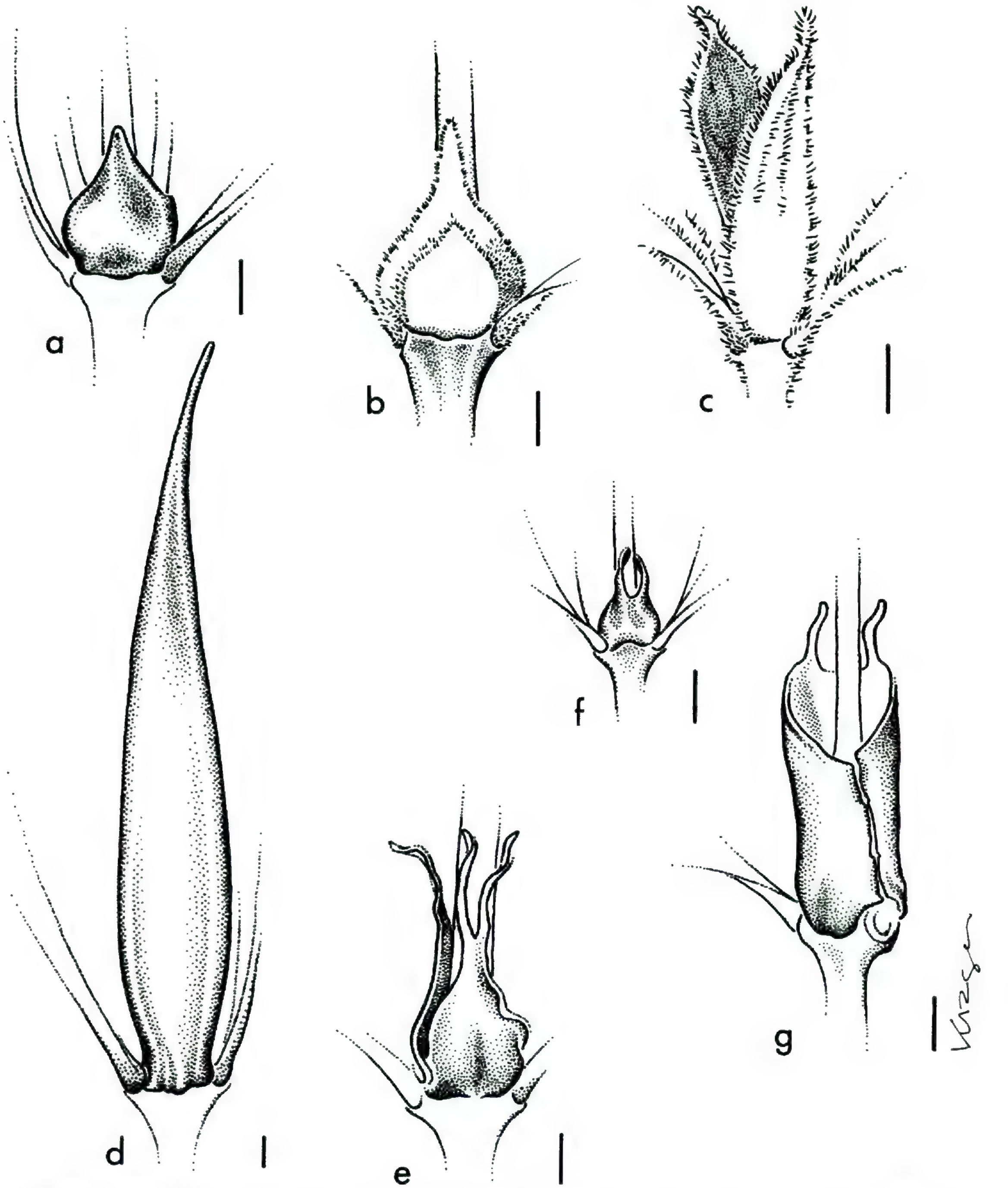


FIGURE 2. Stipule forms found in subg. *Psychotria*.—a. Sheathing, ovate, *P. carthagenensis* (*Croat 10347*).—b. Ovate, the apex cuspidate, with pale center, *P. costivenia* (*Molina & Molina 31059*).—c. Sheathing, lanceolate, *P. erythrocarpa* (*Standley 76317*).—d. Sheathing, lanceolate, *P. panamensis* (*A. Smith 1103*).—e. Ovate, the apex long-biacuminate, *P. tenuifolia* (*Hayden 174*).—f. Ovate to lanceolate, the apex biaristate, *P. orosiana* (*Knapp & Vodicka 5522*).—g. Sheathing, truncate, biaristate from apical corners, *P. psychotriifolia* (*Lewis et al. 2103*). Scale bars = 2 mm.

Tertiary veins in subg. *Psychotria* are generally either: a) orthogonal reticulate, joining each other and the secondaries, intersecting at roughly right angles, or b) percurrent, joining adjacent secondaries, making a ladderlike effect between them (Fig. 5). This distinction is often one of degree, as the major difference is that in percurrent tertiary venation the tertiaries joining the secondaries are more robust than the other reticulate veins, then considered quaternary veins. Few species, such as

P. micrantha, have strikingly percurrent tertiary venation. In several species, especially in the *costivenia* group, tertiary veins known as intersecondary veins intersect the midvein between the secondary intersections and run roughly parallel with the secondaries.

INFLORESCENCES

Inflorescences in subg. *Psychotria* consist generally of panicles of cymes, in which the cyme (dichasium) is the ultimate group of flowers and the panicle comprises the axes leading to the cymes (Fig. 6). The degree of branching of the panicle reflects the maximum branching found in the inflorescence: 2 degrees indicates that there are primary and secondary axes; 3 degrees indicates that there are primary through tertiary axes, etc. (Fig. 6a–c). Similarly, degree of branching of the cymes is also described (Fig. 6d–f). Cymes are often so contracted as to be glomerules of flowers. Bracts and bracteoles are present, though often inconspicuous, on the axes; bracts subtend branches of the panicle, and bracteoles subtend the cymes.

Inflorescence organization provides many of the most useful characters and so is described in great detail (Fig. 7). Secondary axes are borne in ranks along the main axis. The main axis itself is measured; the distance between the base of the main axis and the point of insertion of the basal (first) rank of secondary axes is the peduncle (its length included in the measure of the main axis). Secondary axes are usually two or four per rank; often when there are two or more pairs of axes per rank, the pairs are differentiated into a longer and a shorter pair (Fig. 7a). Often a specified node can have either one or two pairs of axes; measurements of a single pair are included under "the longer pair," while measurements of the "shorter pair" are relevant only when there are two pairs of axes. Sometimes secondary axes are reduced so that a cyme or flower cluster appears sessile on the main axis (Fig. 7b, k). The angle of divergence of the secondary axes (measured as is that of secondary veins) can also provide valuable information: species in the *graciliflora* group often have ca. 90° angles of divergence (Fig. 7h), and *P. stockwellii* shows obtuse angles of divergence (Fig. 7i), in striking contrast to the acute angles characterizing most species.

FLOWERS

The most interesting feature of the flowers of *Psychotria*, as is the case for much of Rubiaceae,

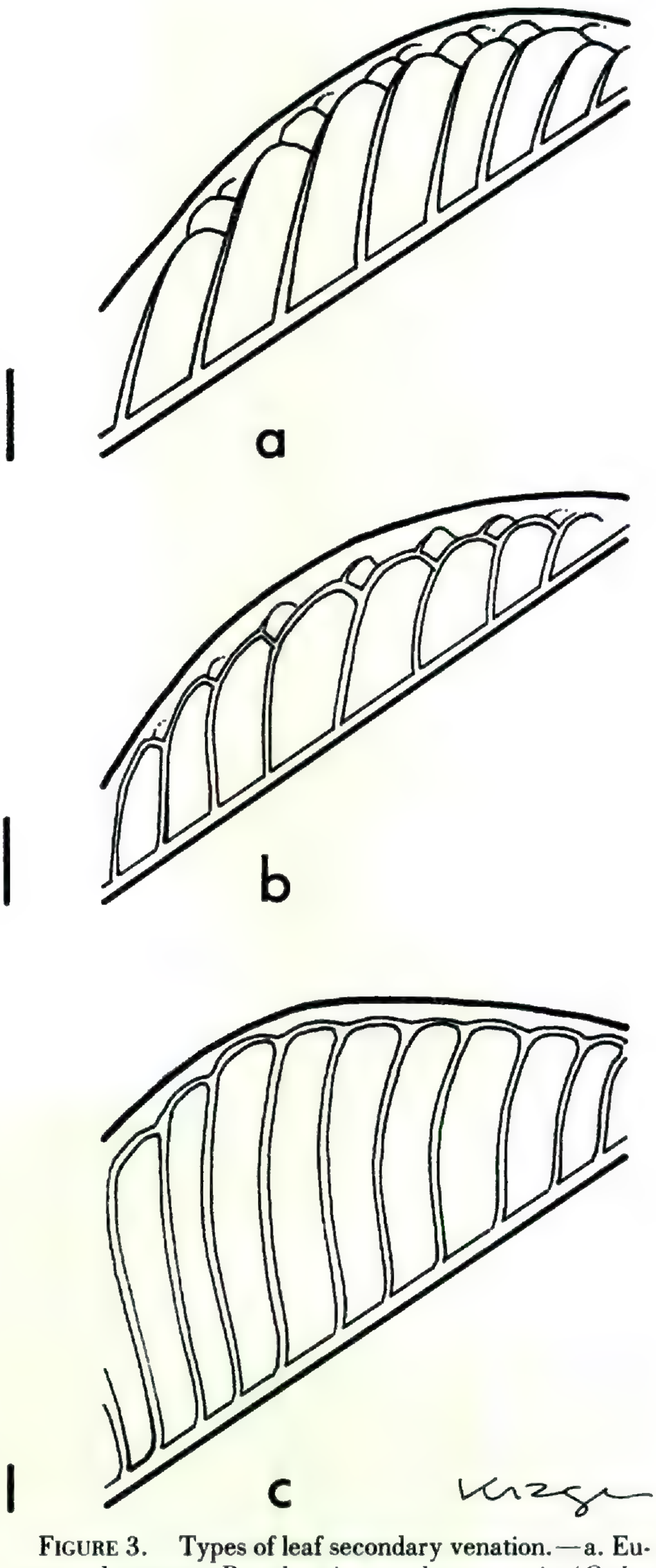


FIGURE 3. Types of leaf secondary venation.—a. Eucamptodromous, *Psychotria carthagenensis* (*Opler 1683*).—b. Brochidodromous, *P. horizontalis* (*Spellman & Newey 1670*).—c. Brochidodromous with collector vein, *P. calophylla* (*Tyson et al. 4556*). Scale bars = 1 cm.

is distyly: within a species many individual plants have flowers with exserted style and inserted stamens ("pin" or "long-style" morph; Fig. 8a–c), and the others have flowers with exserted stamens and inserted style ("thrum" or "short-style" morph; Fig. 8d–f). This is part of an incompatibility system by which pin pollen can fertilize only thrum ovules

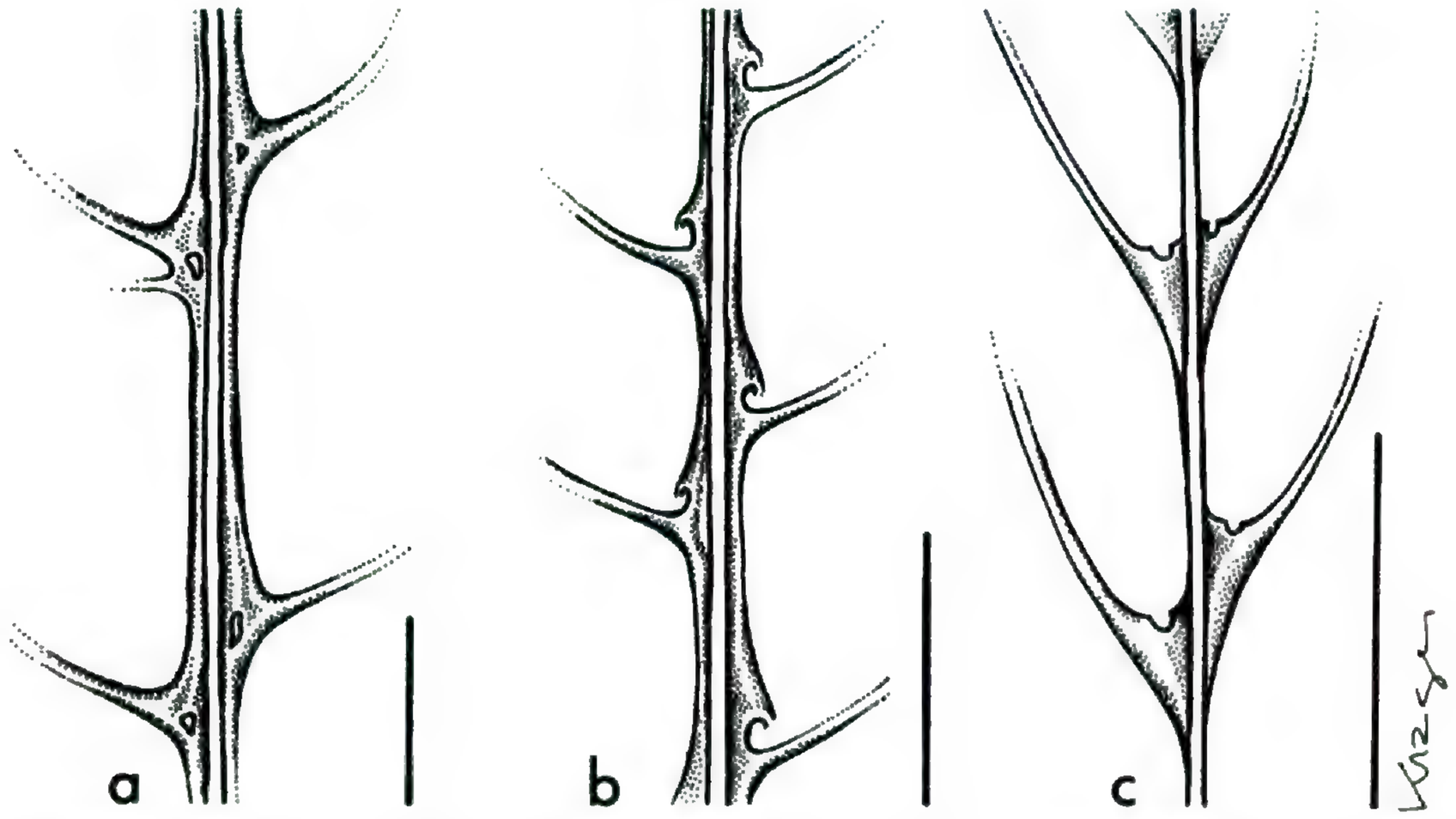


FIGURE 4. Domatia in axils of secondary veins.—a. *Psychotria remota* (*Hartshorn 1444*).—b. *P. marginata* (*Correa & Dressler 1015*).—c. *P. viridis* (*Duke 10230*). Scale bars = 1 cm.

and vice versa, i.e., intramorph incompatibility (Darwin, 1877; Ganders, 1979). From the standpoint of descriptive morphology, it means that flowers of both morphs must be described, with their different filament and style lengths.

Of the 66 taxa in Mesoamerican *Psychotria* subg. *Psychotria*, 40 appear normally distylous, as judged from morphology alone. Five are "long-homostylous," i.e., having only one flower morph, in which stamens and style are both exserted. Five other taxa appear to have only one of the two distylous morphs: two are "pin-monomorphic" and three are "thrum-monomorphic." No cases of dioecy are evident from flower morphology alone. (The remaining 16 taxa cannot be assigned a category because too few flowering specimens were available for analysis.) Nondistylous states of breeding biology are not concentrated in any particular species group (see Infrageneric Relationships) and are

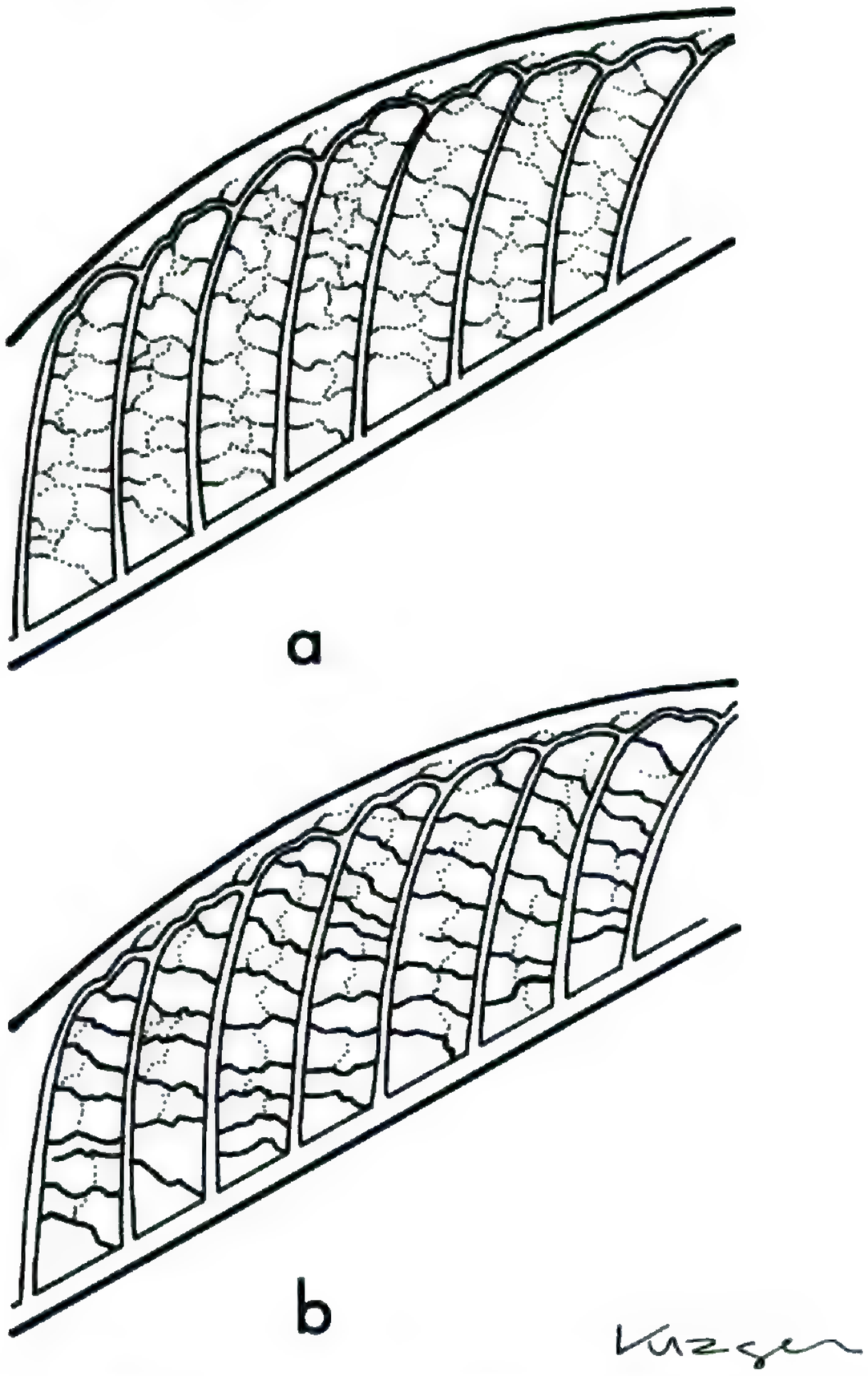


FIGURE 5. Types of leaf tertiary venation.—a. Orthogonal reticulate.—b. Percurrent (with quaternary veins orthogonal reticulate).

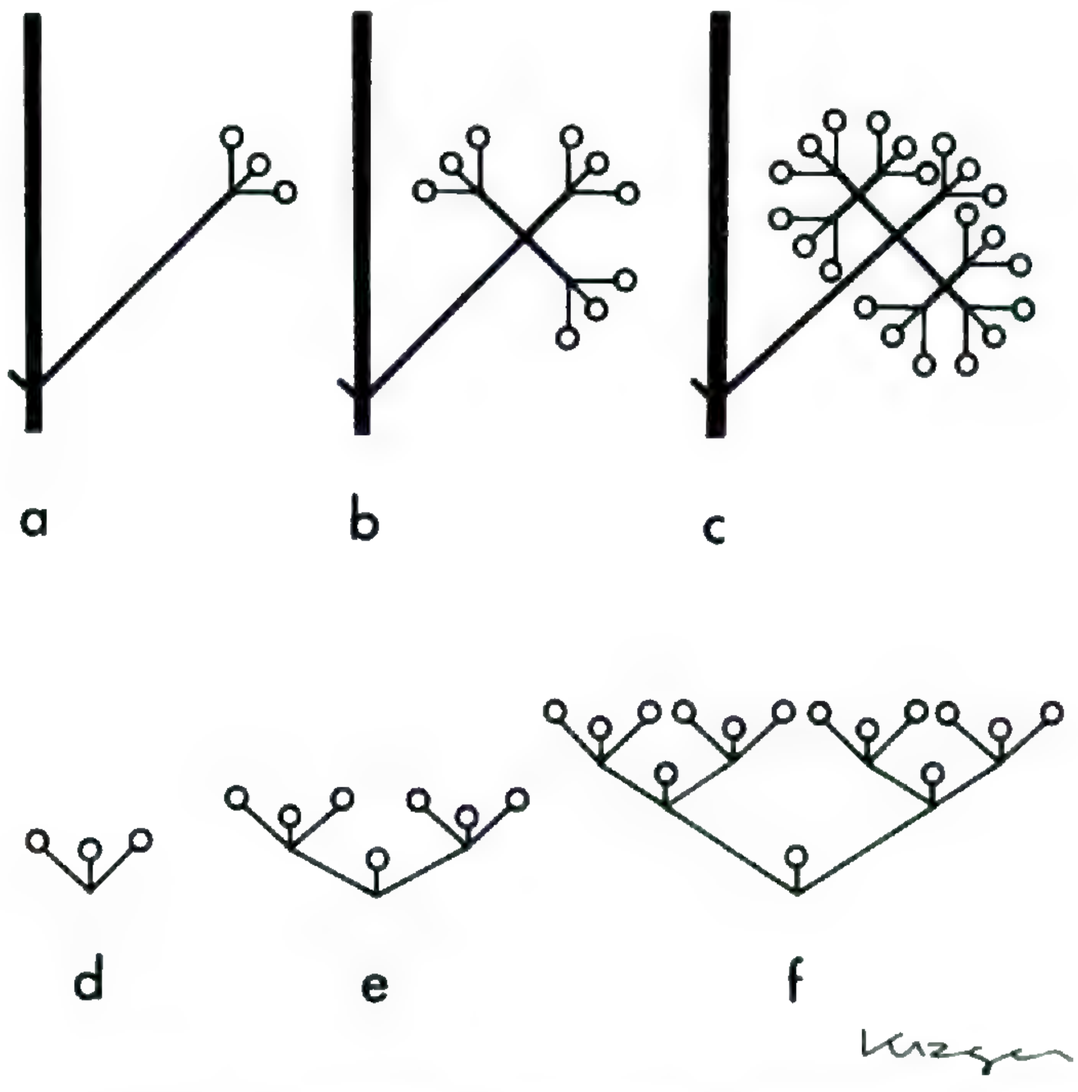
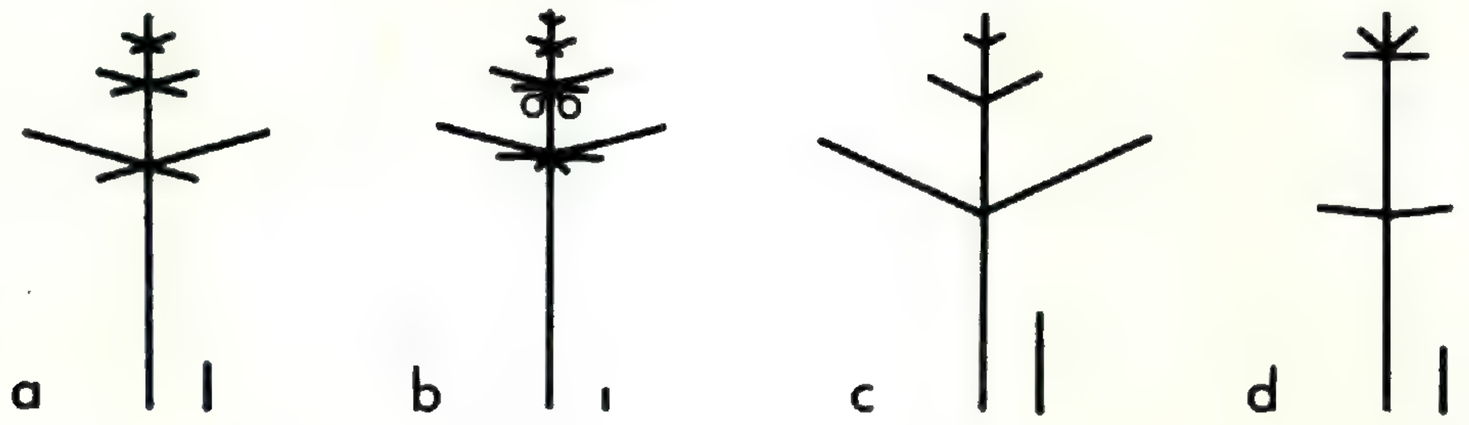


FIGURE 6. Degrees of branching of panicles and cymes. Panicles:—a. Two degrees.—b. Three degrees.—c. Four degrees. Cymes:—d. One degree.—e. Two degrees.—f. Three degrees.



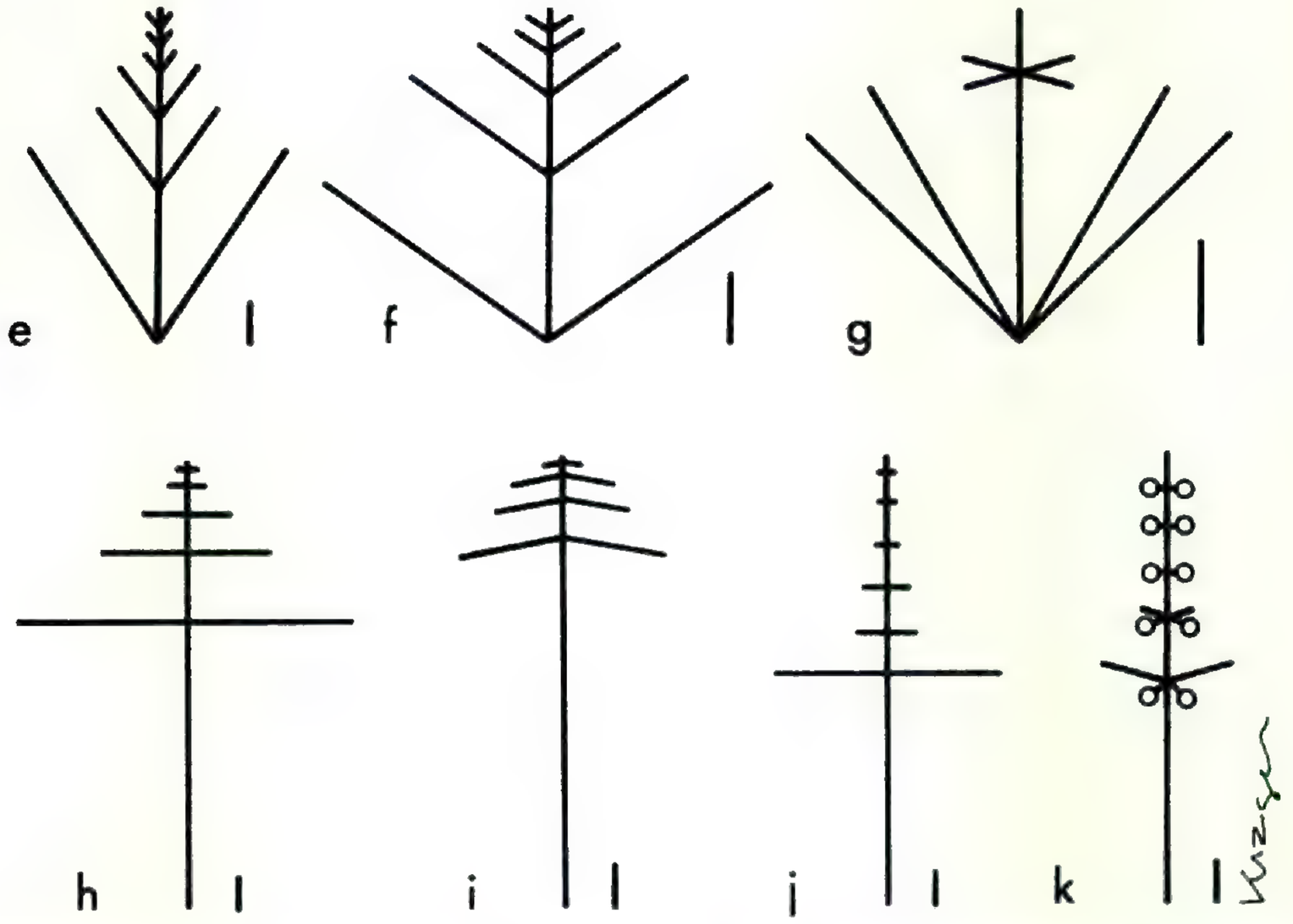


FIGURE 7. Inflorescences in subg. *Psychotria*, showing only main and secondary axes. Circles indicate reduced axes and sessile glomerules.—a. *P. carthagenensis*, with secondary axes in three ranks, two pairs (long vs. short) per rank.—b. *P. flava*, with three pairs of secondary axes in the first two ranks.—c. *P. erythrocarpa*, with one pair of secondary axes per rank.—d. *P. dressleri*, with a cluster of secondary axes at the apex of the primary axis.—e. *P. panamensis*, with no peduncle.—f. *P. limonensis*, with secondary axes of such relative lengths as to give an umbellate shape to the inflorescence.—g. *P. quinqueradiata*, with the first rank of secondary axes almost equal in length to the main axis.—h. *P. marginata*, with secondary axes diverging at right angles.—i. *P. stockwellii*, with secondary axes diverging at obtuse angles.—j. *P. remota*, with all but the first rank of secondary axes very short.—k. *P. viridis*, with almost all secondary axes reduced. Scale bars = 1 cm.

therefore hypothesized to have evolved independently of one another from primitive distyly (Hamilton, in press).

Measurements of corolla tubes and lobes are length followed by maximum width (diameter in the case of the tubes).

Stamen filaments are invariably fused to the corolla tube; their point of separation from the tube is often difficult to ascertain, however, so I have measured the filaments from the base of the corolla tube. Using this measurement and that of style length, one can determine the spatial separation between anthers and stigma. The filaments connect to the anthers usually halfway up the introrse anther thecae.

FRUIT

All fruit measurements are of dried herbarium material and so will differ from those of fresh fruits with fleshy exterior. Fruit shape is a useful character, straightforwardly described. Persistent calyces can also be valuable; Figure 9 indicates the variation within the subgenus and how the relative lengths of calyx tube and lobes can affect the aspect of the fruit.

The two seeds, often called pyrenes (cf. Steyermark, 1972; Dwyer, 1980), are hemispherical in cross section and thus have two surfaces to consider: the rounded, outside "dorsal" surface and the flat, inner "ventral" surface. Longitudinal furrows run along both surfaces, and their number, depth, and regularity serve as important characters. Figure 10 illustrates the variation within the subgenus, with *P. carthagenensis* (Fig. 10a) representing the most common type of cross section. The depth of the furrows on the dorsal surface affects the external appearance of the whole dried fruit: *P. remota* (Fig. 10f) fruit appears deeply ribbed, while that of *P. grandis* (Fig. 10i), with its many shallow irregular furrows, appears smooth.

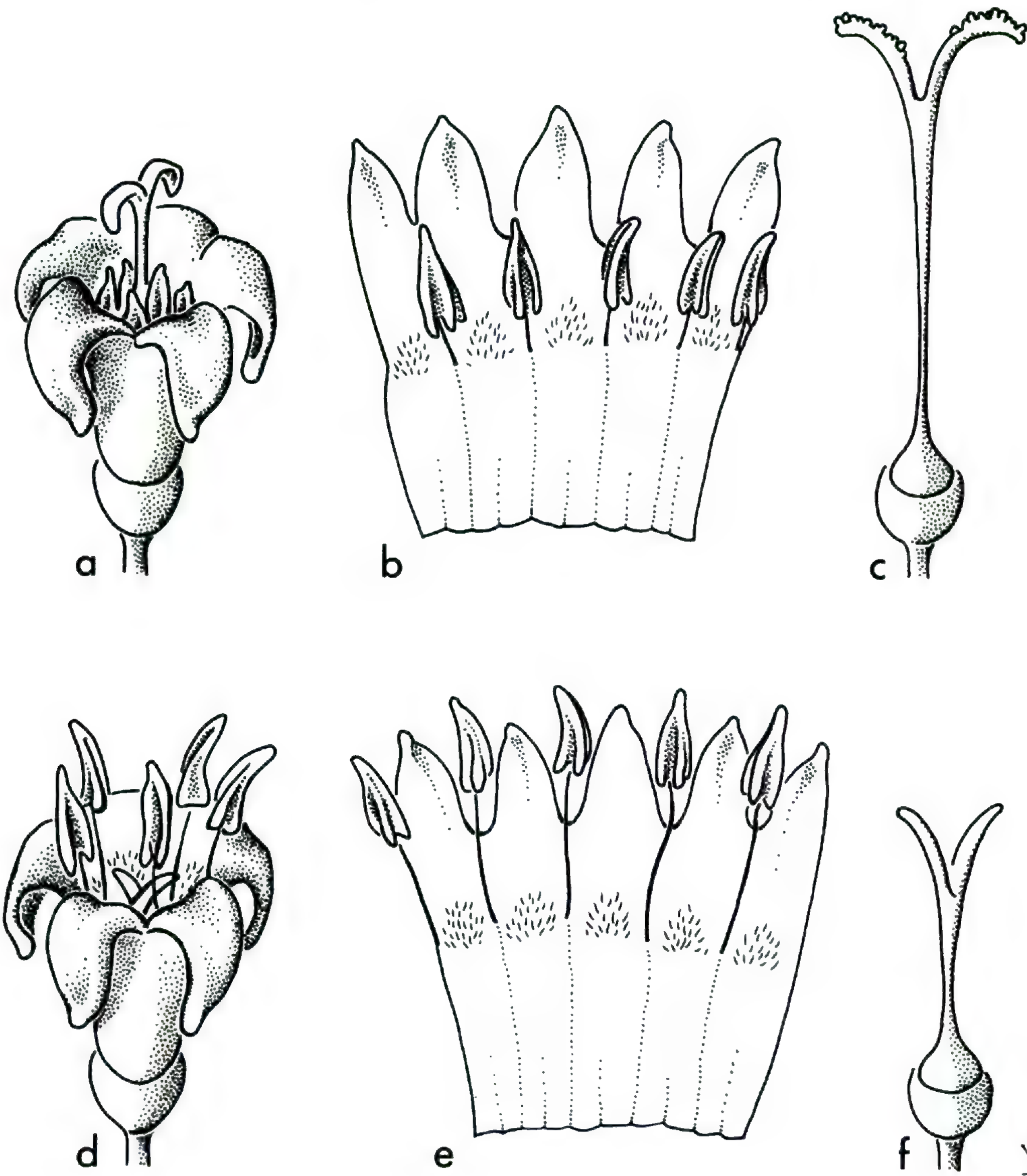


FIGURE 8. Long-style (pin) and short-style (thrum) flower morphs of *Psychotria marginata*.—a–c. Long-style morph (*R. Foster 1696*).—d–f. Short-style morph (*Antonio 2305*). a, d, whole flowers; b, e, dissected corollas; c, f, pistils. Scale bar = 1 mm.

BIOGEOGRAPHY

For purposes of biogeographical analysis I have divided Mesoamerica into nine regions (Fig. 11). The most species and most endemic species of subg. *Psychotria* are found in Panama (40 species; 15 endemics); both diversity and endemism drop somewhat in Costa Rica (32/7). There is a diversity "trough" in middle Mesoamerica (Honduras, El Salvador, and Nicaragua), with absolutely no endemism. A secondary center of diversity includes region 3 (eastern Veracruz, Tabasco, Oaxaca, and Chiapas in Mexico) and region 5 (Guatemala and Belize), both areas having 26 species and a few endemics. Other parts of Mexico have only range extensions of some species found in regions 3 and 5.

The striking pattern of species diversity of subg. *Psychotria* within Mesoamerica appears to represent general diversity patterns of moist- and wet-forest vascular plants (Fig. 11). This pattern—most diversity and endemism in Costa Rica and Panama, a secondary center in southern Mexico

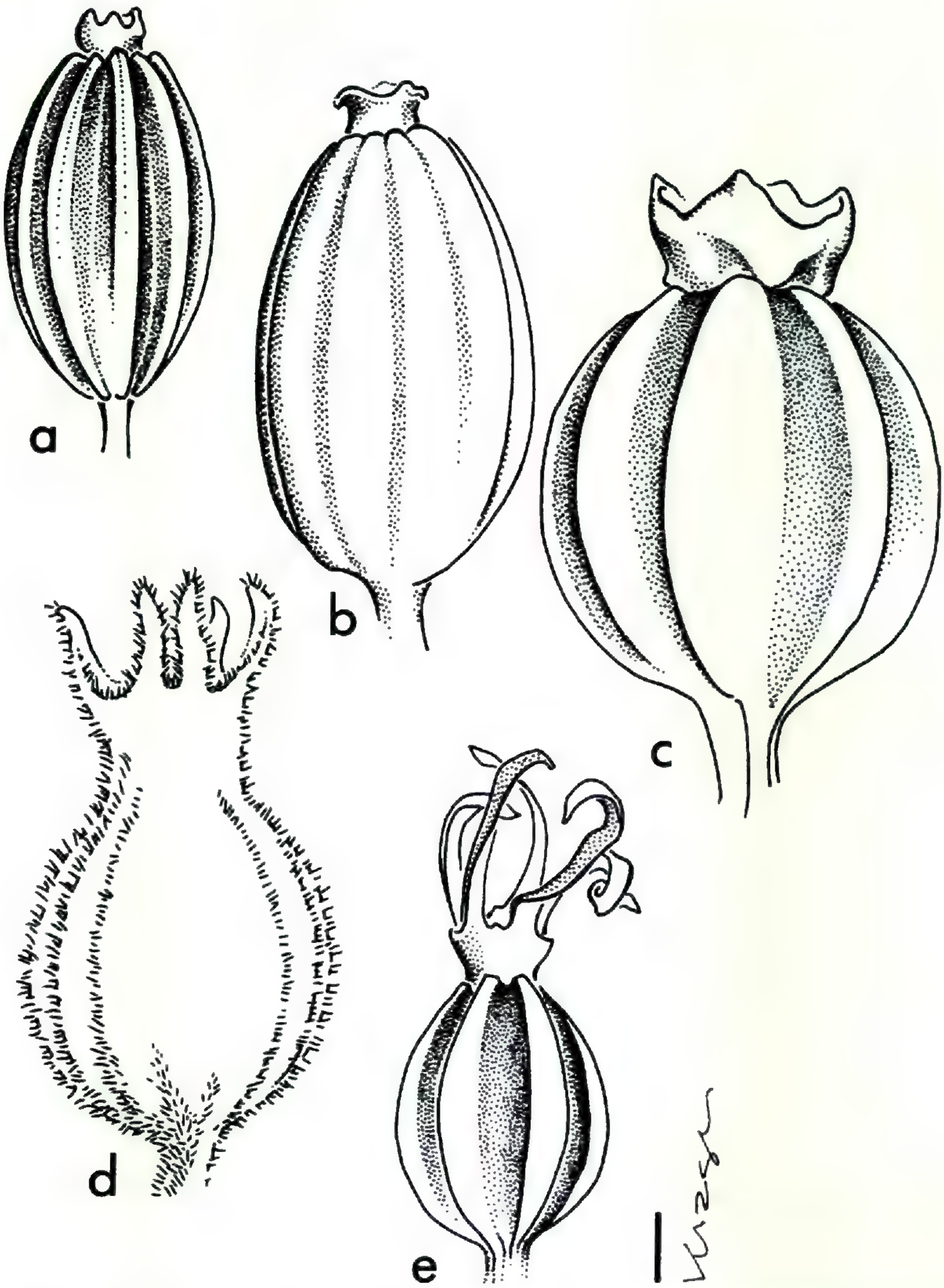


FIGURE 9. Dried fruit with persistent calyces.—a. *Psychotria carthagenensis* (*Standley & Valerio 44926*).—b. *P. papantlensis* (*Contreras 7958*).—c. *P. cocosensis* (*Pittier 12375*).—d. *P. jinotegensis* (*Lauvert & Barkley 39552*).—e. *P. horizontalis* (*Witherspoon & Witherspoon 8693*). Scale bar = 1 mm.

(region 3) and Guatemala, and little between—is found in other recently monographed species-rich taxa of moist- and wet-forest plants (Table 1). The *Anthurium* pattern (tabulated from Croat, 1983, 1986) is an amplified version of that of *P.* subg. *Psychotria*, with nearly seven times as many species in Panama as in Nicaragua. *Cordia* sect. *Micranthae* (Miller, 1985) and *Monochaetum* (Almeda, 1978), with somewhat smaller data sets, also reflect the general trend. *Cavendishia* (Luteyn, 1983) and *Heliconia* with pendent inflorescences (Kress, 1984) also have greatest diversity in Panama and Costa Rica but show no secondary center in Mexico and Guatemala.

All these data sets suggest strongly that the diversity pattern of subg. *Psychotria* represents that of many species-rich taxa and may therefore be of value as an index of regional diversity for tropical flowering plants. The primary value of this would be in pinpointing areas to which we should devote conservation effort in order to preserve the maximum diversity of life. Figure 12, a map of species numbers per one-degree square, reveals great differences in diversity that cannot be dismissed as collecting artifact. It is also noteworthy that all nine squares with significant endemism are in Costa Rica and Panama (Table 2).

Areas in Costa Rica and Panama with particularly high endemism are largely identical to those noted by Croat (1983, 1986) for *Anthurium*, most-

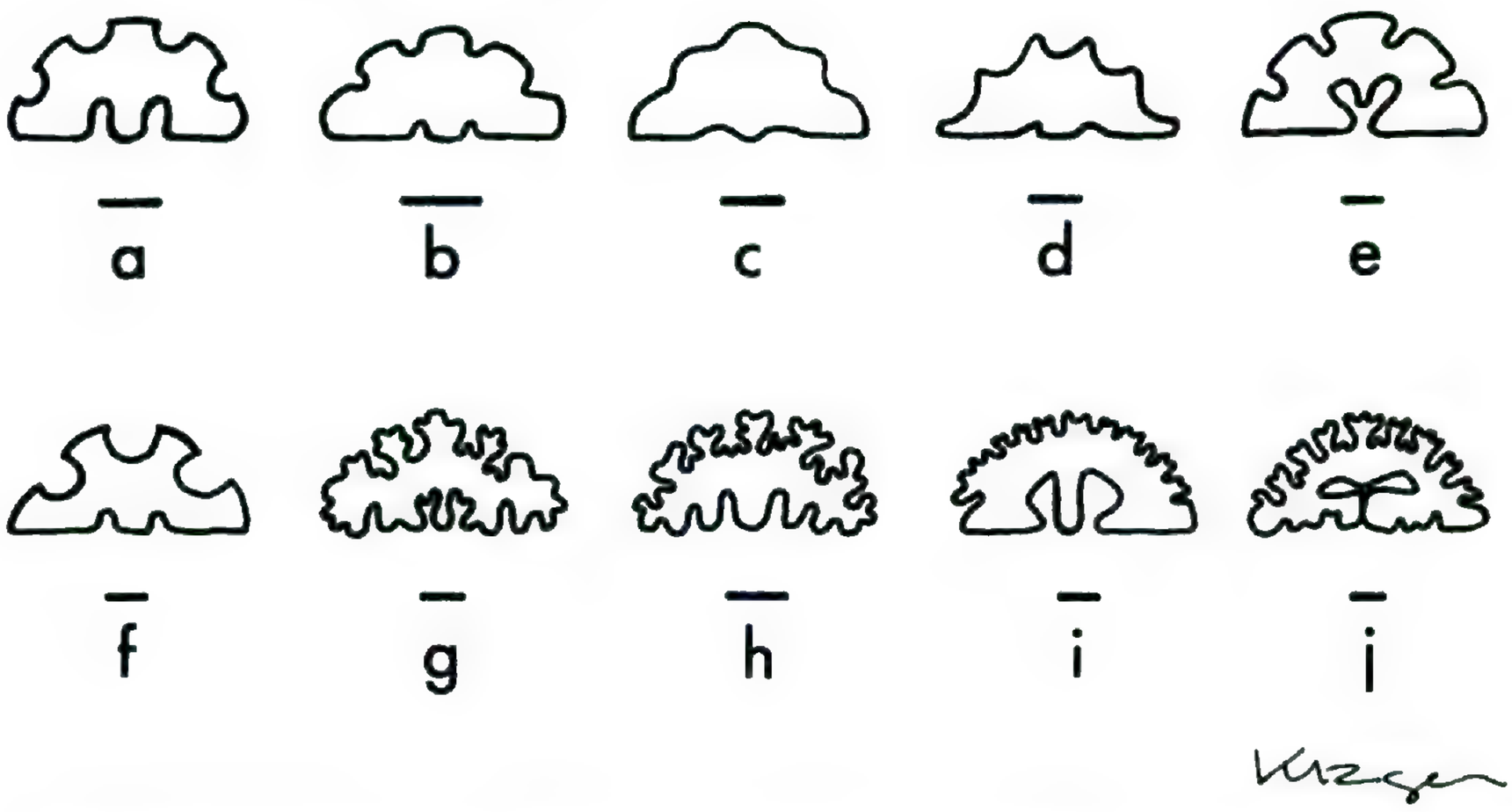


FIGURE 10. Seed cross sections.—a. *Psychotria carthagenensis*, the dorsal surface (d.s.) with 4 deep longitudinal furrows (l.f.), the ventral surface (v.s.) with 2 deep l.f.—b. *P. horizontalis*, the d.s. with 3–5 l.f., the v.s. with 2 l.f.—c. *P. graciliflora*, the d.s. with 4 l.f., the v.s. concave or with 2 broad shallow l.f.—d. *P. orosiana*, the d.s. with 4–5 deep l.f. leaving acute ridges between, the v.s. with 2 shallow l.f.—e. *P. costivenia* var. *costivenia*, the d.s. with 4–5 l.f., the d.s. with 2 deep incompletely divided l.f.—f. *P. remota*, the d.s. with 3 deep l.f., the v.s. with 2 l.f.—g. *P. olgae*, the d.s. with 4 deep and numerous irregular l.f., the v.s. with 2 deep and several irregular l.f.—h. *P. mexiae*, the d.s. with 5–8 deep irregular l.f., the v.s. with 2 deep plus usually 2–4 additional irregular l.f.—i. *P. grandis*, the d.s. with 10–15 shallow irregular l.f., the v.s. with 2 very deep l.f.—j. *P. flava*, the d.s. with 6–10 irregular l.f., the v.s. with 1 often T-shaped l.f. Scale bars = 1 mm.

ly 1,000–2,000 m elevation along the Continental Divide plus isolated hilly areas. Costa Rican endemics *P. chitariana*, *P. monteverdensis*, and *P. sylvivaga* fit this pattern, as does *P. stockwellii*, which extends from Alajuela to western Chiriquí, Panama. The Divide in western Panama has several narrow-ranging species: *P. boquetensis*, *P. hornitensis*, *P. hammelii*, *P. insueta*, and *P. cascajalensis*. Just east of the Canal, the Cerro Azul–Cerro Jefe region has three endemics: *P. liesneri*,

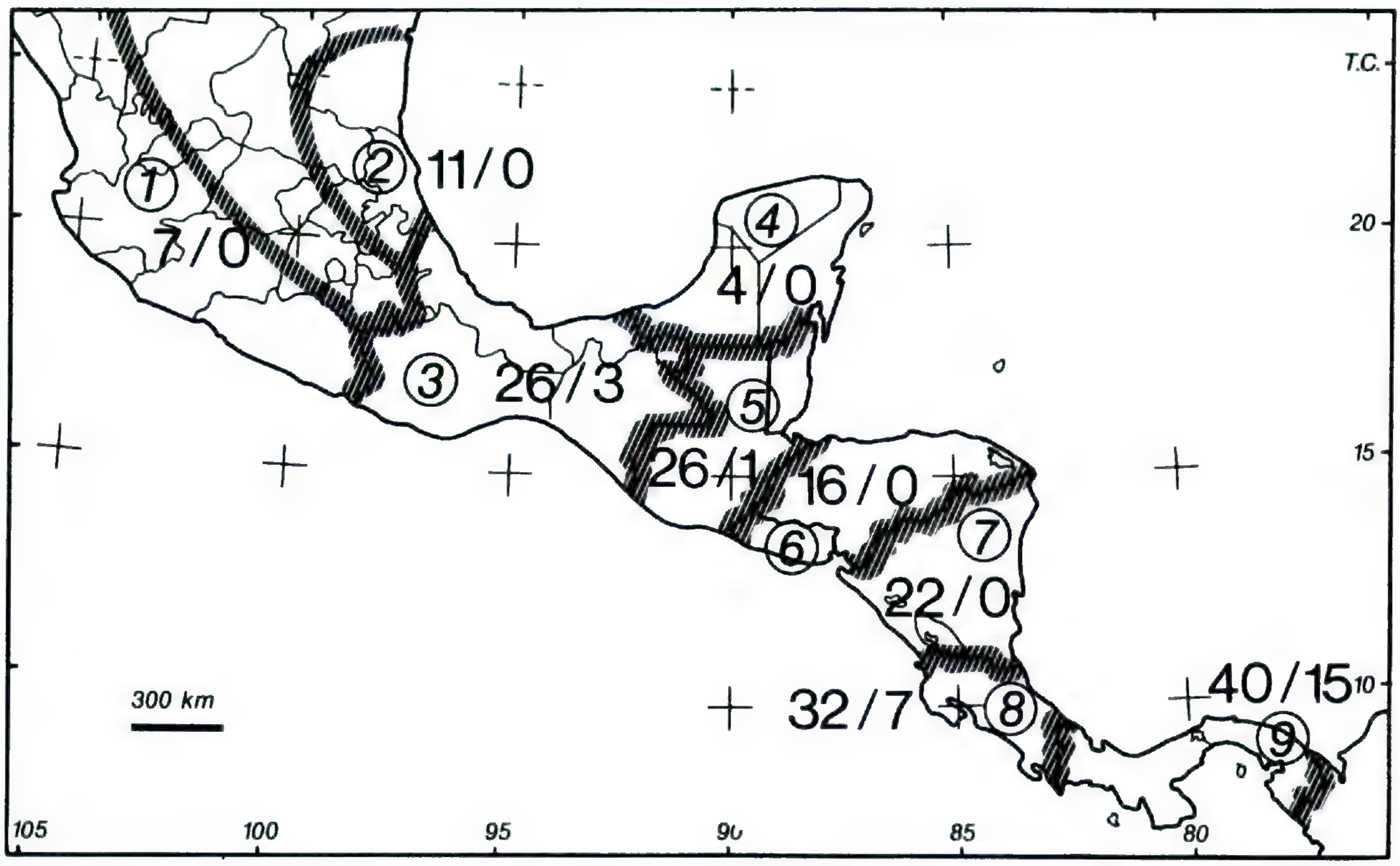


FIGURE 11. Total and endemic species of *Psychotria* subg. *Psychotria* by region. Circled numbers are the region numbers; numbers on the left of the slash are the total species in the area; numbers on the right are the species endemic to the area.

TABLE 1. Numbers of species/endemic species, by region (see Fig. 11), of various taxa.

	Mexico				Guatemala and Belize	Honduras and El Salvador	Nicaragua	Costa Rica	Panama	Total species
	1	2	3	4	5	6	7	8	9	
Psychotria subg. *Psychotria*	7/0	11/0	26/3	4/0	26/1	16/0	22/0	32/7	40/15	61
Anthurium[1]	5/1	2/0	37/22	—	23/3	16/1	22/1	72/18	148/82	207
Cordia sect. *Micranthae*[2]	5/0	2/0	9/0	3/0	10/2	8/0	7/0	12/1	17/6	24
Monochaetum[3]	1/0	3/0	7/3	—	3/1	2/0	2/0	8/5	6/3	18
Cavendishia[4]	—	—	2/0	—	3/0	1/0	3/0	15/6	28/16	36
Heliconia with inflorescence pendent[5]	1/0	—	1/0	—	2/0	2/0	5/0	13/1	16/5	19

[1] Croat, 1983, 1986.
[2] Miller, 1985.
[3] Almeda, 1978.
[4] Luteyn, 1983.
[5] Kress, 1984.

TABLE 2. One-degree squares (see Fig. 12) with significant species endemism in *Psychotria* subg. *Psychotria*.

Square Coordinates[1]	Endemic Species A[2]	B[3]	C[4]	Total *Psychotria* subg. *Psychotria* Species
10°N, 84°W	3	0	2	19
9°N, 84°W	0	2	3	8
9°N, 83°W	1	1	4	20
9°N, 82°W	1	0	2	14
9°N, 79°W	3	0	2	20
8°N, 82°W	2	1	2	13
8°N, 81°W	0	2	1	14
8°N, 80°W	1	1	0	15
8°N, 77°W	2	0	2	20

[1] Coordinates are of the SE corner of the square. Squares are highlighted in Figure 12.
[2] Has been collected only in this square.
[3] Has been collected in only one additional square.
[4] Has been collected in only two or three additional squares.

P. olgae, and *P. pacorensis*. Mountains near the Colombian border support three more: *P. philacra* (Cerro Tacarcuna), *P. rosulatifolia* (Cerro Malí and Cerro Pirre), and *P. insignis* (south of Puerto Obaldía). Three narrow-ranging species, *P. laselvensis*, *P. sixaolensis*, and *P. fendleri*, are found in areas of Caribbean lowlands, which have not been botanized thoroughly. It is beyond the scope of this treatment to speculate on the causes of these patterns—e.g., absolute rainfall, topographical heterogeneity, geological disturbance—but the pattern suggests that Costa Rica and Panama deserve the lion's share of *in situ* conservation focus in Mesoamerica.

The biogeographies of species complexes, within groups, display consistent patterns that suggest hypotheses as to the course of evolution within the complexes (see Infrageneric Relationships). Many species complexes are comprised of one widespread species, for which the complex is named, plus one or more species with much narrower ranges: the *Psychotria quinqueradiata* complex (two species), the *P. micrantha* complex (two species), the *P. horizontalis* complex (two species), the *P. costivenia* complex (seven species), the *P. graciliflora* complex (seven species), the *P. chagrensis* complex (two species), the *P. nervosa* complex (four species), the *P. chiriquina* complex (three species), and the *P. panamensis* complex (six species; see distribution maps in the introductions to each species group in the Systematic Treatment). Seven widespread species, such as *P. carthagenensis* and *P.*

FIGURE 12. Numbers of species of *Psychotria* subg. *Psychotria* per one-degree square. Squares of high endemism (see Table 2) are shaded.

marginata, are not obviously similar to any narrow-ranging species. Group 8, the *calophylla* group, defies even tentative analysis of affinities: most species are narrow endemics in Costa Rica and Panama, with only *P. calophylla* and *P. psychotriifolia* having somewhat wider ranges. The predominant pattern of one widespread plus one or more narrow-ranging species accounts for 35 of the 61 species and suggests that in each complex the widespread species may be ancestral to those with narrow ranges. Careful phylogenetic analysis of the subgenus throughout the Neotropics is necessary to evaluate this hypothesis.

Each species and variety account in the Systematic Treatment includes a characterization of range in terms of habitat and climate. The habitat classification used is that of Holdridge (1967), particularly from life zone maps of Costa Rica (Tosi, 1969) and Panama (Anonymous, 1970). The ranges of many Mexican species are characterized according to a vegetation map of that country (Flores Mata et al., 1971). Climate types are those of Walter et al. (1960), discussed by Walter (1973); the particular climate types referred to herein are six: I equatorial, I(X) equatorial-mountainous, I(II) equatorial-tropical, II(I) tropical-equatorial, II tropical, and II(X) tropical-mountainous. Equatorial and equatorial-mountainous climates may show some seasonality of rainfall, but the ratio of precipitation (in mm) to temperature (in degrees centigrade) never drops below 2:1 in any month. In an equatorial-tropical climate, there is a mild dry season in which the ratio drops slightly below 2:1 for one or two months, usually around March. In a tropical-equatorial climate, the dry season is more extreme, lasting up to four months at the beginning of the year. The dry season in a tropical or tropical-mountainous climate usually lasts November through April, some of those months often having absolutely no precipitation.

Infrasubgeneric Relationships

Formal taxonomic recognition of sections awaits understanding of the subgenus throughout the Neotropics. For the time being, I have divided the 61 Central American species into eight groups comparable to sections. In several cases I refer to species complexes, which are sets of morphologically very similar species within a group.

The following key to species groups indicates major differences among the groups and is primarily didactic; it utilizes characters, such as stipules, that are useful at the species-group level but less so for species identification, e.g., because stipules are caducous and fruits are often not present. For species identification, one should use the key to species in the Systematic Treatment; it relies

largely on leaf and inflorescence characters, which are most consistently evident.

Following the key are brief synopses of the eight species groups, including lists of species, geographic patterns, and noteworthy character states not in the key. More extensive descriptions, with distinctive character states italicized, plus discussions of species relationships, biogeography, and breeding biology will be found at the beginning of each group in the systematic treatment.

Key to Species Groups

1a. Inflorescence axes almost always 4 (or 6) per rank in at least one rank, in usually 2 (or 3) unequal pairs 2
1b. Inflorescence axes generally 2 per rank or, if 4 or clustered, equal in length 3
2a. Leaves drying generally green-brown to red-brown to red-gray ..... Group 1—*carthagenensis* group
2b. Leaves drying generally dull green to yellow-green ..... Group 2—*costivenia* group
3a. Leaf secondary venation eucamptodromous to brochidodromous without a collector vein 4
3b. Leaf secondary venation usually brochidodromous with a collector vein near the margin or, if eucamptodromous, the corolla lobes with apical extensions and/or the inflorescence bracts enlarged 7
4a. Inflorescences generally pedunculate, the secondary axes diverging usually at right angles 5
4b. Inflorescences usually lacking peduncle, the secondary axes generally diverging at acute (obtuse in *P. stockwellii*) angles 6
5a. Leaves drying usually gray-green to green-black or red-black; inflorescence secondary axes elongated in all ranks; seed dorsal surface with 3–5 deep furrows, sometimes plus several irregular longitudinal furrows ..... Group 3—*graciliflora* group
5b. Leaves drying glossy red-brown; inflorescence secondary axes significantly elongated only in the first rank; seed dorsal surface with 3 deep longitudinal furrows ..... Group 4—*remota* group
6a. Plants often ferrugineous-pubescent or tomentose; persistent calyx often conspicuous, 2–5 mm long; seed dorsal surface usually with 4–5 regular longitudinal furrows ..... Group 5—*nervosa* group
6b. Plants not ferrugineous-pubescent or tomentose; persistent calyx inconspicuous or a small beak or rarely a coriaceous cup; seed dorsal surface with 4–10 irregular longitudinal furrows ..... Group 6—*panamensis* group
7a. Inflorescences umbelliform panicles of cymes, the bracts never enlarged; corolla lobes without apical extensions; persistent calyx inconspicuous or to 0.5 mm long ..... Group 7—*tenuifolia* group
7b. Inflorescences panicles of cymes or usually glomerules, the bracts often enlarged; corolla lobes almost always with apical extensions; persistent calyx often a conspicuous tube ..... Group 8—*calophylla* group

Species Group Synopses

Group 1—*carthagenensis* group. Species 1–7.

The *carthagenensis* group comprises seven species: *Psychotria carthagenensis*, *P. clivorum*, *P. lamarinensis*, *P. micrantha*, *P. neillii*, *P. quinqueradiata*, and *P. viridis*. The *Psychotria quinqueradiata* species complex includes that widespread species plus *P. lamarinensis*, which is endemic to northern Costa Rica. The *P. micrantha* complex includes that species plus *P. neillii*, whose range is restricted to Caribbean southern Nicaragua and northern Costa Rica. *Psychotria carthagenensis*, *P. clivorum*, and *P. viridis* are all widespread without obvious close relatives.

In addition to the key characters, members of this group may be recognized by their seeds having (3–)4–5 deep longitudinal furrows on the dorsal surface and 2 longitudinal furrows on the ventral surface.

Group 2—*costivenia* group. Species 8–16.

The *costivenia* group comprises nine species: *P. balancanensis*, *P. costivenia*, *P. fendleri*, *P. flava*, *P. grandis*, *P. horizontalis*, *P. papantlensis*, *P. pleuropoda*, and *P. sylvivaga*. *The Psychotria horizontalis* complex includes the most widespread of the nine plus *P. fendleri*, which is endemic to Caribbean coastal Panama. The *P. costivenia* complex comprises the other seven; *P. costivenia* is only slightly more widespread than *P. grandis*, with the two sharing noteworthy morphological similarity and overlapping ranges. *Psychotria sylvivaga* has been collected only in Costa Rica, and the remaining four species are restricted to southern Mexico, Guatemala, and Belize.

Distinctive character states, in addition to those in the key, include a usually conspicuous persistent calyx in fruit.

Group 3—*graciliflora* group. Species 17–25.

The *graciliflora* group comprises nine species in Mesoamerica: *P. bakeri*, *P. graciliflora*, *P. jimenezii*, *P. laselvensis*, *P. liesneri*, *P. marginata*, *P. orosiana*, *P. parvifolia*, and *P. philacra*. *Psychotria marginata* is the most widespread and frequently collected, and no other species closely resembles it morphologically. In contrast, the also widespread *P. graciliflora* is strikingly similar to six of the other species (the *P. graciliflora* complex) that occur more or less sympatrically with it: *P. parvifolia* and *P. orosiana* (Costa Rica and western Panama), *P. laselvensis* (Costa Rica), *P. bakeri* (Los Santos, Panama), *P. liesneri* (eastern Panama province), and *P. philacra* (eastern Darién, Panama, at higher elevation than *P. graciliflora*). *Psychotria jimenezii* may belong to this complex as well.

Members may be recognized by their key characters plus stipules often biacuminate to biaristate, secondary veins usually brochidodromous and diverging 70°–90°, and inflorescence secondary axes usually delicate.

Group 4—*remota* group. Species 26.

The *remota* group includes several species in South America but only one of those, *P. remota*, in Mesoamerica. An additional recognition character is the winged inflorescence axes, conspicuous especially in the field.

Group 5—*nervosa* group. Species 27–35.

The *nervosa* group comprises nine species: *P. aguilarii*, *P. boquetensis*, *P. chagrensis*, *P. erythrocarpa*, *P. fosteri*, *P. fruticetorum*, *P. jinotegensis*, *P. mirandae*, and *P. nervosa*. Two species complexes, those of *P. nervosa* and of *P. chagrensis*, are discernible; three other fairly widespread species—*P. fruticetorum*, *P. erythrocarpa*, and *P. jinotegensis*—do not closely resemble any others. The *P. nervosa* complex consists of widespread *P. nervosa* and three species of more restricted ranges, all of which occur allopatrically with or at range boundaries of *P. nervosa*: *P. mirandae* in southern Mexico, *P. aguilarii* in higher-elevation southern Guatemala, and *P. boquetensis* in high-elevation western Panama. The *P. chagrensis* complex includes widespread *P. chagrensis* and the probably derived *P. fosteri*, which occurs on Coiba Island, Panama, apparently allopatrically with respect to *P. chagrensis*.

Recognition characters not included in the key are ellipsoidal to narrow-ellipsoidal fruit, and inflorescences reduced to fascicles of flowers or the secondary axes in (2–)3 ranks.

Group 6—*panamensis* group. Species 36–47.

The *panamensis* group comprises 12 species in Mesoamerica: *P. cascajalensis*, *P. chiriquina*, *P. cocosensis*, *P. dwyeri*, *P. hornitensis*, *P. lundellii*, *P. mexiae*, *P. olgae*, *P. panamensis*, *P. sarapiquensis*, *P. stockwellii*, and *P. trichotoma*. The largest species complex is the *P. panamensis* complex. It includes one widespread species, *P. panamensis*, whose var. *ixtlanensis* may owe its origin to introgression from *P. trichotoma* (see under Systematic Treatment), and five narrow-ranging species: *P. dwyeri* (southern Mexico, sympatric with *P. panamensis*), *P. stockwellii* (Costa Rica and Panama, sympatric), *P. cocosensis* (Cocos Island, Costa Rica, allopatric), *P. olgae* (Panama, ± sympatric), and *P. cascajalensis* (Panama, sympatric). The widespread species *P. trichotoma*, *P. sarapiquensis*, and *P. mexiae* are of uncertain affinities; the former two may be closely related to the *P. panamensis* complex. The *P. chiriquina* complex includes two species whose ranges do not overlap (*P. lundellii* south to El Salvador and *P. chiriquina* south from northern Nicaragua) and one narrow endemic, *P. hornitensis* from high-elevation western Panama at the eastern end of the range of *P. chiriquina*.

Group 7—*tenuifolia* group. Species 48, 49.

The *tenuifolia* group includes only two species in Mesoamerica, *P. limonensis* and *P. tenuifolia*, both of which are widespread with extensively overlapping ranges. The group is characterized by minute flowers and secondary veins diverging usually 70°–90°, in addition to the key characters.

Group 8—*calophylla* group. Species 50–61.

The *calophylla* group comprises 12 species: *P. alfaroana*, *P. calophylla*, *P. chitariana*, *P. dressleri*, *P. hammelii*, *P. insignis*, *P. insueta*, *P. monteverdensis*, *P. pacorensis*, *P. psychotriifolia*, *P. rosulatifolia*, and *P. sixaolensis*. Ten of the species have small geographic ranges; only *P. calophylla* and *P. psychotriifolia* are at all widespread, and their ranges are notably discontinuous. *Psychotria dressleri* and *P. rosulatifolia* are quite similar morphologically and occur in eastern Panama, and therefore may be supposed to be related; but beyond that the affinities are very uncertain.

Additional recognition characters are many: herbaceous or suffrutescent habit; usual general pubescence; sheathing stipules, these usually bifurcate or biaristate with the extensions often from corners of the truncate sheath; and ellipsoidal fruit.

Systematic Treatment

Psychotria L., Syst. Nat., ed. 10. 929. 1759 (nom. cons.) subgenus **Psychotria** [sensu Petit, Bull. Jard. Bot. État 34: 1–229. 1964. Also sensu Steyermark, Mem. New York Bot. Gard. 23: 406–484. 1972.] TYPE SPECIES: *Psychotria asiatica* L.

Ouragoga L., Hort. Cliff. 486. 1737. Cf. also Linnaeus, Gen. Pl., ed. 1. 378. 1737.

Myrstiphyllum P. Browne, Civ. Nat. Hist. Jamaica. 152. 1756 (nom. rejic.). Sensu Hitchcock, Annual Rep. Missouri Bot. Gard. 4: 95. 1893.

Psychotrophum P. Browne, Civ. Nat. Hist. Jamaica. 160, t. 13, fig. 1, t. 17, fig. 2. 1756 (nom. rejic.).

Mapouria Aubl., Hist. Pl. Guiane 1: 175, pl. 67. 1775. TYPE SPECIES: *Mapouria guianensis* Aubl. Sensu Oersted, Amér. Centr. 1863. Also sensu Mueller-Argoviensis, Flora 59: 457–466, 495–498. 1876, and in Martius, Fl. Bras. 6(5): 384–428. 1881. Also sensu Bremekamp, Recueil Trav. Bot. Néerl. 31: 248. 1934.

Uragoga Baillon, Adansonia 12: 323. 1879. TYPE SPECIES: *Uragoga ipecacuanha* (Brot. Baill.) Sensu Kuntze, Revis. Gen. Pl. 1: 298–301. 1891.

Shrubs, small trees, or less often herbs or subshrubs; stipules interpetiolar, often sheathing, usually caducous, leaving a pale ridge with red-brown fringe. *Leaves* opposite; blades membranous to coriaceous, drying red-brown or dull greenish or rarely chalky yellow-green; secondary veins eucamptodromous to brochidodromous, sometimes with collector vein, the axils sometimes with domatia or tufts of hairs; tertiary veins orthogonal reticulate to percurrent. *Inflorescences* terminal or pseudoaxillary, panicles of cymes or of glomerules or rarely fascicles of flowers; secondary axes borne in 1–several ranks along the main axis, each rank with 1–3 often size-differentiated pairs of axes. *Flowers* small, (4–)5-merous, almost always distylous; corolla usually white, the tube cylindrical; style 2-branched, the branches bearing the stigmatic surfaces, the ovary 2-celled, the ovules 1 per cell, attached basally. *Fruit* fleshy, maturing red (except reportedly purple or blackish in *P. insueta* and *P. pacorensis*); persistent calyx often conspicuous at distal end of fruit; seeds 2, hemispherical in cross section, the rounded dorsal surface with 3–5 regular to many irregular longitudinal furrows, usually giving the dried fruit a costate aspect, the flat or slightly concave dorsal surface with (1–)2 regular longitudinal furrows often plus several shallow irregular furrows.

A pantropical subgenus of approximately 600 species worldwide, including ca. 200 species in the Neotropics, 61 of which are in Mesoamerica. The subgenus accounts for the majority of species in the Antilles but only for 32 of 242 species treated by Steyermark (1972) for the Guayana Highland.

KEY TO SPECIES OF
PSYCHOTRIA SUBGENUS *PSYCHOTRIA*

1a. Leaf blades with collector veins distinct, straight, or slightly undulating 2
1b. Leaf blades without collector veins 13
2a. Inflorescences reduced to fascicles of flowers 3
2b. Inflorescences with distinct axes 4
3a. Leaf blades (6–)8–12 × (2–)3–5 cm; stipule sheath 8–12 mm long; Coiba Island, Panama ..... (31) *P. fosteri*
3b. Leaf blades (3–)4–7.5(–9.5) × (1–)1.5–2.5(–3.5) cm; stipule sheath 4–7 mm long; widespread ..... (29) *P. chagrensis*
4a. Inflorescence a panicle of glomerules 5
4b. Inflorescence a panicle of cymes 9
5a. Young stems glabrous; western Costa Rica ..... (57) *P. monteverdensis*
5b. Young stems ferrugineous-pubescent or brown-puberulent 6
6a. Leaf blades ovate; secondary veins diverging over 90°; San Blas, Panama ..... (55) *P. insignis*
6b. Leaf blades elliptic or oblanceolate or obovate; secondary veins diverging less than 90° 7
7a. Treelet 3–8(–15) m tall; fruit 10–14 mm long; widespread ..... (51) *P. calophylla*
7b. Shrub or subshrub to 2 m tall; fruit less than 10 mm long 8
8a. Inflorescence lacking peduncle, often with more than 1 pair of secondary axes per rank; corolla tube 1.5 mm long; southern Nicaragua through Panama ..... (59) *P. psychotriifolia*
8b. Inflorescence with peduncle, with 1 pair of secondary axes per rank; corolla tube 4 mm long; Limón, Costa Rica, and Bocas del Toro, Panama ..... (61) *P. sixaolensis*
9a. Young stems ferrugineous-pubescent; inflorescence with secondary axes usually in more than 1 size-differentiated pair per rank; Costa Rica ..... (19) *P. jimenezii*
9b. Young stems glabrous or minute-puberulent; inflorescence with secondary axes in 1 pair or 2 usually equal pairs per rank 10
10a. Inflorescence with bracts 4 mm long; subshrubs or herbs 0.5 m tall; eastern Darién, Panama ..... (60) *P. rosulatifolia*
10b. Inflorescence with bracts to 1.2 mm long; shrubs 0.4–3(–5) m tall 11
11a. Leaves sessile with organic matter accumulating in leaf axils; leaf blades 30–42 cm long; Veraguas, Panama ..... (56) *P. insueta*
11b. Leaves petiolate, not as above; leaf blades to 29 cm long 12
12a. Leaves broad-elliptic, (12–)17–29 × (6–)7.5–15 cm; inflorescence secondary axes in (4–)5–6 ranks; fruit (3.5–)4(–4.5) × (3–)3.5(–4) mm; widespread ..... (48) *P. limonensis*
12b. Leaves narrow-elliptic, (4–)7.5–23 × (1–)2.5–6(–7.7) cm; inflorescence secondary axes in (2–)3(–4) ranks; fruit 4–5 × 3–4.5(–5) mm; widespread ..... (49) *P. tenuifolia*
13a. Fruit obloid (length < diameter); eastern Darién, Panama ..... (25) *P. philacra*
13b. Fruit length ≥ diameter 14
14a. Inflorescence not pedunculate (except rarely) 15
14b. Inflorescence pedunculate (except rarely) 37
15a. Inflorescence reduced to fascicles of flowers 16
15b. Inflorescence not reduced to fascicles of flowers 18
16a. Young stems red-brown tomentose; southern Mexico ..... (34) *P. mirandae*
16b. Young stems glabrous 17
17a. Leaf secondary veins 11–14, diverging 70°–80°; Coiba Island, Panama ..... (31) *P. fosteri*
17b. Leaf secondary veins 6–9(–10), diverging 45°–60°; widespread ..... (6) *P. quinqueradiata*
18a. Inflorescence secondary axes in 2 or more pairs per rank in at least 1 rank (except for rare inflorescences) or in a fascicle 19
18b. Inflorescence secondary axes only in 1 pair per rank (except for unusual inflorescences having 2 pairs in one rank) 23
19a. Young stems glabrous 20

19b. Young stems puberulent, tomentose, or ferrugineous-pubescent 21
20a. Leaf blades usually obovate or oblanceolate, (6–)9–15(–16) × (2–)3–7.5 cm, with secondary veins 6–9(–10) pairs diverging 45°–60°; corolla tubes 4–5 mm long; widespread ..... (6) *P. quinqueradiata*
20b. Leaf blades broad-elliptic, (13–)16–20 × (5–)7.5–9.5 cm, with secondary veins 9–11 pairs diverging 70°–85°; corolla tubes 3 mm long; Alajuela, Costa Rica ..... (3) *P. lamarinensis*
21a. Stipules 4–8 mm long; fruit red-brown tomentose; southern Mexico ..... (34) *P. mirandae*
21b. Stipules at least 10 mm long; fruit glabrous 22
22a. Fruit drying often shiny red-brown; secondary veins often drying reddish below; corolla often drying pink; Mexico through northern Costa Rica ..... (42) *P. mexiae*
22b. Fruit drying dull red-brown or red-black; secondary veins and corolla not as above; widespread ..... (44) *P. panamensis*
23a. Young stems obviously ferrugineous-pubescent or tomentose 24
23b. Young stems glabrous or minutely puberulent 28
24a. Calyx lobes conspicuous, ≥ 0.5 mm long 25
24b. Calyx lobes inconspicuous, ≤ 0.3 mm long 26
25a. Bark longitudinally grooved; stipules bilobed; inflorescence main axis 1.2–2 cm long; Chiriquí, Panama ..... (28) *P. boquetensis*
25b. Bark smooth; stipules not bilobed; inflorescence main axis (2.5–)4–6.5 cm long; Guatemala through Nicaragua ..... (33) *P. jinotegensis*
26a. Leaf blades (1–)1.5–5.2 cm long, the secondary veins inconspicuous to not evident below; Costa Rica and western Panama ..... (24) *P. parvifolia*
26b. Leaf blades at least (6–)9 cm long, the secondary veins conspicuous below 27
27a. Stipules (10–)20–80 mm long; corolla tube diameter greater than half its length; seed dorsal surface with 4 or 7–10 irregular longitudinal furrows; widespread ..... (44) *P. panamensis*
27b. Stipules 6–11 mm long; corolla tube diameter less than half its length; seed dorsal surface with 4–5 regular longitudinal furrows; widespread ..... (35) *P. nervosa*
28a. Persistent calyx cuplike, coriaceous, 1.5 mm long; Cocos Island, Costa Rica ..... (38) *P. cocosensis*
28b. Persistent calyx inconspicuous or a beak to 1 mm long 29
29a. Fruit when dry obovoid or, if ellipsoidal, at least 7 mm long and with inflorescence axes in 3–5 ranks 30
29b. Fruit when dry ellipsoidal or spherical, seldom over 7 mm long and then with inflorescence secondary axes in 5–7 ranks 32
30a. Leaf secondary veins 6–9(–11); Veracruz, Mexico, Costa Rica, and Panama ..... (45) *P. sarapiquensis*
30b. Leaf secondary veins at least 12 31
31a. Leaf blades wide (length/width approximately 2); southern Mexico through Nicaragua ..... (47) *P. trichotoma*
31b. Leaf blades narrow (length/width approximately 3); Oaxaca, Mexico ..... (44b) *P. panamensis* var. *ixtlanensis*
32a. Bark smooth 33
32b. Bark with longitudinal ridges, fissures, or furrows 34
33a. Fruit spherical; southern Mexico ..... (39) *P. dwyeri*
33b. Fruit narrow ellipsoidal; widespread ..... (35) *P. nervosa*
34a. Stipules no more than 10 mm long 35
34b. Stipules rarely as short as 10 mm 36
35a. Inflorescence secondary axes in 2 ranks; corolla tube 3–3.5 mm long; Guatemala ..... (27) *P. aguilarii*
35b. Inflorescence secondary axes in 3 (or 4) ranks; corolla tube 4–6 mm long; Nicaragua through western Panama ..... (37) *P. chiriquina*
36a. Fruit drying often shiny red-brown; secondary veins often drying reddish below; corolla often drying pink; Mexico through northern Costa Rica ..... (42) *P. mexiae*
36b. Fruit drying dull red-brown or red-black; secondary veins and corolla not as above; widespread ..... (44) *P. panamensis*
37a. Inflorescence a panicle of glomerules 38
37b. Inflorescence a panicle of cymes 47
38a. Leaf secondary veins > 10 39
38b. Leaf secondary veins ≤ 10 42
39a. Shrub or subshrub to 1.5 m tall; corolla lobes with apical appendages; eastern Panama ..... (53) *P. dressleri*
39b. Shrub or tree rarely less than 2 m tall; corolla lobes without appendages 40
40a. Young stems and leaf undersides densely ferrugineous-pubescent; fruit when dry 4 mm long; Guatemala, Nicaragua through Panama ..... (4) *P. micrantha*
40b. Young stems and leaf undersides glabrous, puberulent, or short ferrugineous-puberulent; fruit when dry not less than 4.5 mm long 41
41a. Inflorescence main axis (9–)13–26 cm long; leaves often drying chalky yellow-green above; fruit when dry 8–12(–13) mm long; southern Mexico and Guatemala ..... (11) *P. flava*
41b. Inflorescence main axis 1.5–12 cm long; leaves drying red-brown to green-brown; fruit when dry 4.5–8 mm long; widespread ..... (44) *P. panamensis*
42a. Bark smooth 43
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81b. Fruit when dry ellipsoidal, usually red-brown; widespread ..... (44) *P. panamensis*

Group 1. The *carthagenensis* Group

Shrub or sometimes small tree; young stems glabrous or sometimes puberulent or ferrugineous-pubescent; stipules usually sheathing, ovate (Fig. 2) or rarely lanceolate, the apex often acuminate or rarely biacuminate, uniform in color (except *P. viridis* with a darker central triangle), glabrous or sometimes puberulent or ferrugineous-pubescent, sometimes fringed, caducous (Fig. 1). *Leaf* blades usually obovate to elliptic, less commonly oblanceolate, *drying reddish or greenish brown or gray*; secondary veins 6–15 (except (18–)20–26 in *P. micrantha*) pairs, diverging 45°–70°(–85°), eucamptodromous (Fig. 3) or less commonly brochidodromous, the axils usually lacking domatia (except *P. quinqueradiata* and *P. viridis*; Fig. 4); tertiary veins orthogonal reticulate (except percurrent in *P. micrantha* and *P. neillii*; Fig. 5b). *Inflorescences* panicles of cymes or, less commonly, of glomerules (*P. micrantha* and *P. viridis*), pedunculate except for *P. lamarinensis* and *P. quinqueradiata* (Fig. 7g); *secondary axes usually in 2 (or 3) size-differentiated pairs per rank* (Fig. 7a) or sometimes in 4 equal axes per rank (*P. lamarinensis* and *P. quinqueradiata*) or sometimes in 1 pair per rank; bracts not conspicuously enlarged. *Corolla* tubes (1.5–)2–5 mm long, the lobes without apical extensions. *Fruit* when dry ellipsoidal or rarely obovoid; persistent calyx a beak (Fig. 9a) or not evident or rarely (*P. micrantha*) a tube ca. 0.5 mm long; *seed dorsal surface with (3–) 4–5 deep longitudinal furrows, the ventral surface with 2 deep or sometimes shallow longitudinal furrows* (Fig. 10a).

This group includes two pairs of very similar species plus the three other widespread species of unclear affinities, *Psychotria carthagenensis*, *P. clivorum*, and *P. viridis* (Figs. 13, 14). The first pair, the *P. quinqueradiata* complex, includes its widespread namesake plus *P. lamarinensis*, which is endemic to northern Costa Rica (Fig. 15); they share the following distinctive character states: inflorescences lacking peduncles, and inflorescence secondary axes 4 (not size-differentiated) per rank (Fig. 7g). The *P. micrantha* complex—including the widespread *P. micrantha* and *P. neillii*, this endemic to Caribbean southern Nicaragua and northern Costa Rica (Fig. 14)—shares a general ferrugineous vesture, biacuminate stipule apices, percurrent tertiary veins, and shallow longitudinal furrows on the seed ventral surfaces.

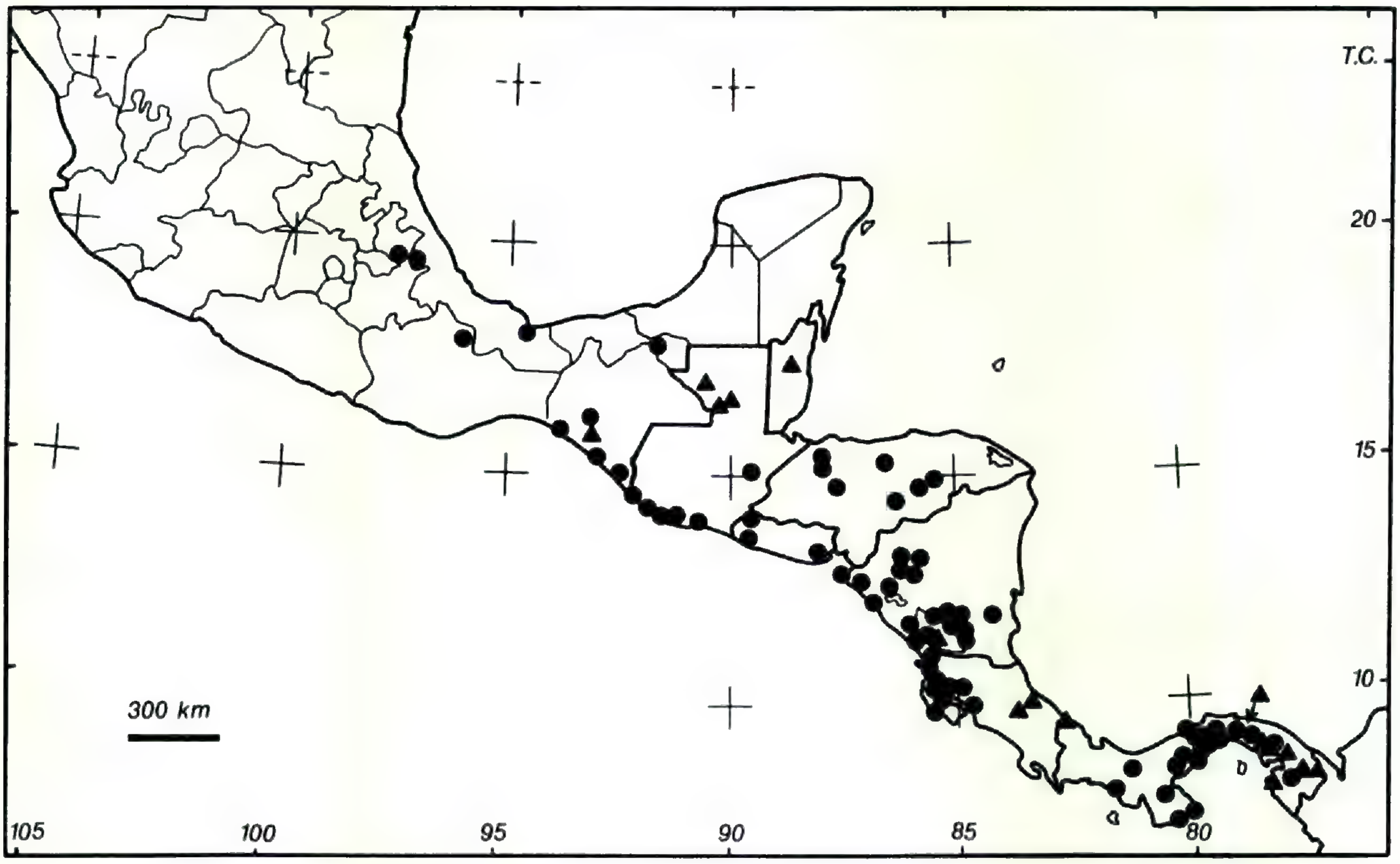

FIGURE 13. Distributions of *Psychotria carthagenensis* (circles) and *P. viridis* (triangles) in Mesoamerica.

Of the seven species in the group, four are apparently normally distylous and one, *Psychotria viridis*, is homostylous (at least in Mesoamerica). The two remaining species are too little collected to determine whether they are distylous or thrum-monomorphic.

1. Psychotria carthagenensis Jacquin, Enum. Syst. Pl. Carib. 16. 1760. Cf. also Select. Stirp. Amer. Hist. 174, fig. 22. 1788. *Uragoga carthagenensis* (Jacq.) O. Kuntze, Revis. Gen. Pl. 2: 959. 1891. *Psychotria carthaginensis* auctt. TYPE: Colombia. Bolívar: Cartagena (fr). (Type material not seen; locality and figure adequate to establish identity.) Figures 1, 2a, 3a, 7a, 9a, 10a, 13.

Psychotria sagraeana Urban, Symb. Antill. 7: 450. 1913. TYPE: Cuba. *Wright 3588* (syntype, US).

Shrub (0.5–)1–3(–6) m tall; young stems glabrous, the bark smooth to irregularly furrowed; stipules sheathing, ovate, 6–8 × 3–5 mm (Fig. 2), irregularly fringed, glabrous, caducous, leaving a pale ridge usually with red-brown fringe (Fig. 1). *Leaves* subsessile to petiolate; petioles to 5(–10) mm long, glabrous, flat above; blades membranous, obovate or rarely elliptic, the apex acuminate, the base attenuate, (6–)7.5–13(–16) × (2–)2.5–5.5(–6) cm, glabrous above and below, drying red-brown to red-gray; secondary veins 7–10 pairs, diverging 60°–70°(–75°), eucamptodromous (Fig. 3), constantly arcuate, prominulous below, glabrous, the axils lacking domatia or hairs; tertiary veins inconspicuous, orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of cymes (Fig. 7a); panicle branched to 3 or 4 degrees; main axis (2–)3.5–8 cm long, the peduncle 1.5–5 cm long; secondary axes in 3(–4) ranks, the first-rank axes 4, the longer pair 1–2.7 cm long, the shorter pair 0.4–1.5 cm long, the second-rank axes (2 or) 4, the longer pair 0.4–1.5 cm long, the shorter pair 0.3–0.8 cm long, the third-rank axes 2 (or 4), the longer pair 0.3–1.0 cm long, the shorter pair 0.1–0.3 cm long, the fourth-rank axes 2, 0.3–0.4 cm long; cymes branched to (2–)3 degrees; bracts and bracteoles prominent, triangular, 1 × 1 mm, the bracts sometimes enlarged to 8 mm long, caducous, glabrous, fringed. *Flowers* sessile to subpedicellate, the pedicels to 0.5 mm long; calyx cup-shaped, the tube 0.5 mm long, the lobes 5, triangular, minute, glabrous; corolla white, the tube cylindrical, 2.5–3 × 1.5 mm, white pubescent in throat, the lobes linear, 1.5–2 × 1 mm; stamens 5, the filaments 3 mm long in pins, 3.5–4.5 mm long in thrums, the anthers 1 mm long; style 5–5.5 mm long in pins, 3–3.5 mm long in thrums, the branches linear. *Fruit* when dry ellipsoidal, 4.5–5.5(–6) mm long, 3.5–4.5 mm diam., maturing red, drying red-brown; persistent calyx

not evident or sometimes a beak (Fig. 9a); seed dorsal surface with 4 deep longitudinal furrows, the ventral surface with 2 deep longitudinal furrows (Fig. 10a).

Distribution (Fig. 13). Common throughout Mexico and Central America, occurring also in Florida (cultivated), Cuba, Colombia, Venezuela, the Guianas, Ecuador, Peru, Brazil, Bolivia, Paraguay, Argentina, and Uruguay. In Central America it is found mostly in Pacific coastal lowlands at elevations of 0–1,400 m, mostly under 400 m, in tropical moist to premontane moist and wet forest with equatorial to tropical climates. It has been collected in flower December–August, primarily February–June, and in fruit throughout the year, primarily September–February.

Selected specimens examined. MEXICO. CHIAPAS: SE of Mapastepec, Guamúchil, 7 Dec. 1950 (st), *Enríquez 6795* (MEXU); bank of Río Salinas, 8 Feb. 1964 (fr), *Lundell 17801* (MO); Tonala, Mojarra, nr. beach, 27 Nov. 1947 (fr), *Matuda 17144* (F, MEXU, NY); Huehuetán, Islamapa, 27 June 1948 (early fr), *Matuda 18002* (MEXU—2 sheets). OAXACA: Tuxtepec, Chiltepec, 7 June 1965 (fl), *G. Martínez C. 13* (F, MEXU—2 sheets, US). PUEBLA: bosque ajenjibre, May 1952 (fl), *Ramírez 9* (MEXU—2 sheets). TABASCO: Balancán, Mercedes, 9–14 May 1939 (fl), *Matuda 3025* (A, F—2 sheets, MEXU). VERACRUZ: San Lorenzo Tenochtitlán, 29 Nov. 1967 (fr), *Chavelas et al. ES-2442* (ENCB, MEXU); 2–3 mi. NW of Acayucan, dirt rd. nr. Hwy. 180, 20 Feb. 1976 (fl), *Croat 32755* (MO). GUATEMALA. ESCUINTLA: Cuyuta, 60 m, Apr. 1890 (fl), *Donnell-Smith 2074* (K, US—2 sheets); Anubis, nr. Obispo, lowland forest, 20 Apr. 1937 (fl), *Muenscher 12370* (F, GH). IZABAL: Dept. Livingston, Río Dulce, 0 m, Mar. 1889 (fl), *Donnell-Smith 1821* (US). RETALHULEU: plains between Nueva Linda and Champerico, 120 m or less, 18 Feb. 1941 (fl), *Standley 87667* (F, US). SAN MARCOS: 1–2 mi. N of Ocós, palmetto flats, 3–5 m, 15 Mar. 1940 (fl), *Steyermark 37866* (F). SUCHITEPÉQUEZ: 7 mi. S of Tiquisate along rd. within 3 mi. of ocean, S of Alotenango Farm, 30–50 m, 19 June 1942 (early fr), *Steyermark 47770* (F). ZACAPA: trail between Río Hondo and waterfall, 250–400 m, 10 Oct. 1939 (fr), *Steyermark 29457, 29458* (F). HONDURAS. COMAYAGUA: unión del Río Yure con Río Humuya, 100 km N del ciudad Comayagua, 200 m, 22 Nov.–31 Dec. 1980 (fr), *C. Nelson et al. 6125* (TEFH). CORTÉS: orilla del Río Humuya, 40 km N de Santa Cruz de Yojoa, 100 m, 1–30 Nov. 1980 (fr), *C. Nelson et al. 5843* (TEFH); San Pedro Sula, 200 m, May 1888 (fl), *Thieme 5278* (US). OLANCHO: midway between Juticalpa and Campamento, along Río Juticalpa, 25 Feb. 1982 (fr), *Blackmore & Heath 1956* (TEFH); matorrales del Río Talgua cerca de la Escuela Granja Demonstrativa de Catacamas, 400 m, 26 Apr. 1957 (fl), *A. Molina R. 8337* (F, MO); Dulce Nombre de Culmí, 600 m, 1 May 1982 (fl), *D. Molina 109* (TEFH). YORO: nr. Coyoles, Aguan River valley, 28 June 1938 (fl), *Yuncker et al. 8040* (F, GH, K, MO, NY, US). EL SALVADOR. SAN MIGUEL: Laguna de Olomega, 75 m, 20 Feb. 1922 (fl), *Standley 21043* (GH, MO, US). SANTA ANA: N shore of Lago de Güija, Hda. La Barra, 470 m, 27 Feb. 1946 (fl), *Carlson 1009* (F). SONSONATE: vic. Sonsonate, 220–300 m, 18–27 Mar. 1922 (fl), *Standley 22336* (GH, NY, US). NICARAGUA. CHINANDEGA: al SW del Volcán Cosigüina, 29 Sep. 1981 (fr), *Fonseca 118* (MO); vic. Chichigalpa, 90 m, 12–18 July 1947 (fl), *Standley 11211* (F, US). CHONTALES: Río Las Vainillas, 12°01′N, 85°14′W, 150 m, 21 Jan. 1983 (fr), *Sandino 3939* (MO); vic. Juigalpa, 160 m, 4–13 June 1947 (fl), *Standley 9303* (F); rd. from Juigalpa NE to La Libertad, ca. 17.4 km NE of Río Mayales, 12°12′N, 85°17′W, 350–400 m, 23–25 Sep. 1977 (fr), *W. D. Stevens 4087* (MO); ca. 5.3 km W of Puente Lóvago, 12°00′N, 85°12′W, 150–170 m, 7 June 1981 (fl, early fr), *W. D. Stevens & Henrich 20521* (MO). ESTELÍ: Hwy. 1, ca. 19.2 km N of entrance into Estelí, 13°16′N, 86°21′W, 650–700 m, 25 Dec. 1978 (fr), *W. D. Stevens 11243* (MO); 25 Dec. 1978 (fl), *W. D. Stevens 11256* (MO). GRANADA: Laguna Juan Tallo, 11°45′N, 85°59′W, 65–70 m, 18 Dec. 1980 (fr), *P. P. Moreno 5449* (MO). JINOTEGA: Sta. Gertrudis, 30 km E de Jinotega, 1,000 m, 20 Jan. 1980 (fl), *Araquistain & Moreno 876* (MO); ca. 5 mi. E of El Jocote, 750 m, 6 Aug. 1977 (fl), *Croat 42883* (MO). LEÓN: ca. 4.0 km SW of La Paz Centro, 12°18′N, 86°42′W, 35 m, 31 May 1983 (fl), *W. D. Stevens 22161* (MO); Río Sinecapa at ford of road, 12°36′N, 86°28′W, 55 m, 15 Sep. 1977 (fr), *W. D. Stevens 3894* (MO). MATAGALPA: Hda. Sta. María de Ostuma, 1,300–1,600 m, 13 Dec. 1976 (st), *Tomlin 126* (MO). RÍO SAN JUAN: rd. to San Carlos 5 km SE of Río Oyate, 11°42′N, 84°57′W, 40 m, 28 Aug. 1983 (early fr), *Miller & Nee 1375* (MO); San Bartolo, 29 July 1972 (fr), *Robbins 6176* (F, GH, MO, NY). RIVAS: Punte de Tola, 40 m, 28 Feb. 1984 (fl), *M. Castro 57* (MO); Isla de Ometepe, N de Volcán Concepción, entrada a Los Angeles, 11°34′N, 85°37′W, 200–250 m, 10 Mar. 1981 (fr), *Sandino 447* (MO). ZELAYA: "San Agustín," al SE de Rama, 12°09′N, 84°12′W, 60 m, 22 May 1984 (fl), *Robleto 544* (MO). COSTA RICA. GUANACASTE: Nicoya, 200 m, 22 May 1903 (fl), *Cook & Doyle 672* (US); Finca La Pacifica, 5 km NW of Cañas, 80 m, 22 Feb. 1969 (fl), *Davidse & Pohl 1473* (F, MO, NY); playa de Sámara, al S de Nicoya, 10 m, 23 Mar. 1963 (fl), *A. Jiménez M. 520* (CR, F); Santa Rosa National Park, 10°48′N, 85°40′W, 0–20 m, 21 Jan. 1978 (fr), *Liesner 4250* (CR, MO); Río Sapoá, 4 km N of La Cruz, 11°06′N, 85°35′W, 2 Feb. 1978 (fr), *Liesner 4863* (MO); Comelco, 5 km NW of Bagaces, 150 m, 30 Jan. 1973 (fl), *Opler 1683* (CR, F, MO—2 sheets); Ballena Rd., 17 July 1918 (early fr), *Rowlee & Rowlee 166* (US); vic. Líbano, 260–360 m, 15 Jan. 1926 (fr), *Standley & Valerio 44926* (US); banks of Río Corubici, 17 Aug. 1967 (fr), *Whitmore 28* (DUKE, F, MO, NY). PUNTARENAS: 8 km N of Barranca, 1 km N of Miramar turn-off, Qda. Negros, 10°02′N, 84°45′W, 20–30 m, 30 Apr. 1983 (fl), *Liesner et al. 15125* (CR, MO). PANAMA. CANAL AREA: Barro Colorado Island, 23 May 1970 (fl), *Croat 10347* (DUKE, F, MO, NY); Fort Clayton, Apr. 1965 (fl), *Dwyer & Robyns 8* (MO—2 sheets); N of Gamboa, 9°05′N, 79°45′W, 25 m, 22 Mar. 1983 (fl), *Hamilton 3677* (CR, MO); Parque Soberania nr. Las Cruces trail, 9°15′N, 79°45′W, 12 Mar. 1983 (fl, fr), *Hamilton et al. 3296* (MO); Mount Hope, 7 Apr. 1921 (fl), *Heriberto 74* (US); 1 mi. from Gaillard Hwy. on track off Chiva Chiva Road, 9°00′N, 79°37′W, 0–25 m, 26 Apr. 1982 (fl), *Knapp & Schmalzel 4841* (MO); Balboa, Nov. 1923–Jan. 1924 (fr), *Standley 25501* (GH, US). CHIRIQUÍ: Río Viguí, border of Chiriquí and Veraguas at Panam. Hwy., 8°10′N, 81°30′W, 100 m, 10 Jan. 1983 (fr), *Stein et al. 1319*

(MO). COCLÉ: El Valle de Antón, 300–600 m, 2–3 Dec. 1967 (fr), *Lewis et al. 3543* (MO); Chorrerita, 21 Sep. 1973 (fr), *L. Medina 6* (DUKE); vic. Penonomé, 15–300 m, 23 Feb.–22 Mar. 1908 (fr), *R. S. Williams 59* (NY—2 sheets, US). DARIÉN: nr. Yaviza, ca. 0 m, 8 Jan. 1975 (fr), *Gentry 13490* (GH, MO). HERRERA: vic. Ocú, Río Pasoancho, 19 Feb. 1963 (fl, fr), *Stern et al. 1735* (MO, US). LOS SANTOS: Pedasí, bank of beach, 10 Aug. 1962 (early fr), *Dwyer 2489* (MO, US); Río Tonosí, vic. Tonosí, 25 May 1967 (fl), *Lewis et al. 1540* (DUKE, MO); along Río Tonosí ca. 9 mi. N of Tonosí, 17 July 1970 (early fr), *Luteyn & Foster 1387* (DUKE, F, MO). PANAMÁ: Río Majé, ca. 30 speedboat minutes from confluence with Río Bayano, 30 m, 19 Apr. 1976 (fl), *Croat 34403* (MO, NY); Cermeño, 7 Apr. 1965 (fl), *Dwyer 6588* (MO); 2 mi. W of Chepo, 6 Apr. 1972 (fl), *Gentry 4971* (F, MO, NY); Río Ipetí, S of Panam. Hwy., 9°03′N, 78°25′W, 100 m, 17 Sep. 1982 (st), *Hamilton & D'Arcy 1336* (MO); falls of La Chorrera, 5 Apr. 1969 (fl), *Lewis et al. 5205* (MO); Río Crystal de Nuevo Arraiján, 4 Dec. 1971 (fr), *L. Salazar 15* (DUKE, MO); Cerro Azul, nr. lake, 600 m, 27 May 1966 (fl), *Tyson & Blum 4066* (MO); marshy area 2 mi. S of Tocumen Airport, 25 July 1969 (early fr), *Tyson & Clewell 5875* (DUKE, MO). VERAGUAS: just S of Santa Fe, 450 m, 17 Nov. 1973 (fr), *Nee 8036* (MO, US).

Modern authors have perpetuated an early misspelling of the specific epithet by spelling it "*carthaginensis*" instead of the correct original "*carthagenensis*" (D. Nicolson, pers. comm.). A collection by Vahl, from the type region of Cartagena, resides in Berlin (*Willdenow 4083*) and has been annotated as *P. carthagenensis*; it is, however, *P. nervosa* and is clearly not the type of Jacquin's species.

Psychotria carthagenensis may be recognized by its obovate leaves drying dull red-brown, eucamptodromous secondary venation (Fig. 3), secondary inflorescence axes in two unequal pairs per rank (Fig. 7a), corolla drying red, ellipsoidal fruit drying reddish, and seed in cross section with the dorsal surface having four deep furrows and the ventral surface having two deep furrows (Fig. 10a). It is expected that careful analysis will reveal that this species exhibits more primitive character states than any other neotropical species in the subgenus. Mexican and Guatemalan collections suggest that the leaf blades are larger there than elsewhere in Central America.

2. Psychotria clivorum Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 87. 1944. Based on *Psychotria limonensis* var. *angustifolia* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 17: 282. 1937 (see protologue of *P. clivorum*). TYPE: Guatemala. Suchitepéquez: Finca Mocá, 1,020 m, 7 Jan. 1935 (fl), *Skutch 2073* (holotype, F; isotype, A). Figure 14.

Shrub or small tree, 2.5–6 m tall; young stems red-brown puberulent, the bark smooth to irregularly furrowed; stipules sheathing, ovate, the apex sometimes biaristate, 8–9(–14) × 4–4.5(–5) mm, glabrous to puberulent, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 4–10 mm long, glabrous, grooved above; blades membranous, elliptic, the apex cuspidate, the base attenuate, (9–)12–22 × (3–)4–6.5(–8.5) cm, glabrous above, glabrous below with the midvein sometimes sparsely puberulent, drying red-gray to gray-green; secondary veins 9–13 pairs, diverging 55°–70°, eucamptodromous to brochidodromous, straight then arcuate near margin, prominulous below, glabrous to minute puberulent below, the axils lacking domatia or hairs; tertiary veins evident to conspicuous, orthogonal reticulate to slightly percurrent. *Inflorescences* terminal or pseudoaxillary, elongate panicles of cymes; panicle branched to 4 degrees; main axis 6–8.5 cm long, the peduncle 2.5–5 cm long; secondary axes in (3–)4(–5) ranks, the first-rank axes 4 or rarely 2, the longer pair 1.5–2.5 cm long, the shorter pair 0.6–1.5 cm long, the second-rank axes 4, the longer pair 0.8–1.3 cm long, the shorter pair 0.4–1 cm long, the third-rank axes 2 or 4, the longer pair 0.4–0.7 cm long, the shorter pair 0.1–0.3 cm long, the fourth-rank axes 2, 0.3–0.6 cm long, the fifth-rank axes 2, 0.3 cm long; cymes branched to 1–3 degrees; bracts linear, to 2 mm long, puberulent; bracteoles minute, irregular, to 0.6 mm long, puberulent. *Flowers* sessile to subpedicellate, the pedicels to 1 mm long; calyx cup-shaped, the tube 0.3–0.5 mm long, the lobes 5, triangular to barely evident, to 0.3 mm long, puberulent; corolla white, the tube cylindrical to campanulate, 2–2.5 × 1.5 mm, white pubescent in throat, the lobes 5, linear, 2 × 0.8 mm; stamens 5, the filaments 2.5 mm long in pins, 3.5–4 mm long in thrums, the anthers 1 mm long; style 3.5–4 mm long in pins, 2–2.5 mm long in thrums, the branches short, clublike. *Fruit* when dry ellipsoidal, 5–6 mm long, 4–4.5 mm diam., maturing red, drying deep red-brown; persistent calyx not evident or sometimes a beak; seed dorsal surface with 4 deep longitudinal furrows, the ventral surface with 2 deep longitudinal furrows.

Distribution (Fig. 14). Not commonly collected but widespread from southern Mexico to western Panama, occurring at low elevations, 0–200 m, in Veracruz and Oaxaca, Mexico, and Bocas del Toro, Panama, and higher elevations, 600–1,400 m, in other parts of the range. It has been found in tropical moist and premontane rain

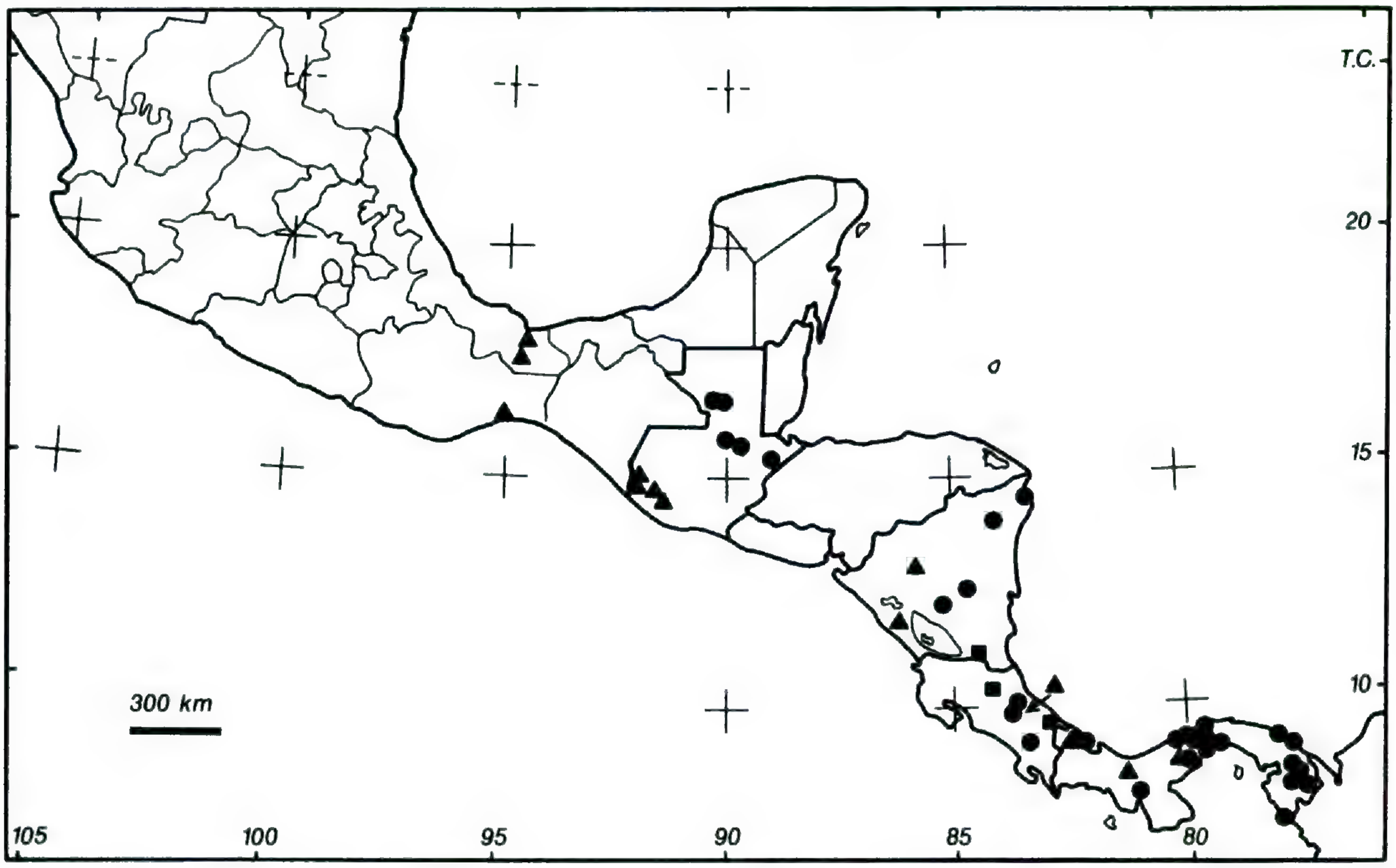

FIGURE 14. Distributions of *Psychotria clivorum* (triangles), *P. micrantha* (circles), and *P. neillii* (squares) in Mesoamerica.

forest with equatorial to tropical climate. It has been collected in flower January–May, especially March–April, and in fruit November–March.

Selected specimens examined. MEXICO. OAXACA: Juchitán, Montaña de la Pedrera, Palomares, 90 m, 14–17 Apr. 1970 (fl), *MacDougall s.n.* (NY). VERACRUZ: Mpio. Hidalgotitlán, del km 3 al km 5 del camino de Plan de Arroyos al Alvaro Obregón, 17°15′N, 94°40′W, 130–150 m, 2 Apr. 1974 (fl), *B. Dorantes 2731* (MEXU—2 sheets, MO); Mpio. Hidalgotitlán, campamento Hermanos Cedillo a 2 km por el camino a La Laguna, 150 m, 1 Apr. 1975 (fl), *Ortíz & Martiniano 71* (MEXU—3 sheets); Mpio. Hidalgotitlán, brecha Hermanos Cedillo–Agustín Melgar, 17°13′N, 94°35′W, 153 m, 26 Apr. 1974 (fl), *B. Vázquez 418* (MEXU, MO); Fortuño, Coatzacoalcos River, 30–50 m, Mar. 1937 (fl), *Ll. Williams 8677* (F). GUATEMALA. QUEZALTENANGO: between Finca Pirineos and Finca Soledad, lower south-facing slopes of Volcán Santa María, between Santa María de Jesús and Calahuaché, 1,300–1,400 m, 5 Jan. 1940 (fr), *Steyermark 33543* (F, US). SAN MARCOS: Río Mopá, below Rodeo, 600 m, 14 Mar. 1939 (fl), *Standley 68772, 68783* (F); Volcán Tajumulco, Finca El Porvenir, along Río Cabús above Potrero Matasán, 1,000–1,300 m, 12 Mar. 1940 (fl), *Steyermark 37628* (A, F). NICARAGUA. CARAZO: 1 km E of San Marcos, ravine at edge of coffee plantation, 2 May 1976 (fl), *Neill 285* (MO). MATAGALPA: Macizo de Peñas Blancas, Finca San Sebastián, 1,050 m, 24 Nov. 1981 (fr), *Tellez et al. 5156* (MO), *5200* (MEXU). COSTA RICA. CARTAGO: Tucurrique, 650–700 m, Mar. 1899 (fl), *Tonduz 13018* (US). PANAMA. BOCAS DEL TORO: vic. Almirante, Jan.–Mar. 1928 (fr), *Cooper 453* (F); Jan.–Mar. 1928 (fl), *Cooper 566* (F, GH, NY). COCLÉ: El Valle, 800–1,000 m, 28 June 1967 (early fr), *Duke 13151* (MO—3 sheets); Cerro Pilón, to 930 m, 19 Jan. 1968 (fr), *Dwyer 8326* (MO); Cerro Pilón, 600–800 m, 28 Mar. 1969 (fr), *Dwyer et al. 4553* (MO). VERAGUAS: N of Santa Fe, Cerro Tute, Escuela Agricola Alto de Piedra, 1,000–1,200 m, 4 Feb. 1977 (fr), *Folsom 1603* (MO); 17 Oct. 1974 (early fr), *Mori & Kallunki 2541* (MO).

Psychotria clivorum may be recognized by its elliptic leaves drying red-gray to gray-green, secondary veins well-spaced and diverging 55°–70°, inflorescence secondary axes in two unequal pairs per rank, the higher ranks decreasing in size uniformly, corolla drying red, ellipsoidal fruit, and seed cross section with four deep longitudinal furrows on the dorsal surface and two deep longitudinal furrows on the ventral surface. *Psychotria clivorum* shares many character states with *P. carthagenensis*, but the former differs in having stipules often biaristate, larger elliptic (versus obovate) leaf blades, more secondary veins, often brochidodromous secondary venation, and larger inflorescences.

Stipule morphology varies geographically, as Guatemalan plants appear more often biaristate while Nicaraguan plants have exceptionally large stipules. Secondary venation is generally eucamptodromous, but in Nicaragua the secondary loops are sufficiently robust to appear brochidodromous.

3. Psychotria lamarinensis C. Hamilton, Phytologia 64: 227. 1988. TYPE: Costa Rica. Ala-

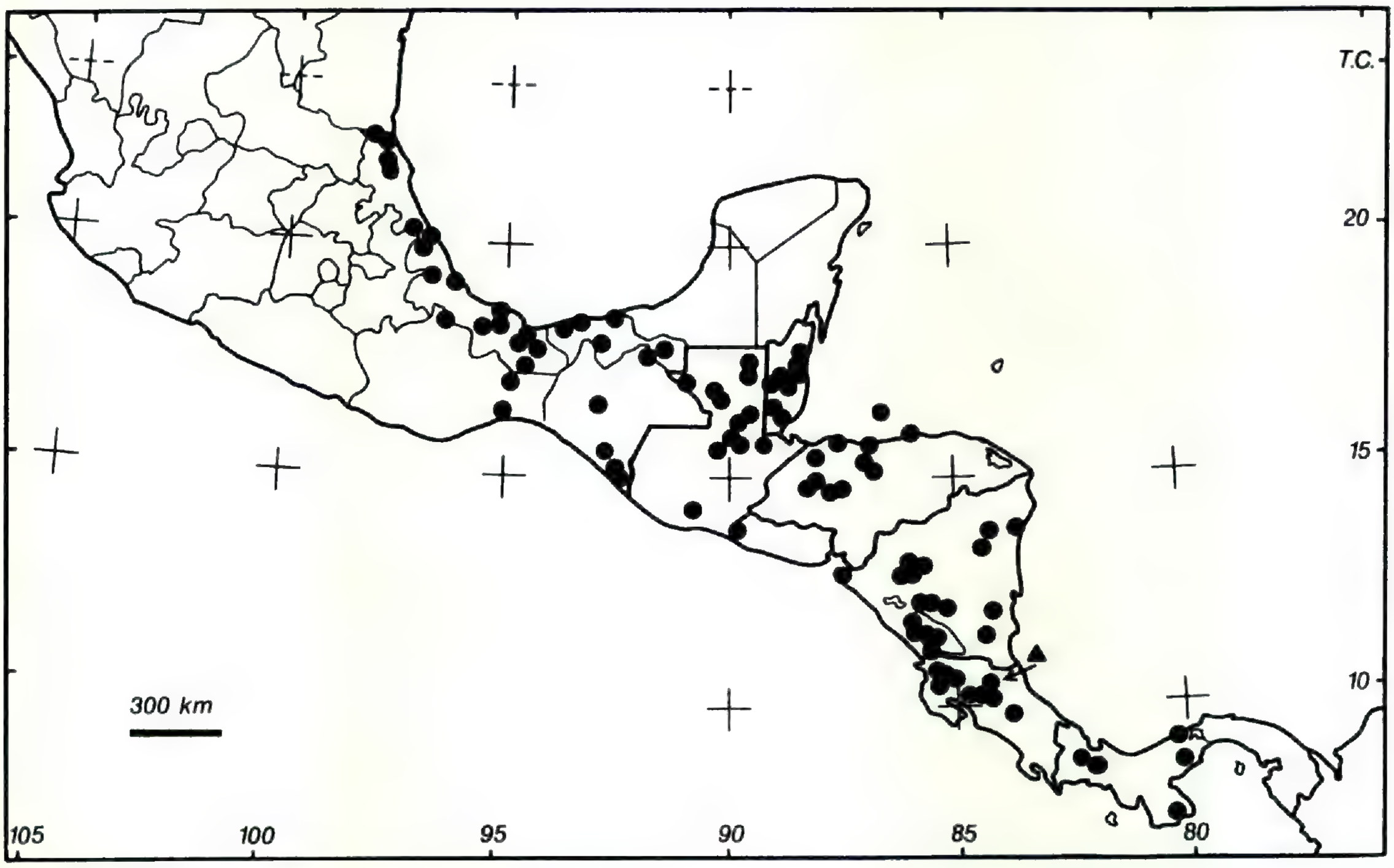

FIGURE 15. Distributions of *Psychotria lamarinensis* (triangle) and *P. quinqueradiata* (circles) in Mesoamerica.

juela: E of Río San Rafael, W of La Marina, 10°23′N, 84°23′W, 500 m, 19 May 1968 (fl), *Burger & Stolze 5062* (holotype, NY; isotype, MO). Figure 15.

Shrub 1.8–2 m tall; young stems glabrous, the bark pale, smooth; stipules ovate, 12 × 8 mm, glabrous, caducous, leaving a pale ridge with thick red-brown fringe. *Leaves* petiolate; petioles 5–7 mm long, glabrous, terete; blades membranous, elliptic, the apex acuminate, the base attenuate to attenuate-truncate, (13–)16–20 × (5–)7.5–9.5 cm, glabrous above and below, drying green-brown above, red-brown below; secondary veins 9–11 pairs, diverging 70°–85°, eucamptodromous, constantly arcuate, elevated below, glabrous, the axils lacking domatia or hairs; tertiary veins evident, orthogonal reticulate. *Inflorescences* terminal, condensed globose panicles of cymes; panicle branched to 3 degrees; main axis 1.5–2 cm long, the peduncle lacking; secondary axes in 2–3 ranks, the first-rank axes 4, subequal, 0.5–1.5 cm long, the second-rank axes 4, subequal, 0.4–0.7 cm long, the third-rank axes 4, subequal, 0.2 cm long; cymes branched to 1–2 degrees; bracts triangular, 2 mm long, glabrous; bracteoles not evident. *Flowers* pedicellate, the pedicels 0.5–1.5 mm long; calyx cup-shaped, 0.5 mm long, the lobes not evident to barely evident, glabrous; corolla white, the tube cylindrical, 3 × 1 mm, white pubescent in throat, the lobes 5, linear with 1.5 mm linear extension from near apex, 2 × 1 mm; stamens 5, the filaments not seen in pins, 3.5–4 mm long in thrums, the anthers 0.7 mm long; style not seen in pins, 2–2.5 mm long in thrums, the branches linear. *Fruit* not seen.

Distribution (Fig. 15). Known only from the type locality near La Marina, Alajuela, Costa Rica, at ca. 500 m elevation in a region of tropical wet to premontane wet forest with equatorial-mountainous climate. It was collected in flower on May 19.

Additional specimen examined. COSTA RICA. ALAJUELA: E of Río San Rafael, W of La Marina, 10°23′N, 84°23′W, 500 m, 19 May 1968 (fl), *Burger & Stolze 5069* (MO, NY).

Psychotria lamarinensis may be recognized by its large, broad-elliptic leaves with the base narrowly subcordate, reduced globose inflorescence drying red-brown, and broad-ovate stipules. *Psychotria lamarinensis* may be a local derivative from *P. quinqueradiata*, from which the former differs in having much larger leaves with secondary veins diverging 70°–85° instead of 45°–60° and shorter (3 mm vs. 4–5 mm) corolla tubes.

Only a short-style flower morph has been seen, but only two flowering collections do not suffice to suggest that the species is thrum-monomorphic.

4. Psychotria micrantha Kunth in Humboldt, Bonpland and Kunth, Nov. Gen. Sp. 3: 363, pl. 284. 1819. *Uragoga micrantha* (Kunth) Kuntze, Revis. Gen. Pl. 2: 961. 1891. *Mapouria micrantha* (Kunth) Wernham, Kew Bull. 1914: 69. 1914. TYPE: Peru(?) (fl), *Bonpland s.n.* (holotype, P, n.v., fragment, F). Figure 14.

Psychotria rufescens Roemer & Schultes, Syst. Veg. 5: 192. 1819, non Kunth in H.B.K. (which is a synonym of *P. nervosa* Sw.), Nov. Gen. Sp. 3 (fasc. 12): 364. 1819. TYPE of *P. rufescens* Roem. & Schultes: Colombia. Río Magdalena, *Humboldt s.n.* (holotype, B—*Willdenow 4107*).

Tree 1.5–5(–8) m tall; young stems densely ferrugineous-pubescent, the bark slightly furrowed longitudinally; stipules sheathing, ovate, the apex biacuminate, 13–18(–22) × (5–)6–7(–8) mm, ferrugineous-pubescent, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 1–2.2 cm long, ferrugineous, grooved above; blades membranous, elliptic, the apex acuminate, the base cuneate to attenuate, (12–)20–32 × (5–)8–13 cm, puberulent above, the veins ferrugineous-pubescent, ferrugineous-pubescent below, drying green-brown to red-brown; secondary veins (18–)20–26 pairs, diverging (60°–)65°–70°, eucamptodromous to sometimes brochidodromous, constantly arcuate or straight then arcuate near margin, elevated below, ferrugineous, the axils lacking domatia or hairs; tertiary veins evident to conspicuous, percurrent, the quaternaries orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of glomerules; panicle branched to 4 degrees; main axis 10.5–17 cm long, the peduncle 6–8.5 cm long; secondary axes in 3–4 ranks, the first-rank axes 4 or 6, the long pair 2.5–5.5 cm long, the medium pair 1–2.5 cm long, the short pair 0–0.5 cm long, the second-rank axes 4 or 6, the long pair 0.5–2 cm long, the medium pair 0.2–0.8 cm long, the short pair 0–0.2 cm long, the third-rank axes 4, the longer pair 0.4–0.8 cm long, the shorter pair 0–0.4 cm long, the fourth-rank axes 4, the longer pair 0.4 cm long, the shorter pair 0.1 cm long; bracts ovate-acuminate, to 6 mm long, ferrugineous-pubescent. *Flowers* sessile; calyx cup-shaped, the tube 0.2–0.5 mm long, the lobes 5, barely evident to triangular, to 0.3 mm long, white pubescent without; corolla white, the tube cylindrical, 2 × 1 mm, short white pubescent in throat, the lobes 5, ovate, 1–1.5 × 1 mm; stamens 5, the filaments 1.5 mm long in pins, 3 mm long in thrums, the anthers 1 mm long; style 3.5–4 mm long in pins, 2–2.5 mm long in thrums, the branches linear. *Fruit* when dry ellipsoidal, 4 mm long, 2.5–3(–3.5) mm diam., maturing red, drying black or sometimes red-brown, sparsely ferrugineous; persistent calyx a tube ca. 0.5 mm long, drying pale brown; seed dorsal surface with 4–5 deep longitudinal furrows, the ventral surface with 2 shallow longitudinal furrows.

Distribution (Fig. 14). Guatemala and Nicaragua through Panama, mostly on the Caribbean side, at elevations of 0–600 m in usually tropical moist to wet forest with equatorial to sometimes tropical-equatorial climate. It occurs also in Colombia, Venezuela, Ecuador, Peru, and Bolivia. *Psychotria micrantha* has been collected in flower April–September, December, and January, and in fruit July–March, primarily September–December.

Selected specimens examined. GUATEMALA. ALTA VERAPAZ: Sebol, WNW of the village, nr. Río Sebol, 11 July 1964 (fl), *Contreras 5281* (LL); Chahal, Sepur Ranch, bordering Río Chahal, 8 Oct. 1968 (fr), *Contreras 7866* (LL, NY). IZABAL: trail from Los Amates to Izabal, 31 May 1919 (fl), *Blake 7755* (US). PETÉN: Río Pucte, on La Libertad trail ca. 4.5 km ENE of El Pucte Camp, 3 Mar. 1964 (fr), *Lundell 18245* (LL, MEXU); forest between Finca Yalpemech along Río San Diego and San Diego on Río Cancuen, 50 150 m, 25 Mar. 1942 (st), *Steyermark 45415* (F, US). NICARAGUA. CHONTALES: vic. La Libertad, 500–700 m, 29 May–1 June 1947 (fl), *Standley 9097* (F). ZELAYA: Guamil o breñas a lo largo del Río Grande, 24 Apr. 1949 (fl), *A. Molina R. 2370* (F, GH); Comarca del Cabo, 25 km al S de Tronquera cerca de Río Wawa, San Mateo, 35 m, 22 Aug. 1965 (fl), *A. Molina R. 15088* (F, NY, US); Mpio. de Siuna, Danlí, 100–130 m, 31 Sep. 1982 (fr), *Ortíz 204* (MO). COSTA RICA. CARTAGO: El Bron, entre Turrialba y Florencia, 600 m, 16 July 1965 (fl), *A. Jiménez M. 3308* (F); Turrialba, terrenos del Instituto, 600 m, 26 Oct. 1949 (fr), *León 1872* (US); Turrialba, Puente Cajón, 625 m, 31 May 1972 (fl), *Poveda 129* (MO). LIMÓN: Goldengrove, drenaje de Río Reventazón, 15 m, 23 Oct. 1951 (fr), *Shank & Molina 4399* (F, GH, US). PUNTARENAS: nr. Buenos Aires, between Qda. Grande and Qda. Guajiniquil, 350 m, 1 Mar. 1966 (fr), *A. Molina R. et al. 18146* (CR, F, MO, NY). PANAMA. BOCAS DEL TORO: Milla, 26 July 1971 (fl, fr), *Croat & Porter 16272* (ENCB, F, MO, NY); Old Bank Island, 23 Jan. 1941 (fl, fr), *Wedel 1869* (GH, MO); Little Bocas, Chiriquí Lagoon, 9 July 1941 (fl), *Wedel 2508* (F, GH, MO). CANAL AREA: Barro Colorado Island, 20 Sep. 1968 (fr), *Croat 6235* (DUKE, F, MO, NY); 25 June 1968 (fl), *Foster 641* (DUKE); rd. between Locks and Fort Sherman, 10 July 1971 (fl), *Croat 15361* (MO, NY); Madden Dam, Boy Scout Rd., 23 July 1968 (fl), *Dwyer & Lallathin 8822* (F, MO, NY); along old Las Cruces Trail between Fort Clayton and Corozal, 31 Dec. 1923 (fr), *Standley 29198* (US). COLÓN: N side of Río Guanche, 0.5 km upstream Puerto Pilón–Portobelo Hwy. bridge, 5–30 m, 22 Sep. 1973 (early fr), *Nee 7104* (F, GH, MO); Palmas Bellas, 30 May 1971 (fl), *Thoms 35* (DUKE, F, MO). DARIÉN: confluence of Río Chucunaque and Río Canglón, 5 July 1962 (fl), *Duke 5114* (GH, MO, US); Río Chico across from

Boca de Tesca, 18 July 1962 (fl), *Duke 5217* (GH, MO, US); Cocalita, 13 Aug. 1963 (fl), *Dwyer 4398* (US); Río Paya, trail from Paya to Pucro, 11 June 1959 (fl), *Stern et al. 222* (GH, MO, US); trail between Cana and Boca de Cupe, vic. El Real, 16 June 1959 (fl), *Stern et al. 611* (GH, MO, US). PANAMÁ: 2 mi. above Interamerican Hwy. to Cerro Campana, 10 Sep. 1970 (early fr), *Croat 12045* (F, MO); E of Río Tocumen, 11 Dec. 1923 (fr), *Standley 26604* (A). SAN BLAS: headwaters of Río Mulatupo, 17 Aug. 1967 (early fr), *Elias 1729* (GH, MEXU, MO, US); mainland opposite Ailigandi, 7–8 Dec. 1966 (fl, fr), *Lewis et al. 156* (F, GH, MO, NY, US). VERAGUAS: Río de Jesús, Río Trinidad, 3 Aug. 1961 (fl), *Dwyer 1319* (GH).

Psychotria micrantha may be recognized by its densely ferrugineous vesture, large (20–32 × 8–13 cm) elliptic leaves with many (20–26) secondary veins and conspicuous percurrent tertiary veins, large panicles of glomerules, and small (4 × 2.5–3 mm) pubescent ellipsoid fruits.

5. Psychotria neillii C. Hamilton & Dwyer in C. Hamilton, Phytologia 64: 231. 1988. TYPE: Nicaragua. Río San Juan: Río Sábalo, 2 km al O de Sta. Eduviges, 11°03′N, 84°29′W, 80 m, 18 Feb. 1984 (fl, fr), *P. P. Moreno 23060* (holotype, MO). Figure 14.

Shrub or small tree, 1–4 m tall; young stems ferrugineous-pubescent, the bark smooth; stipules sheathing, lanceolate, the apex biacuminate, 10–14 × 3–5 mm, ferrugineous-pubescent, ciliate, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 4–8 mm long, ferrugineous-pubescent, terete; blades membranous, oblanceolate, the apex acuminate, the base cordate, 10–18 × 4–7.5 cm, glabrous above, the midvein basally ferrugineous-pubescent, sparsely ferrugineous-pubescent below, drying green-brown to red-brown; secondary veins 12–15 pairs, diverging (60°–)65°–75°, brochidodromous, constantly arcuate, elevated below, ferrugineous-pubescent below, the axils lacking domatia or hairs; tertiary veins evident to conspicuous, percurrent, the quaternaries orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of cymes; panicle branched to 3–4 degrees, the axes delicate; main axis (6–)9–15 cm long, the peduncle (3.5–)6–8 cm long; secondary axes in 3 ranks, the first-rank axes 4, the longer pair (1.5–)3–6 cm long, the shorter pair (0.8–)1–3.5 cm long, the second-rank axes 2 or 4, the longer pair (0.8–)1.4–3.2 cm long, the shorter pair ca. 1.5 cm long, the third-rank axes 2, 0.6–1.4 cm long; cymes branched to 2–3 degrees; bracts triangular, 4 mm long, ferrugineous-pubescent; bracteoles linear, 0.5 mm long, ferrugineous-pubescent. *Flowers* sessile to pedicellate, the pedicels to 1 mm long; calyx cup-shaped, the tube 0.3 mm long, the lobes 5, triangular, 0.2 mm long, ferrugineous-pubescent; corolla cream, the tube cylindrical, 1.5–2 × 1 mm, white pubescent in throat, red-brown pubescent without, the lobes 5, triangular, 1 × 0.8 mm; stamens 5, the filaments not seen in pins, 2.5 mm long in thrums, the anthers 0.8 mm long; style not seen in pins, 2 mm long in thrums, the branches linear. *Fruit* when dry ellipsoidal to obovoid, 5–7 mm long, 3–3.5 mm diam., maturing red, drying dark red-brown, sometimes puberulent; persistent calyx inconspicuous or a minute beak; seed dorsal surface with 3 deep longitudinal furrows, the ventral surface with 2 shallow longitudinal furrows.

Distribution (Fig. 14). Known from Caribbean coastal Costa Rica and just north into Nicaragua, at 80–400 m elevation in tropical moist to wet forest with equatorial climate. It has been collected in flower in January, February, and April and in fruit in February and May.

Additional specimens examined. NICARAGUA. RÍO SAN JUAN: nr. Caño Chontaleño, 20 km NE of El Castillo, 200 m, 18–21 Apr. 1978 (fl), *Neill & Vincelli 3503* (MO). COSTA RICA. HEREDIA: Magsasay, entre el campamento Canta Rana y Río Peje, 400 m, 14 Jan. 1983 (fl), *Chacón 76* (MO). LIMÓN: 7 km SW of Bribrí, 100–250 m, 4 May 1983 (early fr), *L. D. Gómez et al. 20357* (MO—2 sheets).

Psychotria neillii may be recognized by its great resemblance to *P. micrantha* and its delicate ferrugineous-pubescent inflorescence axes. *Psychotria neillii* differs from *P. micrantha* in having smaller (10–18 vs. 20–32 cm long) mature leaves with fewer (12–15 vs. 20–26) secondary veins, delicate inflorescence axes, and larger (5–7 mm vs. 4 mm long) fruit.

All three flowering collections are thrums; additional collections are necessary to determine whether the species is distylous or thrum-monomorphic.

6. Psychotria quinqueradiata Polakowsky, Linnaea 41: 570. 1877. *Uragoga quinqueradiata* (Polak.) Kuntze, Revis. Gen. Pl. 2: 962. 1891. TYPE: Costa Rica: prope San José et in silvis primaevis Carpinterae, June–Aug. (fl), *Polakowsky 135* (lectotype, B, destroyed, photos, GH, US). Figures 7g, 15.

Mapouria obovata Oersted, Amér. Centr. 17, t. 14, figs. 3, 4. 1863. *Psychotria obovata* (Oersted) Hemsley, Biol. Cent.-Amer. Bot. 2: 50. 1881, *non Psychotria obovata* Ruiz & Pavón, Fl. Peruv. Prodr. 2: 58. 1799. *Uragoga oerstedtiana* Kuntze, Revis. Gen. Pl. 2: 957. 1891. *Psychotria oerstediana* (Kuntze)

Standley, Contr. U.S. Natl. Herb. 23: 1390. 1926. TYPE: Mexico: *Liebmann s.n.* (holotype, C, n.v.).

Psychotria morae Polakowsky, Linnaea 41: 570. 1877. *Uragoga morae* (Polak.) Kuntze, Revis. Gen. Pl. 2: 961. 1891. TYPE: Costa Rica: San José, June 1875 (fl), *Polakowsky 171* (holotype, B, destroyed, photos, GH, US).

Shrub 0.5–2(–5) m tall; young stems glabrous, the bark pale, irregular; stipules sheathing, ovate-acuminate, 4–6 × 2–5 or 10–15 × 8 mm, glabrous, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 0.3–1 cm long, glabrous, grooved above; blades membranous to subcoriaceous, obovate to oblanceolate or medium- to broad-elliptic, the apex acute to short (–long)-acuminate, the base narrow-subcordate or attenuate, the margin sometimes crenate, (6–)9–15(–16) × (2–)3–7.5 cm, glabrous above and below, drying red-brown to green-brown, paler below; secondary veins 6–9(–10) pairs, diverging 45°–60°, eucamptodromous to usually brochidodromous, the secondary loops usually far from margin, increasingly arcuate toward margin, prominulous below, glabrous, the axils with domatia sometimes with tufts of hairs below; tertiary veins evident, orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of cymes (Fig. 7g), sometimes reduced to appear as fascicles of flowers behind terminal stipule; panicle branched to (2–)3 degrees; main axis 0.5–3.5 cm long, the peduncle lacking or rarely present, ca. 1.5 mm long; secondary axes in (1–)2(–3) ranks, the first-rank axes 4, subequal to equal, 0.5–3.5 cm long, the second-rank axes 4, subequal, 0.1–0.6 cm long, the third-rank axes 4, equal, 0.1–0.2 cm long; cymes branched to 1–2 degrees; bracts and bracteoles not evident. *Flowers* pedicellate, the pedicels 0.5–1 mm long; calyx cup-shaped, the tube 0.3–0.5 mm long, the lobes not evident or 5, barely evident, glabrous; corolla white, the tube cylindrical, 4–5 × 1–1.5 mm, white pubescent in throat, the lobes 5, lanceolate, 1.5–2 × 1 mm; stamens 5, the filaments 3–3.5 mm long in pins, 5.5–6.5 mm long in thrums, the anthers 1–1.5 mm long; style 5.5–7.5 mm long in pins, 4–5 mm long in thrums, the branches linear. *Fruit* when dry ellipsoidal, 5.5–7 mm long, 4–5.5 mm diam., maturing red, drying red-brown; persistent calyx inconspicuous; seeds 2, the dorsal surface with 4–5 longitudinal furrows, the ventral surface with 2 sometimes shallow longitudinal furrows.

Distribution (Fig. 15). Widespread fom Veracruz, Mexico, through western Panama, at 0–1,300 m elevation in tropical moist to premontane wet forest with equatorial to tropical climate. This species has been collected in flower throughout the year, primarily January–June, and in fruit throughout the year.

Selected specimens examined. MEXICO. CAMPECHE: Santa Leonor, E of Río San Pedro, 20 Apr. 1963 (fr), *Barlow 14/4* (GH). CHIAPAS: Mpio. Tenejapa, Tanate River below Habenal, paraje of Mahben Chauk, 930 m, 13 July 1964 (early fr), *Breedlove 6334* (F, NY); Mpio. Huixtla, 6–8 km NE of Huixtla along rd. to Motozintla, 200 m, 30 June 1972 (fr), *Breedlove 25966* (ENCB, MEXU—2 sheets, MO, NY); ca. 8.5 mi. NE of Escuintla, rd. to El Triunfo, 250 m, 21 Aug. 1977 (early fr), *Croat 43826* (MO); 19 mi. E of Zapata on Zapata–Balancán rd., 20 m, 9 Aug. 1975 (fr), *Davidse & Davidse 9428* (NY); Huehuetán, Islamapa, 27 June 1948 (fr), *Matuda 17985* (MEXU). OAXACA: km 47 camino Cedillo–Sarabia, San Juan Guichicobi, 150 m, 7 Dec. 1974 (fr), *J. Dorantes et al. 3779* (MEXU); Tehuantepec, July 1936 (fl), *Matuda 2277* (MEXU); Temazcal, 19 Oct. 1962 (st), *Sousa 1749* (MEXU—2 sheets). TABASCO: outskirts of Villahermosa, June 1964 (fl), *Barlow 3/5A* (MEXU); Balancán, Reforma, 22–26 May 1939 (fr), *Matuda 3146* (A, F, K, MEXU, NY); Frontera, 5 Mar. 1911 (fl), *Seler 5441* (GH, US); Mpio. Paraíso, La Unión, 0 m, 26 Aug. 1983 (fr), *Ventura 20640* (ENCB, MO); Laguna Mecoacán, Arroyo Atascadero, mound, 22 Mar. 1963 (fl), *West 3/5* (GH). VERACRUZ: San Andrés Tuxtla, Cerro Vaxin S del Volcán San Martín, 1,150 m, 15 June 1972 (fl), *Beaman 6183* (F); Estación Biología de Los Tuxtlas, Feb. 1971 (fl), *Calzada 157* (ENCB, F, GH, MEXU, US); Mpio. Ozuluama, 8 km from Ozuluama, 8 July 1970 (fr), *Chiang 251* (F, MEXU); Hidalgotitlán, km 0–3 camino Cedillo la Laguna, 140 m, 10 May 1974 (fl), *B. Dorantes 3022* (MEXU); Casitas-Gutiérrez Zamora, 30 m, 21 June 1970 (fl), *Gómez-Pompa & Nevling 1158* (GH, MEXU); Mpio. de Pajapán, Laguna del Ostión, 0–4 m, 5 Jan. 1980 (fl, fr), *L. Gutiérrez C. 39* (MEXU); Laguna Tamiahua, 50 mi. S of Tampico, 5 Mar. 1939 (fl), *LeSueur 352* (F); Santa Lucrecia, 3 Mar. 1930 (fl), *Mell 676* (NY); Catemaco, Laguna de Sontecomapan, 18°34′N, 95°00′W, 5 m, 25 Mar. 1973 (fl), *Menéndez 114* (F, MEXU, MO); vic. Pánuco, 20–25 Apr. 1910 (fl), *Palmer 347* (GH, K, MO, NY); vic. Pueblo Viejo, 2 km S of Tampico, 10–25 Feb. 1910 (fl), *Palmer 384* (US); Coatzacoalcos, Isthmus of Tehuantepec, Feb. 1895 (fl, fr), *C. Smith 590* (F, GH, MEXU—2 sheets, MO, NY—3 sheets, US); Gulf Coastal Plain, 24 mi. SE of Veracruz, 24 mi. WNW of Alvarado, coastal hammock in savanna, 28 June 1970 (fl), *Thorne & Lathrop 40456* (ENCB); 2 km despues del Pedregal, 800 m, 18 June 1972 (fr), *C. Vázquez Y. 537* (MEXU); carret. a Plan de las Hayas, a 21.5 km de la desviación, 720 m, 24 June 1972 (fr), *C. Vázquez Y. 781* (F, MEXU); Mpio. de Nautla, Nautla, 0 m, 25 Mar. 1976 (fl), *Ventura 12563* (ENCB, MEXU); Mpio. de Alto Lucero, Laguna Verde, 20 Feb. 1978 (fl), *Ventura 15007* (ENCB, MEXU). GUATEMALA. ALTA VERAPAZ: Chahal, 3.7 km E of airport, 12 Oct. 1968 (fr), *Contreras 7906* (NY); 1.5–2 mi. S of Cubilgüitz, 300–350 m, 1 Mar. 1942 (st), *Steyermark 44480* (F, US); along Río Sebol to junction with Río Santa Isabel, 125–150 m, 20 Apr. 1942 (fl), *Steyermark 45802* (US). ESCUINTLA: 8 km S of Palín, 8 July 1970 (fr), *Harmon & Dwyer 2961* (ENCB, MO). IZABAL: Petén–Guatemala rd., 27 May 1971 (fl), *Contreras 10864* (MO). PETÉN: Uaxactún, nr. aguada, 24 Apr. 1931 (fl), *Bartlett*

12722 (A, F, US); Dos Lagunas, ca. 10 km W of village, in tintal, 27 Dec. 1960 (fl), *Contreras 1762* (NY); Dolores, 300 m W of rd. at km 82, 22 May 1961 (fl), *Contreras 2368* (NY); La Cumbre, on Pusila River, ca. 8 km from village, 17 May 1967 (fl), *Contreras 6936* (DUKE, F, MEXU); Tikal National Park, Aguada El Pital, on new Uaxactún rd., 21 Apr. 1968 (fl), *Contreras 7724* (F, MEXU); San Luis, km 116 en el camino para Poptún, 6 Dec. 1970 (fl), *Ortíz 1477* (F, US); along Río Santa Isabel, between mouth of Río Sebol and El Porvenir, 100 m, 21 Apr. 1942 (fl), *Steyermark 45836* (F); along Río San Martín, between Cerro Ceibal and Ceibal, 50 m, 1 May 1942 (fl), *Steyermark 46172* (F). BELIZE. BELIZE: Burrel Boom, thicket nr. ferry, 9 June 1973 (fr), *Dwyer 11060* (F, MO, NY); Gracie Rock, 27–28 May 1974 (fl), *Dwyer 12451* (GH, MO—2 sheets); Maskalls, 6 Apr. 1934 (fl), *Gentle 1255* (A, F, GH, K, MO, NY, US). CAYO: El Cayo, 2 May 1931 (fl), *Bartlett 13002* (F, US); Teakettle, 12 May 1931 (fl), *Bartlett 13143* (A, F, K); Vaca, 10 May 1938 (fl), *Gentle 2595* (A—2 sheets, F, K, MEXU); ca. 250 m W of Hummingbird Hwy. 2.5 mi. S of Western Hwy., 50 m, 17 July 1970 (fr), *Spellman & Newey 1701* (MO). TOLEDO: 2 km S of Mayan village of San José, ca. 8 km W of Columbia Forest Station, 12 June 1973 (fl), *Croat 24311* (F, MO); between Punta Gorda–San Antonio Rd. and Moho River, in broken cohune ridge, 28 May 1949 (fl), *Gentle 6754* (DUKE, F). HONDURAS. ATLANTIDA: vic. Tela, 0 m, 20 May 1926 (fl), *Mitchell 87* (F, GH, US); base of hills S of San Alejo nr. Río San Alejo, 150–270 m, 22–27 Apr. 1947 (fl), *Standley 7728* (F); foothills back of La Ceiba, bank of Cangrejal River, 29 July 1938 (fr), *Yuncker et al. 8673* (F, GH, K, MO, NY, US). COLÓN: N bank of Río Guaimoreto between old bridge and opening of Laguna Guaimoreto, 15°57′N, 85°54′W, 17 Oct. 1980 (fl), *Saunders 635* (F, MO). COMAYAGUA: San Luis, Coyocutena, 120 m, 25 May 1932 (fl), *J. B. Edwards P-297* (F, GH); 3 km de La Libertad, cerca de Qda. La Jutera, 600 m, 20 May 1956 (fl), *A. Molina R. 7048* (F, GH, US). CORTÉS: NE de San Pedro Sula, Cordillera de Omoa, 200 m, 19 Apr. 1956 (fl), *A. Molina R. 6710* (F, GH, US); 50 km N Lago de Yojoa, Ocote Arrancado, 600 m, 1–30 Nov. 1980 (fr), *C. Nelson et al. 6022* (TEFH). ISLAS DE LA BAHÍA: Roatán Island, nr. town of Roatán, 50 m, 16 Aug. 1970 (fr), *Harmon & Dwyer 3953* (MO). SANTA BARBARA: mountains above Las Vegas, 1,050 m, 21 June 1970 (fl), *Barkley & Smith 40856* (TEFH). YORO: 19 km SE of Río Viejo (Atlantida), 820 m, 27 June 1970 (fl), *Davidse & Pohl 2204* (F, MO, NY); nr. Coyoles, Aguan River valley, 28 June 1938 (fr), *Yuncker et al. 8038* (GH, K, MO, NY, US). EL SALVADOR. AHUACHAPÁN: rd. to Tacuba, 2–3 mi. NW of San Francisco Menéndez, 500 m, 28 July 1977 (early fr), *Croat 42077* (MO). NICARAGUA. BOACO: W slope of Cerro Mombachito, 12°24′N, 85°33′W, 900–1,000 m, 8 Oct. 1979 (fr), *W. D. Stevens & Grijalva 14773* (MO). CHINANDEGA: falda NW de Volcán Cosigüina, 12°56′N, 87°31′W, 400–500 m, 18 June 1983 (fl, early fr), *Sandino & Aldubin 4379* (MO). CHONTALES: 2.8 km N of Cuapa, 12°17′N, 85°23′W, 400–500 m, 30 Dec. 1983 (fr), *W. D. Stevens 22696* (MO); 1.9 km S of La Libertad, 12°12′N, 85°10′W, 530 m, 7 June 1980 (fl), *W. D. Stevens & Montiel 17516* (MO). GRANADA: upper slopes of Volcán Mombacho, 1,100 m, 19 Mar. 1977 (fl), *Croat 39118* (MO); Isla Zapatera, costado E de Hda. El Cerro, 11°41′N, 85°46′W, 400–500 m, 24 Nov. 1982 (fr), *Grijalva 1961* (MO); NW de Volcán Mombacho, 11°49′N, 85°56′W, 19 Aug. 1981 (fr), *Sandino 1283* (MO). JINOTEGA: Sta. Gertrudis, 30 km E de Jinotega, 1,000 m, 20 Jan. 1980 (fl), *Araquistain & Moreno 833* (MO). MATAGALPA: La Estancia "El Comelar," carret. Matagalpa–Waslala, costado NE del Cerro Peñas Blancas, 13 Sep. 1982 (fr), *Grijalva & Moreno 1063* (MO); El Tuma, beside Río Tuma, 350 m, 19 May 1976 (fl), *Neill 335* (GH); Sta. María de Ostuma, 1,300–1,500 m, 19–21 Feb. 1963 (fr), *L. O. Williams et al. 24669* (F, NY, US). RIVAS: Isla Ometepe, faldas del lado N del Volcán Maderas, 11°27′N, 85°30′W, 900–1,200 m, 19 Jan. 1983 (fl), *P. P. Moreno 19688* (MO); Isla de Ometepe, N de Volcán Concepción, 11°32′N, 85°38′W, 800–1,000 m, 7 Aug. 1982 (fr), *Sandino 3450* (MO); Hda. Fátima, Montaña La Victoria, SW de Sapoa, 11°10′N, 85°40′W, 12 Sep. 1982 (fr), *Sandino 3585* (MO). ZELAYA: Cerro Livico, 7 km NE of Siuna, 500 m, 28 Apr. 1978 (fl), *Neill 3651* (MO); Cerro Waylawás, E slope of northern range, 13°39′N, 84°49′W, 80 m, 11 Mar. 1979 (fr), *Pipoly 4377* (MO); ca. 6.3 km S of bridge at Colonia Yolania on rd. to Colonia Manantiales, 11°36′N, 84°22′W, 200–300 m, 29–31 Oct. 1977 (fr), *W. D. Stevens 4877* (MO); ca. 8.9 km E of Río Kukalaya on rd. from Puerto Cabezas to Rosita, 14°07′N, 84°02′W, 200–300 m, 3 May 1978 (fl), *W. D. Stevens 8705* (MO); Salto La Oropendola, Río Rama, 11°57′N, 84°17′W, 15–25 m, 17 May 1978 (fl), *W. D. Stevens 8956* (MO). COSTA RICA. ALAJUELA: Colinas de San Pedro de San Ramón, 4 June 1931 (fl), *Brenes 14310* (A, CR, F, NY); Santa María Park, 10°37′N, 85°17′W, 600 m, 7 Feb. 1978 (fl), *Liesner 5060* (MO); 22 km NE of Quesada, 4 km W of Muelle San Carlos, 10°28′N, 84°30′W, 9 Apr. 1983 (fl, early fr), *Liesner 14099* (MO); nr. Los Angeles, llanura de San Carlos, 100 m, 21 Feb. 1966 (fl), *A. Molina R. et al. 17649* (MO, NY). CARTAGO: Agua Caliente del Llano, 11 May 1906 (fl), *Brenes s.n.* (NY). GUANACASTE: Parque Nacional Rincón de la Vieja, SE slopes of Volcán Sta. María, 10°47′N, 85°18′W, 900–1,200 m, 27–28 Jan. 1983 (fr), *Davidse et al. 23342* (CR, MO); entre Guayabo y La Unión, Bagaces, 4 Oct. 1963 (fl), *Jiménez 1150* (CR, F); 3 km NW of Río Naranjo, lower slope of Volcán Miravalles, 1,000 m, 31 Mar. 1972 (fl), *Opler 662* (CR, F); above Hda. Tenorio, 14 Feb. 1956 (fr), *Schubert 1052* (A, F); vic. Tilarán, 500–650 m, 10–31 Jan. 1926 (fl), *Standley & Valerio 44986* (US). LIMÓN: La Colombiana Farm of the United Fruit Co., 70 m, 6–7 Mar. 1924 (fl), *Standley 36956* (US). PUNTARENAS: E of Monteverde, 10°18′N, 84°48′W, 1,300–1,450 m, 29 Oct.–2 Nov. 1975 (fl, fr), *Burger & Baker 9630* (CR, F). PANAMA. CHIRIQUÍ: rd. to Cerro Hornito, 12 mi. from Gualaca, 1,300 m, 1 Sep. 1979 (fr), *Antonio 1754* (MO); Cerro Colorado Mine, 2 mi. from Lower Elevation Camp, 1,250 m, 30 May 1980 (fl), *Antonio 4908* (ENCB, MO). COCLÉ: N rim of El Valle, 4 June 1939 (fl), *Alston 1853* (GH, MO, NY, US); El Valle de Antón, 900 m, 4 June 1939 (fl), *Alston 8716* (US); behind Club Campestre, El Valle, 700 m, 2 July 1967 (early fr), *Duke 13246* (MO—3 sheets). COLÓN: between Palmas Bellas and Salud, ca. 0 m, 7 July 1976 (early fr), *Croat 36867* (MO). LOS SANTOS: Los Toretos, 10 Aug. 1962 (fl), *Dwyer 2445* (US).

Psychotria quinqueradiata and *P. morae* were published simultaneously by Polakowsky and serve as the only instance known to me where pin and thrum morphs of the same species were named as different species. I chose to retain the former ep-

ithet for its reference to the five equal axes radiating from the base of the inflorescence, an important recognition character (Fig. 7g).

The glabrous, obovate leaves drying red-brown to green-brown, with secondary veins usually brochidodromous making loops far from the margin, also aid in recognition. *Psychotria quinqueradiata* resembles *P. carthagenensis* in most vegetative and fruit characters but differs in its distinctive inflorescence and brochidodromous venation.

Stipule shape is invariable in the range of the species, but size varies greatly, from the typical 4–6 × 2–3 mm in Nicaragua and Costa Rica to 4–6 × 5 mm in Panama to 10–15 × 8 mm in Guatemala.

7. Psychotria viridis Ruiz & Pavón, Fl. Peruv. Prodr. 2: 61, pl. 210, fig. b. 1799. *Uragoga viridis* (Ruiz & Pavón) Kuntze, Revis. Gen. Pl. 2: 963. 1891. TYPE: n.v. Figures 4c, 7k, 13.

Psychotria glomerata Kunth in Humboldt, Bonpland and Kunth, Nov. Gen. Sp. 3: 362. 1819. *Uragoga glomerata* (Kunth) Kuntze, Revis. Gen. Pl. 2: 960. 1891. TYPE: Colombia? *Kunth s.n.* (holotype, P, n.v.).

Psychotria microdesmia Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 36. 1853. *Uragoga microdesmia* (Oersted) Kuntze, Revis. Gen. Pl. 2: 961. 1891. TYPE: Costa Rica: Jaris, 900 m, *Oersted 11610* (holotype, C, n.v., photo, F neg. 22840; isotypes, K, US).

Psychotria trispicata Grisebach, Pl. Wright., Pars II: 509. 1862 (cf. also Mem. Amer. Acad. Arts, n.s. 8: 508. 1863). *Uragoga trispicata* (Griseb.) Kuntze, Revis. Gen. Pl. 2: 963. 1891. TYPE: Cuba: San Andres, 1860–1864 (fr), *Wright 1280* (lectotype, NY; isolectotype, NY).

Tree 2–4 m tall; young stems glabrous, the bark pale, smooth; stipules ovate, the apex often acuminate, darker in central triangle, 8–15 × 3–6 mm, irregularly fringed, caducous, leaving a pale ridge with long red-brown fringe. *Leaves* subsessile to petiolate; petioles to 8 mm long, glabrous, flat above; blades membranous, elliptic-obovate, the apex short-acuminate to acute, the base attenuate, (6.5–)9–15 × (3–)4–5(–6) cm, glabrous above and below, drying dull red-brown to green-brown; secondary veins 7–10 pairs, diverging 45°–55°, eucamptodromous, straight then arcuate ⅔ to margin, elevated below, glabrous, the axils often with domatia below especially near apex (Fig. 4c); tertiary veins inconspicuous, orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of glomerules (Fig. 7k); panicle branched to 3 degrees; main axis 6.5–12 cm long, the peduncle 2–6 cm long; secondary axes in (4–)5 ranks, the first-rank axes 4, the longer pair (0.6–)1–2.5 cm long, the shorter pair usually reduced or to 0.3 cm long, the second-rank axes 2 or 4, reduced and thus flowers disposed in glomerules along main axis, the longer pair when present 0.5–0.8 cm long, the third-rank axes 2 or rarely 4, reduced, the longer pair when present 0.4 cm long, the fourth-rank axes 2, reduced, the fifth-rank axes 2, reduced; tertiary axes reduced and thus flowers disposed in glomerules along secondary axes; bracts and bracteoles irregular, to 1 mm long, red-brown ciliate. *Flowers* sessile; calyx cup-shaped, ca. 0.5 mm long, the lobes not evident or rarely 5, triangular, to 0.2 mm long, glabrous; corolla white, the tube cylindrical, 1.5 × 1 mm, thick white pubescent in throat, the lobes 5, lanceolate, 1 × 0.6 mm; stamens 5, the filaments 2 mm long, the anthers 0.5 mm long; style 2.5 mm long, the branches clublike. *Fruit* when dry ellipsoidal, 4.5–5 mm long, 3–3.5 mm diam., maturing red, drying red-brown; persistent calyx a beak to 0.5 mm long; seed dorsal surface with 4–5 deep longitudinal furrows, the ventral surface with 2 deep longitudinal furrows.

Distribution (Fig. 13). Very sparse distribution throughout Central America at 0–1,000 m elevation, collected most commonly in the lowlands of eastern Panama, in tropical moist to premontane wet forest with equatorial to tropical climate. *Psychotria viridis* occurs also in Cuba, Hispaniola, Colombia, Venezuela, Ecuador, Peru (where it is extremely common), Brazil, and Bolivia. In Central America it has been collected in flower September–March and in fruit January–June and in September.

Selected specimens examined. MEXICO. CHIAPAS: Río Salinas, in riverbank forest, above mouth of Río Pasión, 8 Feb. 1964 (early fr), *Lundell 17811* (LL). GUATEMALA. PETÉN: Dolores, km 78–79 on Santo Toribio Rd., 20 Apr. 1961 (fr), *Contreras 2140* (DUKE); Chinchilá, Sebol rd., forest in corozal and zapotal, 7 Mar. 1971 (fr), *Contreras 10610* (F); Río de la Pasión, Ceibal, in corozal on ruins, 3 Feb. 1964 (fr), *Lundell 17649* (DUKE, F, LL); Cerro Ceibal (Sierra Mojada), between mouth of Río Sta. Monica and mouth of Río San Martín, on W side of Río Cancuen, 75–150 m, 30 Apr. 1942 (fr), *Steyermark 46100* (F). BELIZE. CAYO: Cocquericot, 10 Mar. 1931 (fr), *Bartlett 12038* (F, NY, US). NICARAGUA. RIVAS: Isla Ometepe, Lago de Nicaragua, Volcán Maderas, N slope, cloud forest, 800–1,000 m, 24 Feb. 1978 (early fr), *Neill & Vincelli 3270* (MO). COSTA RICA. CARTAGO: CATIE, 3 km E of Turrialba, Río Reventazón, 9°54′N, 83°39′W, 525–600 m, 9 May 1983 (fr), *Liesner et al. 15301* (CR, MO). LIMÓN: La Palma, Sixaola, 1 Mar. 1924 (fl), *Dunlap 470* (F, K, US); drenajes de los ríos Parismina y Reventazón, 0 m, 3 Oct. 1951 (early fr), *Shank & Molina 4261* (GH, US); entre Barra Parismina y Río Chiquero, 9 Oct. 1951 (fl), *Shank & Molina 4330* (F, GH); drenaje

de Río Valle Estrella, Montaña Andromeda, 26–28 Oct. 1951 (early fr), *Shank & Molina 4518* (F, GH, US). SAN JOSÉ: vic. El General, 700 m, Jan. 1939 (fl), *Skutch 3904* (A, K, MO, NY, US). PANAMA. DARIÉN: ca. 2 mi. N of Santa Fe, ca. 25 m, 15 Feb. 1967 (fr), *Duke 10230* (ECON, MO); S slope of Cerro Tacarcuna, 700–1,000 m, 25 Jan. 1975 (early fr), *Gentry & Mori 13902* (MO); SE of Río Chico, ca. 10 km upstream from Nazareht, 8°15′N, 77°25′W, 200 m, 20 Dec. 1980 (early fr), *W. Hahn 123* (MO); base of Cerro Sapo, 400 m, 30 Jan. 1975 (early fr), *Hammel 1136* (MO). PANAMÁ: Serranía de Majé, S of Ipetí, to 360 m, 17 Sep. 1982 (early fr), *D'Arcy 15115* (MO); 17 Sep. 1982 (fr), *D'Arcy 15123* (MO); nr. Jenine, Río Cañita, 23 Sep. 1961 (fl, early fr), *Duke 3852* (GH, MO—2 sheets); Panam. Hwy. 28 km E of Bayano bridge, 22 Jan. 1977 (fr), *Folsom 1388* (MO); base of Serranía de Cañazas, ca. 15 km SW of Cañazas nr. Río Tortí, 8°52′N, 78°22′W, 150 m, 15 Jan. 1983 (fr), *Stein 1337* (MO).

Psychotria viridis may be readily recognized by its inflorescence: all ranks of secondary axes except the first and second are reduced so that flowers and fruit appear in clusters along the main axis (Fig. 7k). *Psychotria viridis* is, in its vegetative and fruit characters, almost identical to *P. carthagenensis*; the distinctive inflorescence may be viewed as a reduction in secondary and tertiary axes of that of *P. carthagenensis*.

There appears to be only one flower morph, a homostyle, in Central American *P. viridis*, with no spatial separation between the exserted anthers and stigma. Leaves in Guatemala and Belize have fewer secondary veins than elsewhere in Central America.

GROUP 2. THE *COSTIVENIA* GROUP

Shrub or tree; young stems glabrous or puberulent or rarely tomentose or ferrugineous-pubescent; stipules usually not sheathing, ovate, uniform in color or often with a pale central triangle or keel (Fig. 2b), glabrous or puberulent or ferrugineous-pubescent or sometimes fringed, caducous or often persistent at terminal 2–6 nodes. *Leaf* blades elliptic or ovate or obovate or oblanceolate, *drying usually yellow-green or sometimes green*, green-brown, or red-brown, *often dull* or pale, sometimes chalky above, sometimes darker below; secondary veins (6–)7–19(–21) pairs, diverging (45°–)60°–85°, eucamptodromous or brochidodromous, the axils usually lacking domatia or hairs (except sometimes *P. horizontalis* and *P. sylvivaga*); tertiary veins orthogonal reticulate or less commonly percurrent, the intersecondaries often conspicuous, the tertiary loops sometimes evident (*P. fendleri* and *P. horizontalis*). *Inflorescences* panicles of cymes or rarely of glomerules (*P. flava*), pedunculate (except rarely in *P. horizontalis*); *secondary axes usually in 2 or 3 size-differentiated pairs per rank* (Fig. 7b) or sometimes 2 or rarely 4 subequal; bracts not conspicuously enlarged (to 5 mm long in *P. flava* and *P. pleuropoda*). *Corolla* tubes 2–3.5 mm long (4–5 mm in *P. papantlensis*), the lobes without apical extensions. *Fruit* when dry spherical to ellipsoidal (sometimes slightly obovoid in *P. flava*); *persistent calyx a beak or a tube* Fig. 9b) *or of linear lobes* (Fig. 9e) or not evident, over 1 mm long only in *P. fendleri* and *P. horizontalis*; dorsal seed surface with 3–5 regular (Fig. 10b) or 6–15 irregular longitudinal furrows (Fig. 10i, j), the ventral surface with 2 often incompletely divided longitudinal furrows (Fig. 10e) or one often T-shaped longitudinal furrow (*P. flava*; Fig. 10j) rarely plus 4 irregular longitudinal furrows (*P. sylvivaga*).

This subgroup may be subdivided into two species complexes. The *Psychotria horizontalis* complex includes the widespread *P. horizontalis* and *P. fendleri*, the latter endemic to Caribbean coastal Panama (Figs. 16, 17); they share the distinctive character states of immediately caducous stipules, brochidodromous secondary venation with connecting loops far from the blade margin plus evident tertiary connecting loops, and persistent calyx at least 1 mm long. The *P. costivenia* complex, which includes the remaining seven species, has in common often persistent stipules usually with a paler central triangle or keel, often conspicuous intersecondary veins, and persistent calyx a beak or tube no longer than 1 mm. Two species are widespread—*P. costivenia* (Mexico through Nicaragua; Fig. 18) and *P. grandis* (Guatemala through Panama; Fig. 19), both also in the Greater Antilles—and five have small ranges: *P. balancanensis* (Tabasco, Mexico; Fig. 19), *P. flava* (southern Mexico and Petén, Guatemala; Fig. 17), *P. papantlensis* (southern Mexico through Belize; Fig. 16), *P. pleuropoda* (southern Mexico through Belize; Fig. 17), and *P. sylvivaga* (central Costa Rica; Fig. 17).

Of the nine species in the group, six appear distylous; two of those, *Psychotria papantlensis* and *P. pleuropoda*, show some between-morph asymmetry in floral part lengths. Only one species, *P. fendleri*, apparently has evolved a derived state, thrum-monomorphy. Too few specimens of *P. balancanensis* have been seen to determine its breeding system.

8. Psychotria balancanensis C. Hamilton, Phytologia 64: 219. 1988. TYPE: Mexico. Tabasco: Balancán, La Palma, 1–6 June 1939

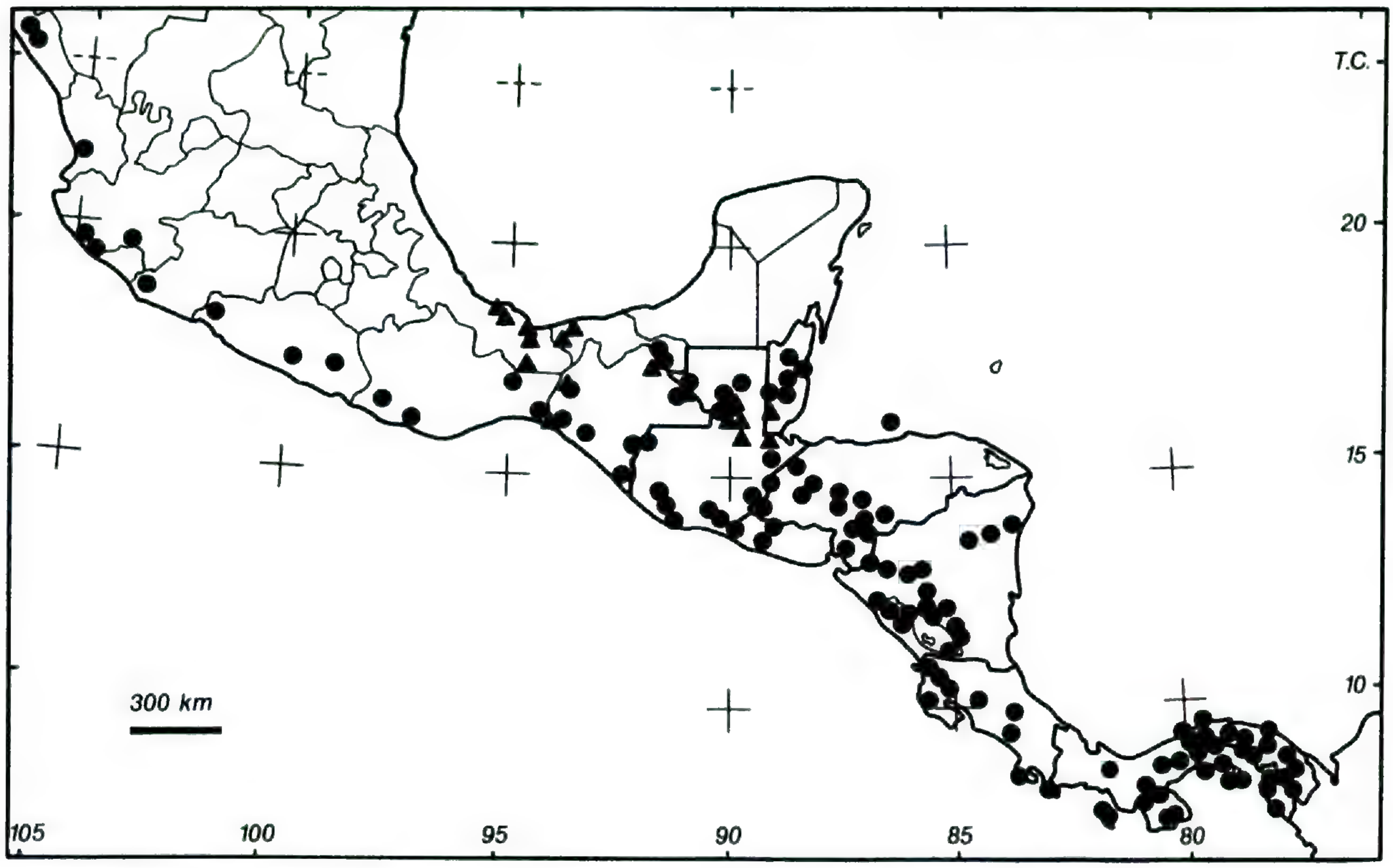

FIGURE 16. Distributions of *Psychotria horizontalis* (circles) and *P. papantlensis* (triangles) in Mesoamerica.

(fl), *Matuda 3286* (holotype, F; isotypes, A, MEXU, NY). Figure 19.

Shrub ca. 2.5 m tall; young stems glabrous, the bark smooth, sometimes with shallow fissures; stipules ovate-triangular, 6.5–7.5 × 3–4 mm, fringed, glabrous, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 0.9–2 cm long, glabrous, flat above; blades membranous, elliptic to slightly obovate, the apex acuminate, the

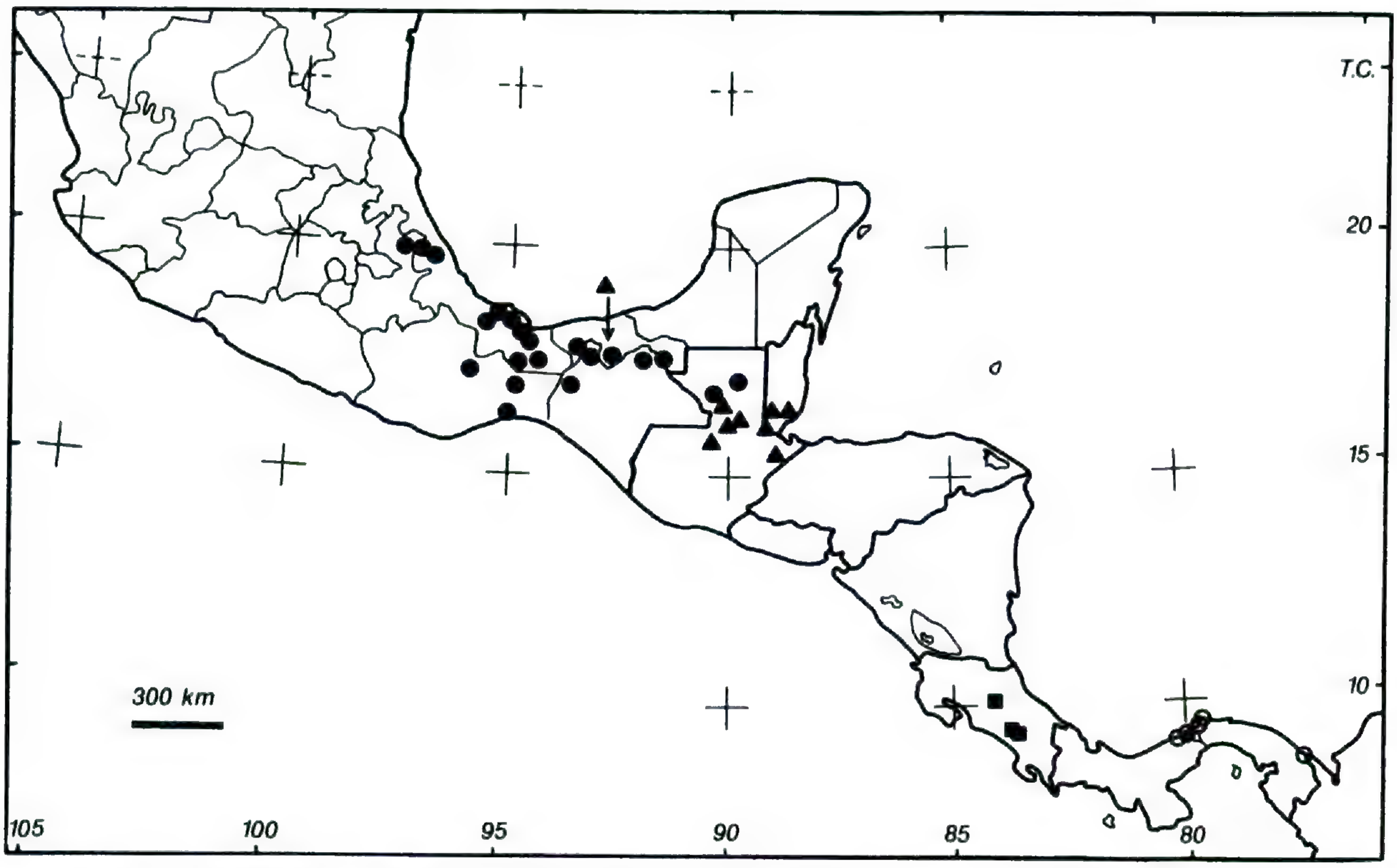

FIGURE 17. Distributions of *Psychotria fendleri* (open circles), *P. flava* (solid circles), *P. pleuropoda* (triangles), and *P. sylvivaga* (squares).

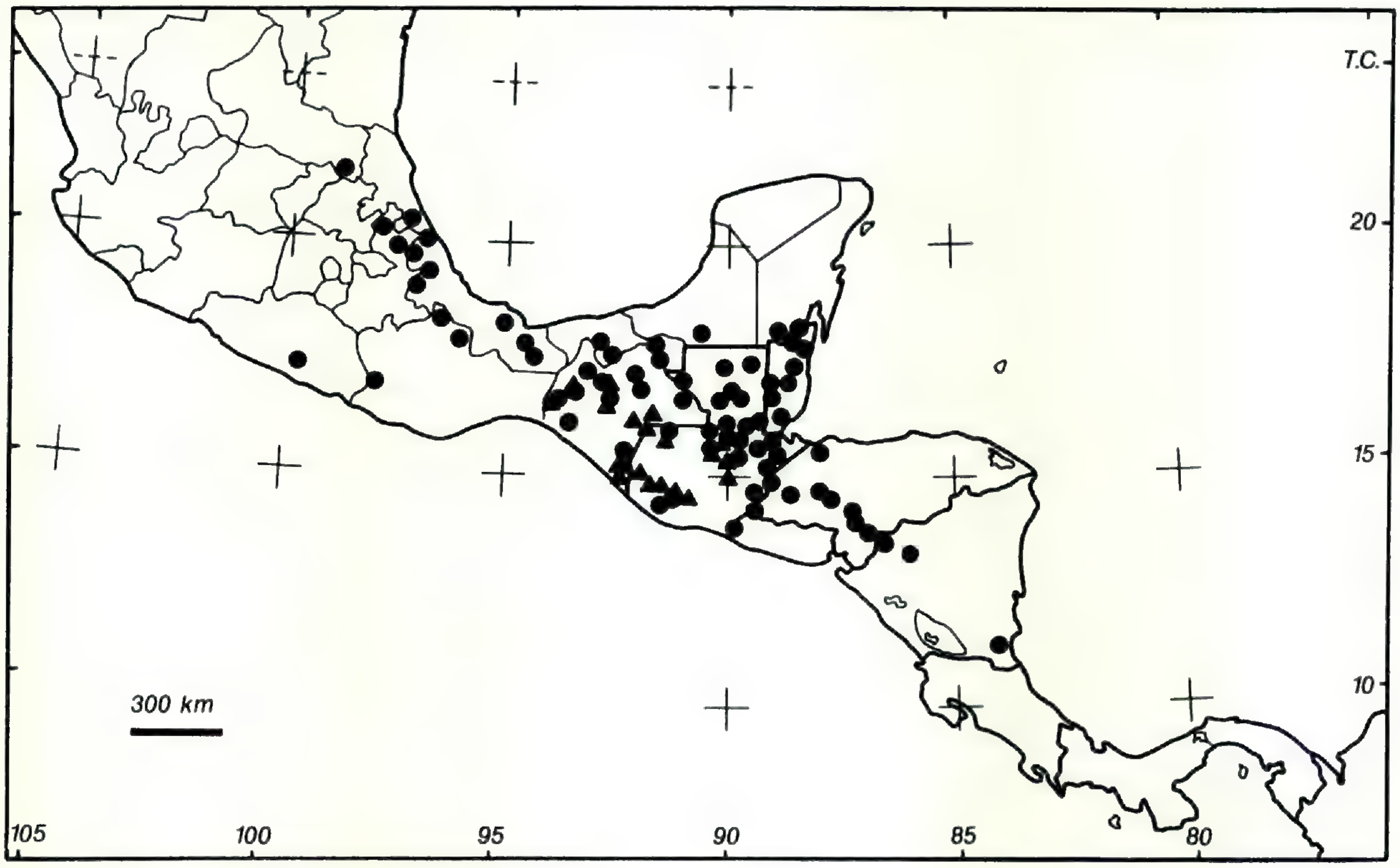

FIGURE 18. Distributions of *Psychotria costivenia* var. *altorum* (triangles) and *P. costivenia* var. *costivenia* (circles) in Mesoamerica.

base attenuate, (6–)7–11(–13) × (2–)3–6 cm, glabrous above and below, drying dull green; secondary veins 8–10 pairs, diverging 65°–75°, eucamptodromous to brochidodromous, constantly arcuate, elevated below, glabrous, the axils lacking domatia and hairs; tertiary veins evident, orthogonal reticulate to percurrent. *Inflorescences* terminal, panicles of cymes; panicle branched to 3–

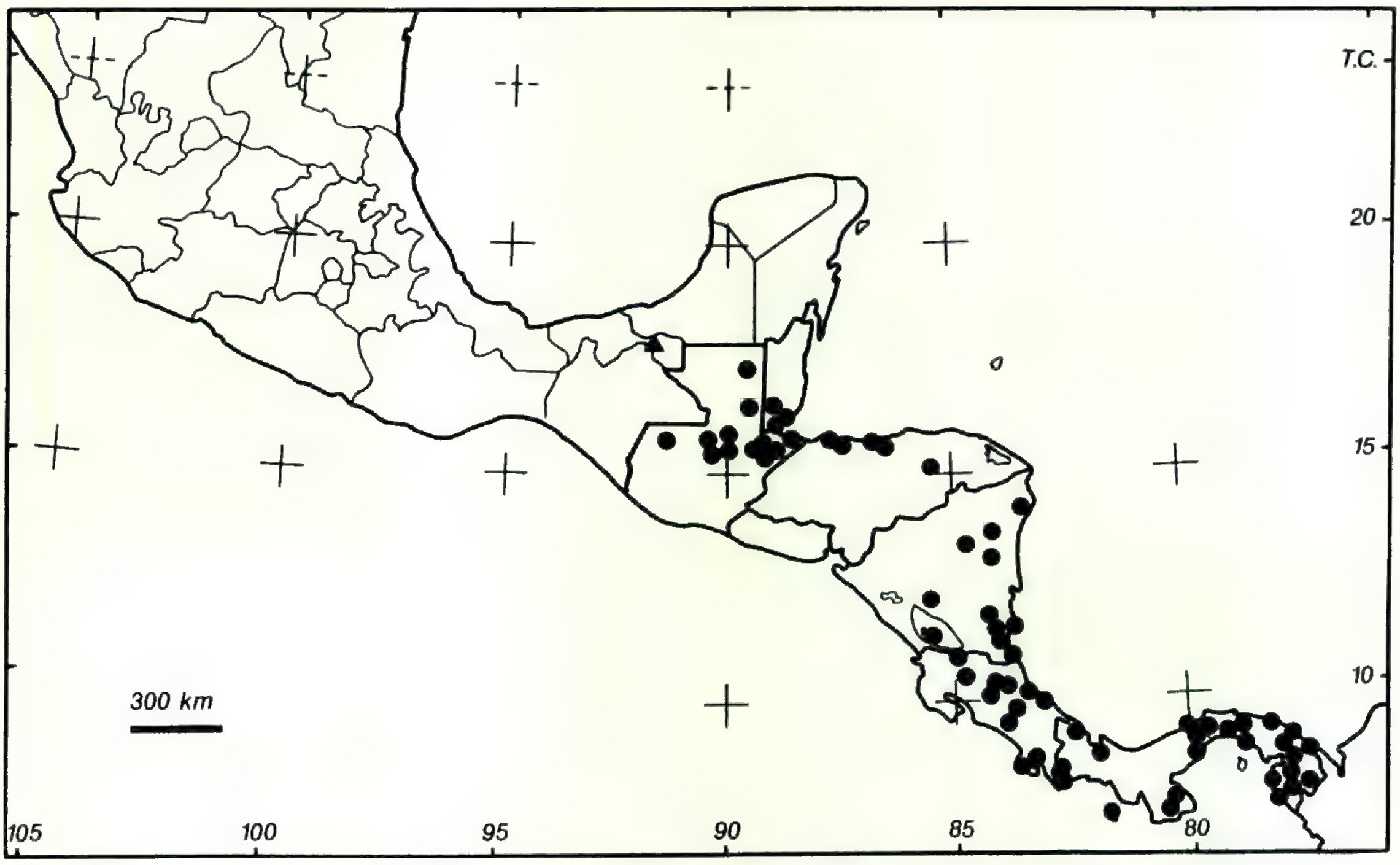

FIGURE 19. Distributions of *Psychotria balancanensis* (triangle) and *P. grandis* (circles) in Mesoamerica.

4 degrees; main axis 3.5–9 cm long, the peduncle 2.5–7 cm long; secondary axes in 2 ranks, the first-rank axes 2 or 4, the longer pair 0.8–1.2 cm long, the shorter pair 0.2–0.8 cm long, the second-rank axes 4, equal, 0.3–0.7 cm long; cymes branched to 1–2 degrees; bracts and bracteoles irregular triangular, 0.7 × 0.8 mm, puberulent, fringed. *Flowers* pedicellate; pedicels 0.7–1 mm long; calyx cup-shaped, the tube 0.3–0.5 mm, the lobes 5, broadly triangular to barely evident, 0.2–0.3 × 0.5 mm, fringed; corolla white, the tube cylindrical, 2.5–3 × 1.2 mm, white pubescent in throat, the lobes 5(–6), triangular, spreading, 1.5 × 1 mm; stamens 5(–6), the filaments 2.5–3 mm long in pins, not seen in thrums, the anthers 1 mm long; style 4.5 mm long in pins, not seen in thrums, the branches linear. *Fruit* not seen.

Distribution (Fig. 19). Known only from the type collection from eastern Balancán, Tabasco, in a region of evergreen forest and savanna with equatorial-tropical climate. It was collected in flower in early June.

Psychotria balancanensis may be recognized by its moderate-sized (7–11 cm long) broad-elliptic leaves drying dull green to green-brown with conspicuous intersecondary veins and by its inflorescence with the secondary axes in two ranks near the apex of the main axis. This species differs from *P. costivenia* in having broader-elliptic leaves and smaller inflorescences with fewer (two vs. four) ranks of secondary axes.

Only the pin morph has been collected, but the one flowering specimen seen is not sufficient to suggest that the species is pin-monomorphic.

9. Psychotria costivenia Grisebach, Pl. Wright., Pars II: 508. 1862. (Cf. also Mem. Amer. Acad. Arts, n.s. 8: 508. 1863.) *Uragoga costivenia* (Griseb.) Kuntze, Revis. Gen. Pl. 2: 960. 1891. TYPE: Cuba. Oriente: prope villam Monte Verde dictam, Jan.–July 1859 (fr), *Wright 242* (lectotype designated herein, GH). Figures 2b, 10e, 18.

Shrub 0.5–5(–6) m tall; young stems glabrous to red-brown puberulent to sparsely tomentose, the bark often pale, smooth; stipules ovate, the apex cuspidate or aristate or biaristate, 6–10(–11) × 3–7(–10) mm, with pale center and often evident central keel (Fig. 2b), glabrous to red-brown subtomentose, often fringed especially near apex, caducous, sometimes persistent at the terminal 2–3 nodes, leaving a pale ridge with red-brown fringe. *Leaves* sessile to petiolate; petioles to 1.5(–2) cm long, glabrous to puberulent, flat and sometimes shallowly grooved above; blades membranous to rarely subcoriaceous, elliptic or rarely obovate, the apex acute to acuminate, the base attenuate, (4–)4.5–17(–22) × (1–)1.5–6(–8) cm, glabrous above and below, drying green, yellow-green, red-brown, or green-brown; secondary veins 7–12 (–18) pairs, diverging 65°–80°, eucamptodromous to brochidodromous, straight or constantly arcuate, elevated below, glabrous, the axils lacking domatia or hairs; tertiary veins evident, orthogonal reticulate, the intersecondaries particularly conspicuous. *Inflorescences* terminal or pseudoaxillary, panicles of cymes; panicle branched to 3–4 degrees; main axis 3.5–22 cm long, the peduncle (0.7–)2.5–11.5 cm long; secondary axes in (2–)3–4(–5) ranks, the first-rank axes 2 or 4, the longer pair 0.5–4.7 cm long, the shorter pair 0.3–2.3 cm long, the second-rank axes 2 or 4, the longer pair 0.3–2.5 cm long, the shorter pair 0.2–1.5 cm long, the third-rank axes 2 or 4, the longer pair 0.1–1.5 cm long, the shorter pair 0.1–0.5 cm long, the fourth-rank axes 2 or 4, the longer pair 0.1–0.8 cm long, the shorter pair 0.4 cm long, the fifth-rank axes 2, 0.1 cm long; cymes branched to 1–3 degrees; bracts linear, 2–5 mm long, puberulent, sometimes fringed; bracteoles irregular, to 1 mm long, red-brown pubescent. *Flowers* sessile or pedicellate, the pedicels to 1.5 mm long; calyx cup-shaped, the tube 0.3–0.7 mm long, the lobes 5, barely evident to triangular to linear, to 0.8 mm long, to 0.6 mm wide, fringed, often puberulent outside; corolla white, the tube cylindrical, 2–3.5 × 1–2 mm, white pubescent in throat, the lobes 5, linear, 1.5–2 × 0.7–1 mm; stamens 5, the filaments 2–3 mm long in pins, 3.5–5 mm long in thrums, the anthers 0.8–1 mm long; style (3–)3.5–5 mm long in pins, 2.5–3.5 mm long in thrums, the branches short, clublike. *Fruit* when dry spherical to ellipsoidal, 5–7(–8.5) mm long, 4–6(–7) mm diam., maturing red, drying red-brown or black; persistent calyx not evident or as a beak, drying green or red-brown; seed dorsal surface with 4–5 longitudinal furrows, the ventral surface with 2 deep longitudinal furrows, incompletely divided (Fig. 10e).

Distribution (Fig. 18). Mexico through Nicaragua at elevations of 20–2,800 m.

Psychotria costivenia may be recognized by its stipules usually persisting at the terminal two or three nodes and having a paler central triangle (Fig. 2b), its elliptic leaves drying usually green or yellow-green with secondary veins drying paler and intersecondaries particularly conspicuous, and its

inflorescence secondary axes in one or two unequal pairs per rank, the higher ranks decreasing in size fairly uniformly.

KEY TO VARIETIES OF *PSYCHOTRIA COSTIVENIA*

1a. Leaf blades generally 4.5–10 × 1.5–3 cm, drying red-brown or green brown; inflorescence main axis 3.5–6 cm long ..... 9a. *P. costivenia* var. *altorum*

1b. Leaf blades generally 8–17 × 3.5–6 cm, drying green or yellow-green; inflorescence main axis 5.5–22 cm long ..... 9b. *P. costivenia* var. *costivenia*

9a. Psychotria costivenia Grisebach var. **altorum** (Standley & Steyermark) C. Hamilton, Phytologia 64: 223. 1988. *Psychotria altorum* Standley & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 86. 1944. TYPE: Guatemala. Quezaltenango: Montaña Chicharro, on lower SE-facing slopes of Volcán Sta. María, 2–4 mi. S of Sta. María de Jesús, 1,400–1,500 m, 17 Jan. 1940 (fl), *Steyermark 34302* (holotype, F). Figure 18.

Shrub: stipules ovate, the apex aristate or biaristate, 4–4.5 × 3 mm, the extensions 1.5–3 mm long, caducous, never persistent at the terminal 2–3 nodes. *Leaves:* blades narrow-elliptic, (4–)4.5–10(–12) × (1–)1.5–3(–4) cm, drying red-brown or green-brown; secondary veins 7–9(–11) pairs. *Inflorescences* few-branched panicles of cymes; panicle branched to 3(–4) degrees; main axis 3.5–6 cm long, the peduncle (0.7–)2.5–4 cm long; secondary axes in 3–4(–5) ranks, the first-rank axes 2 (or 4), 0.5–1.6 cm long, the shorter pair 0.3–1 cm long, the second-rank axes 2 or 4, 0.3–0.8 cm long, the shorter pair 0.2–0.5 cm long, the third-rank axes 2 (or 4), 0.1–0.5 cm long, the shorter pair 0.2 cm long, the fourth-rank axes 2, 0.1–0.3 cm long, the fifth-rank axes 2, 0.1 cm long; cymes branched to 1–2 degrees. *Flowers:* calyx lobes triangular to linear, 0.3–0.8 mm long. *Fruit:* drying red-brown; persistent calyx not evident or sometimes as a beak, drying red-brown.

Distribution (Fig. 18). Chiapas, Mexico, and southern Guatemala mostly at elevations of 1,000–2,800 m in areas of pine–oak forest with tropical climate. It has been collected in flower January–June and once in November and in fruit mostly September–February and rarely in May and June.

Selected specimens examined. MEXICO. CHIAPAS: Chamula, Yal Ichin, 1,800 m, 3 Apr. 1965 (fl), *Breedlove 9537* (NY); Mpio. La Trinitaria, Lago Tsiskaw, 30 mi. E of La Trinitaria, 1,350 m, 14 Apr. 1965 (fl), *Breedlove 9744* (ENCB, F, NY); Mpio. Ocozocoautla de Espinosa, rd. to Mal Paso, 900 m, 25 June 1972 (fl), *Breedlove 25671* (ENCB, F, MO); Mpio. San Cristobal de Las Casas, rd. to Chanalo 16–20 km E of Chilil, 2,380 m, 10 Nov. 1976 (fr), *Breedlove 41341* (MO); Mpio. La Independencia, rd. from Las Margaritas to Campo Alegre, 1,600 m, 30 Sep. 1981 (fr), *Breedlove 53213* (MEXU); Mpio. La Trinitaria, Comitán River at its sumidero, Lagos de Montebello, 42 km NE of La Trinitaria, 23 Oct. 1971 (fr), *Breedlove & Thorne 21156* (ENCB, MEXU, MO, NY); Mpio. Tapachula, Soconusco, 140 m, 20 Sep. 1977 (fr), *Lamas 368* (MEXU); Volcán Tacaná, 2,800 m, 30 Mar. 1939 (fl), *Matuda 2926* (F, GH, K, MEXU, NY); Tonalá, Paderon, 14–20 Jan. 1946 (fl), *Matuda 16302* (MEXU). GUATEMALA. ALTA VERAPAZ: Chamal, margenes del Río Cobán, 1,200 m, 13 May 1963 (fr), *A. Molina R. & A. Molina 12183* (F—2 sheets, NY, US—2 sheets); along Río Carchá, between Cobán and San Pedro Carchá, 1,360 m, 26–27 Mar. 1941 (fl), *Standley 90065* (F); 10–15 km W of San Cristobal, "El Derrumbe," canyon of Río Chixoy (Negro), 15°25′N, 90°27′W, 1,200–1,600 m, 2–4 Feb. 1969 (fr), *L. O. Williams et al. 40581* (F). BAJA VERAPAZ: Union Barrios, E of km 155/156 on Cobán rd., 13 Apr. 1975 (fl), *Lundell & Contreras 19180* (LL); Sierra de las Minas ca. 5 km S of Purulhá, 1,600 m, 2 Jan. 1973 (fl), *L. O. Williams et al. 41958* (F). CHIMALTENANGO: lower and middle SW slopes of Volcán Fuego, above Finca Montevideo, along Barranco Espinazo and tributary of Río Pantaleón, 1,200–1,600 m, 20 Sep. 1942 (fr), *Steyermark 52059* (F, US). EL PROGRESO: Montaña Canahui, between Finca San Miguel and summit, nr. upper limits of Finca Caieta, 1,600–2,300 m, 10 Feb. 1942 (fr), *Steyermark 43776* (F, NY). HUEHUETENANGO: Barillas, Finca San Isidro, 1,300 m, 22 Apr. 1948 (fl), *Holdridge 2331* (F, US). QUEZALTENANGO: above Mujulía, between San Martín Chile Verde and Colomba, 1,800 m, 1 Feb. 1941 (fl), *Standley 85583* (F); lower S-facing slopes of Volcán Santa María, between Santa María de Jesús and Calahuaché, along great barranco between Finca Pirineos and San Juan Patzulín, 1,300–1,500 m, 6 Jan. 1940 (fl, fr), *Steyermark 33690* (A, F). SAN MARCOS: Barrancos 10 km S and W of Tajumulco, NW slopes of Volcán Tajumulco, 2,300–2,800 m, 26 Feb. 1940 (fr), *Steyermark 36714* (F); above Finca El Porvenir, up Cerro de Mono, S-facing slopes of Volcán Tajumulco, 1,400–1,700 m, 9 Mar. 1940 (fl), *Steyermark 37388* (F). SOLOLÁ: Volcán Atitlán, S-facing slopes, 1,700–3,800 m, 11 June 1942 (fr), *Steyermark 47337* (F, GH). SUCHITEPÉQUEZ: Volcán Atitlán, S slope, 1,600 m, 22 Oct. 1934 (fr), *Skutch 1486* (F, GH); Volcán Santa Clara, between Finca El Naranjo and upper slopes, 1,250–2,650 m, 23 May 1942 (fr), *Steyermark 46615* (F—2 sheets, US).

Psychotria altorum has been reduced to a variety within *P. costivenia* because the distinguishing features (see varietal key) are not sufficient to distinguish a species, though varietal recognition is useful.

Leaf blades of this variety appear to have more secondary veins in Mexico than in Guatemala; persistent calyces are beaklike in Mexico and not evident in Guatemala.

9b. Psychotria costivenia Grisebach var. **costivenia.** Figure 18.

Mapouria miradorensis Oersted, Amér. Centr. 17, t. 14, fig. 9. 1863. *Psychotria miradorensis* (Oerst.) Hemsley, Biol. Cent.-Amer. Bot. 50. 1881. *Uragoga miradorensis* (Oerst.) Kuntze, Revis. Gen. Pl. 2: 961. 1891. TYPE: Mexico. Veracruz: Mirador, 900 m, 1841–1843 (fl), *Liebmann 11662* (lectotype, C, photo F neg. no. 22839; isolectotype, US).

Shrub: stipules ovate, the apex cuspidate, 6–10(–11) × 3.5–7(–10) mm, caducous, often persistent at the terminal 2–3 nodes. *Leaves:* blades elliptic or rarely obovate, (7–)8–17(–22) × (3–)3.5–6(–8) cm, drying green, yellow-green, or less often green-brown; secondary veins (8–)9–12(–18) pairs. *Inflorescences* many-branched panicles of cymes; panicle branched to 3–4 degrees, the axes often winged; main axis 5.5–22 cm long, the peduncle 2.5–11.5 cm long; secondary axes in (2–)4 ranks, the first-rank axes (2 or) 4, the longer pair (0.6–)1–4.7 cm long, the shorter pair (0.3–)0.5–2.3 cm long, the second-rank axes 2 or 4, the longer pair 0.5–2.5 cm long, the shorter pair 0.2–1.5 cm long, the third-rank axes 2 or 4, the longer pair (0.2–)0.4–1.5 cm long, the shorter pair 0.1–0.5 cm long, the fourth-rank axes 2 or 4, the longer pair 0.1–0.8 cm long, the shorter pair 0.4 cm long; cymes branched to 1–3 degrees. *Flowers:* calyx lobes barely evident to triangular, to 0.3 mm long. *Fruit:* drying black; persistent calyx not evident or often as a beak, to 1 mm long, drying green.

Distribution (Fig. 18). Widespread in Mexico through Nicaragua, at elevations of 20–1,500 m, usually at 1,000 m or lower, in evergreen to subevergreen forest with equatorial to tropical climate. It has been collected in flower January–June, principally March–May, and in fruit throughout the year.

Representative specimens examined. MEXICO. CAMPECHE: Campo Experimental Forestal Tropical "El Tormento," km 5 carr. Escárcega a Candelaria, 20 Apr. 1966 (fl, fr), *Chavelas & E. Hernández X. ES-794* (MEXU). CHIAPAS: Mpio. Jitotol, Río Hondo 4 mi. N of Jitotol on rd. to Pueblo Nuevo Solistahuacán, 1,650 m, 20 Aug. 1965 (fr), *Breedlove 12034* (NY); Mpio. Rayón, 10 km above Rayón Mezcalapa along rd. to Jitotol, 1,700 m, 12 Dec. 1971 (fr), *Breedlove 23196* (F, MO); Mpio. Berriozábal, 13 km N of Berriozábal nr. Pozo Turipache and Finca El Suspiro, 1,000 m, 24 July 1972 (fl), *Breedlove 26314* (ENCB, MO, NY); 900 m, 25 Dec. 1972 (fr), *Breedlove & Thorne 30828* (MO, NY); Mpio. Ocosingo, 6–8 km N of Ocosingo along rd. to Bachajón, 900 m, 24 Sep. 1972 (fr), *Breedlove 27877* (MEXU, NY); Mpio. Ocozocoautla de Espinosa, 32 km N of Ocozocoautla along rd. to Mal Paso, 750 m, 19 Oct. 1965 (fr), *Breedlove & Raven 13568* (DUKE, ENCB, NY); Mpio. Cintalapa, 16 km NW of Rizo de Oro along a logging road to Colonia Figueroa, 1,600 m, 3 Nov. 1971 (fr), *Breedlove & Smith 21713* (ENCB, MEXU, MO, NY); La Grandeza, 2,016 m, 19 May 1945 (fl), *Matuda 5573* (F, LL, MEXU); Mpio. Ocosingo, Centro Arqueológico Bonampak, 350 m, 24 Dec. 1982 (fr), *Meave et al. B-127* (MEXU); Mpio. Tenajapa, barrio of Tih Ha', paraje of Mahben Chauk, 1,080 m, 28 Oct. 1966 (fr), *Ton 1428* (ENCB, F, NY); Mpio. Angel Albino Corzo, nr. Rancho Viejo of the Finca Prusia, 720 m, 23 Jan. 1968 (fr), *Ton 3525* (ENCB); Mpio. Yajalon, 67 km al S de Palenque, sobre carret. a Ocosingo, 17°10′N, 92°09′W, 450 m, 3 Dec. 1979 (fr), *Wendt et al. 2345* (ENCB). GUERRERO: Mpio. Atoyac, 19 km NE of Atoyac, nr. Santiago La Unión, 770 m, 3 Nov. 1979 (fr), *Koch et al. 79288* (MEXU). OAXACA: Mpio. Tuxtepec, Isla de Málsaga en la Presa Miguel Alemán, 24 Oct. 1964 (fr), *L. González Q. 1789* (ENCB, MEXU); Putla, Arroyo Limón, 1,350 m, 16 Dec. 1970 (fl), *MacDougall H153* (ENCB, NY); Tuxtepec, Chiltepec and vic., 20 m, 28 Aug. 1940 (fr), *G. Martínez-Calderón 147* (GH, MEXU, US). PUEBLA: km 247.3 de la carret. México–Tuxpán, 1 May 1962 (st), *Sarukhán et al. 2119* (MEXU); Mpio. Hueytamalco, Paxta, 250 m, 31 Jan. 1978 (fr), *Ventura 14951* (ENCB, MEXU). QUINTANA ROO: 8 km N of Unión, 110 km SW of Chetumal by road, 100 m, 7 May 1982 (fr), *Davidse et al. 20178* (MO). SAN LUIS POTOSÍ: Axtla, ladera margosa, 250 m, 17 Apr. 1956 (fl), *Rzedowski 7529* (ENCB, MEXU). TABASCO: Mpio. Macuspana, rd. along Río Chinal (Río Macuspana) between Macuspana and El Carmen, 29 Sep. 1944 (fr), *Gilly & E. Hernández X. 378* (GH, MEXU); 13.6 km de Tenosique, por la carret. a Zapata, 1 Dec. 1966 (fr), *González & Hernández GH134* (ENCB, MEXU); a 11 km de Villahermosa, 2 km al S de Escárcega, 28 Dec. 1965 (fl), *González & Pérez 3896* (ENCB); Balancán, La Palma, 1–6 June 1939 (fr), *Matuda 3264* (A, F—2 sheets, MEXU). VERACRUZ: Teocelo, Trapiche, 1,220 m, 2 May 1980 (fl), *Barrera et al. 228* (MEXU); Papantla, Tajin, 1947 (fl), *Kelly 183* (DUKE); 5 km limite Puebla–Veracruz, carret. Tlapacoyan–Teziutlán, 900 m, 13 July 1971 (fr), *Nevling & Gómez-Pompa 1667* (GH, MEXU); banks of Arroyo Zacuapan, Mar. 1930 (fl, fr), *Purpus 14398* (A—2 sheets, F—2 sheets); Hidalgotitlán, Brecha Hnos. Cedillo–La Escuadra, 200 m, 7 Mar. 1974 (fl), *B. Vázquez 123* (MEXU—2 sheets); Mpio. de Nautla, La Martinica, 50 m, 25 Mar. 1971 (fl, fr), *Ventura 3338* (ENCB); Mpio. de Totutla, El Mirador, 1,000 m, 17 Apr. 1978 (fl), *Ventura 15208* (MEXU, MO); Mpio. Minatitlán, 4.5 km al E del Río Grande, 17°17′N, 94°30′W, 170 m, 27 Feb. 1981 (fl), *Wendt et al. 2939* (ENCB, MEXU). GUATEMALA. ALTA VERAPAZ: Sebol, ca. 800 m W of village, bordering arroyo, 15 Apr. 1964 (fl), *Contreras 4319* (MO); Chahal, airport, on El Moxpin, 14 Oct. 1968 (fr), *Contreras 7933* (MO); 14 km up rd. to Oxec, gravel rd. N from Hwy. 7E between Tucurú and El Estor ca. 6 km NE of Panzós, 800 m, 20 July 1977 (fr), *Croat 41692* (MO); Rubelsanto, Río Salinas, 15 July 1975 (early fr), *Lundell & Contreras 19517* (MO); 1.5–2 mi. S of Cubilgüitz, 300–350 m, 1 Mar. 1942 (fl), *Steyermark 44444* (F). CHIQUIMULA: Montaña Castilla, nr. Montaña Cebollas, along Río Lucía Saso, 5 km SE of Quezaltepeque, 1,200–1,500 m, 6 Nov. 1939 (fr), *Steyermark 31300* (F). HUEHUETENANGO: between Ixcán and Finca San Rafael, Sierra de los Cuchumatanes, 200–800 m, 24 July 1942 (fr), *Steyermark 49405* (F, US). IZABAL: Puerto Méndez, on Río Dulce Rd., km 10, 10 Sep. 1970 (fr), *Contreras*

10245 (MO); 18 km E of Los Amates, 13 June 1970 (fl), *Harmon 2569* (F, GH, MO—2 sheets); hills above Eximbal mining area W of El Estor, 9 Apr. 1970 (fr), *Harmon & Dwyer 4332* (ENCB, F, GH, MO); between Milla 49.5 and Cristina, 65–70 m, 30 Mar. 1940 (fl), *Steyermark 38476* (F—2 sheets). PETÉN: Tikal National Park, on Aguada Aurora, in zapotal, 15 June 1960 (fl), *Contreras 1098* (MO); Lacandón, El Caribal, low forest, 16 Mar. 1962 (fl), *Contreras 3540* (MO); Dos Lagunas, on Ixcanrio Rd., in zapotal, 20 Apr. 1969 (fl), *Contreras 8364* (MO); Chinchilá, Sebol Rd., 10 Mar. 1971 (fl), *Contreras 10706* (F); Carmelita, in thicket bordering aviation field, 29 June 1942 (early fr), *Egler 42-264* (F); 5 km S of Poptún, 1,500 m, 10 June 1970 (fl), *Harmon 2513* (ENCB, F, MO); 13 km S of Flores, 200 m, 28 June 1970 (early fr), *Harmon & Dwyer 2786* (MO); La Cumbre, Cerro la Cueva, 3 km E, in zapotal, 22 Mar. 1977 (fl), *Lundell & Contreras 20637* (MO); entre La Libertad y Subín, 50 km al S de Sta. Elena, 100 m, 10 Nov. 1965 (fr), *A. Molina R. 15498* (F—2 sheets, NY); Tikal National Park, orilla del camino para El Remate, en el km 58, 7 Sep. 1970 (fr), *Ortíz 1296* (ENCB, F, MO, NY); ca. 200 m de Dolores, en orillando el camino para el arroyo Dolores, 16 Feb. 1971 (fr), *Ortíz 1586* (ENCB, F, MO, NY); en el camino que conduce al campamento chiclero Mushanal, a 1.5 km de la aldea de Uaxactún, 16 May 1973 (fl), *Ortíz 2561* (ENCB, F, MO, NY); low forest along Río Chinajá, N of Chinajá on trail towards Zacatal, 50–70 m, 28 Mar. 1942 (fr), *Steyermark 45452* (F). SOLOLÁ: pine woods bordering Río Bravo, nr. Finca Mocá, S-facing slopes of Volcán Atitlán, 1,000–1,100 m, 21 June 1942 (fr), *Steyermark 48002* (F, GH). SUCHITEPÉQUEZ: Finca Mocá, 1,260 m, 8 Jan. 1935 (fl), *Skutch 2087* (A, F). BELIZE. BELIZE: mi. 20–35, Northern Hwy., 2 June 1974 (fl), *Dwyer 12595* (DUKE, F, GH, MO, NY, US); Maskall, Nov. 1933 (fr), *Gentle 928* (A, F, MO, NY, US); 19 Apr. 1934 (fl), *Gentle 1215* (A, F, MO, NY); Big Fall Pine Ridge, 14 June 1933 (fl), *Lundell 4195* (F, K). CAYO: El Cayo, 1 Apr. 1931 (fl), *Bartlett 12907* (F, NY, US); Benque Viejo, bordering Río Mopan, on Bañas Rd., 22 Oct. 1967 (fr), *Contreras 7170* (MO); Roaring Creek and Hummingbird Hwy., 20 Aug. 1969 (fr), *Dwyer 9123* (MO); Millionario, rd. to Cuevas, 29 May 1973 (fl), *Dwyer 10828* (F, GH, MO—2 sheets, NY); Vaca, 5 Mar. 1938 (fl), *Gentle 2307* (A, F, K). COROZAL: 1.5 km W of Northern Hwy., 1.5 km N of Buena Vista, 23 June 1973 (fr), *Dwyer 11373b* (GH); high ridge, 1931–1932 (fr), *Gentle 532* (F, MEXU). ORANGE WALK: along Northern Hwy., mi. 58, 23 June 1973 (fr), *Dwyer 11391a* (F—2 sheets, MO, NY); Honey Camp, Nov. 1928 (fr), *Lundell 107* (F, K, US). TOLEDO: Golden Stream River, upper reach, Bolo Camp, 16 Apr. 1944 (fl), *Gentle 4539* (LL); between Orange Point and Pablow, Broken Cohune ridge, 3 Sep. 1955 (fr), *Gentle 7737* (K, MO). HONDURAS. COMAYAGUA: Villa de Taulabé, Qda. La Caliche, 600 m, 12–13 June 1976 (early fr), *C. Nelson et al. 3542* (MO, TEFH). COPÁN: 6 km NE of Santa Rita, Qda. Jaral, 700 m, 28 Aug. 1975 (fr), *A. Molina R. & A. Molina 30835* (F). CORTÉS: La Cumbre desprendimiento de Sierra de Omoa, 190 m, 30 Nov. 1950 (fr), *A. Molina R. 3466* (GH). EL PARAISO: Qda. Tapahuasca, 1,300 m, 14 Aug. 1964 (fr), *A. Molina R. 14623* (F, NY, US). DISTRITO CENTRAL: Barranco y Qda. de Zambrano, entre Zambrano y La Piramide, 1,500 m, 26 June 1964 (early fr), *A. Molina R. 14245* (F, NY); Río Rancho Quemado, SE of Tegucigalpa, km 20–25 rd. to Sabana Grande, 1,300 m, 9 Nov. 1966 (fr), *A. Molina R. 18652* (F, GH, NY). FRANCISCO MORAZÁN: Qda. Quemada, km 21 vic. Cerro de Hule, 1,300 m, 26 Feb. 1970 (fr), *A. Molina R. 25412* (F, MO, NY). LEMPIRA: Qda. Bañaderos cerca de Lepaera, 1,200 m, 27 Sep. 1963 (fr), *A. Molina R. 12991* (F—2 sheets, NY). OCOTEPEQUE: Lempa River between Sta. Anita and Sta. Fe, 700 m, 3 Sep. 1975 (fr), *A. Molina R. & A. Molina 31059* (ENCB, F, MO). SANTA BARBARA: Montaña Sta. Barbara, above Sauce nr. Lake Yojoa, 1,000 m, 7 Aug. 1948 (fr), *L. O. Williams & A. Molina R. 14513* (GH, MO, US). EL SALVADOR. AHUACHAPÁN: sin. loc., 1922 (fr), *Padilla 303* (US); Sierra de Apaneca, in the region of Finca Colima, 17–19 Jan. 1922 (fr), *Standley 20062* (US). NICARAGUA. JINOTEGA: N slope of Volcán Yalí, 13°15′N, 86°10′W, 1,200–1,400 m, 25 Oct. 1979 (fr), *W. D. Stevens & Grijalva 15136* (MO). NUEVA SEGOVIA: Loma Fria ridge W of Río Las Manos, 20 km NW of Ocotal, 1,200 m, 16 June 1977 (fl), *Neill 2201* (MO). ZELAYA: Río Punta Gorda, Atlanta, desembocadura del Caño el Guineo, 11°33′N, 84°02′W, 10 m, 11 Nov. 1981 (fr), *P. P. Moreno & Sandino 12850* (MO).

Psychotria miradorensis, described from Mexico, is indistinguishable from *P. costivenia*, described from Cuba; the latter name was published only a few months prior to the former.

Leaf blades from Zelaya, Nicaragua, at the southern end of the geographical range, have 15–18 secondary veins, numbers rarely reached in the rest of the range. Inflorescences tend to be smaller in Honduras, El Salvador, and Nicaragua than farther north. The corolla appears generally wider (2 mm) in Honduras than in the rest of the range.

10. Psychotria fendleri Standley, Contr. U.S. Natl. Herb. 18: 129. 1916. TYPE: Panama. Canal Area: Chagres, Isthmus of Panama, 25 Feb. 1850 (fl), *Fendler 59* (holotype, US; isotypes, GH, MO). Figure 17.

Shrub 1–2 m tall; young stems glabrous to minute puberulent, the bark smooth to longitudinally striate; stipules ovate, 5–9 × 3–4 mm, glabrous, caducous, leaving a pale ridge with red-brown fringe. *Leaves* subsessile; petioles to 3 mm long, glabrous, flat and furrowed above; blades coriaceous, stiff, obovate, the apex acute to acuminate, the base attenuate, the margins inrolled, (5–)7–9(–10) × (3–)3.5–5(–5.5) cm, glabrous above and below, drying bright chalky yellow-green above, dull green below, often partly red-brown; secondary veins (6–)8–10 pairs, diverging 50°–70°, brochidodromous, straight, elevated below, glabrous, the secondary loops far from margin, the axils lacking domatia or hairs; tertiary veins inconspicuous, orthogonal reticulate, the tertiary loops between secondary loops and margin evident. *Inflorescences* terminal, panicles of cymes; panicle branched to 3(–4) degrees; main axis 5.5–9 cm

long, the peduncle 3–7 cm long; secondary axes in 2(–3) ranks, the first-rank axes (2 or) 4, the longer pair 0.5–1.5 cm long, the shorter pair 0.2–0.8 cm long, the second-rank axes 2 (or 4), subequal, 0.2–1 cm long, the third-rank axes 2, 0.2 cm long; cymes branched to 1–2 degrees; bracts broad, irregular, ca. 2 mm long, glabrous to puberulent; bracteoles triangular, 0.5 mm long, puberulent. *Flowers* pedicellate, the pedicels 1 mm long; calyx cup-shaped, the tube 1.5 mm long, the lobes 5, triangular, 0.5 × 0.7 mm, glabrous; corolla white, the tube cylindrical, 2.5 × 1.5 mm, white pubescent in throat, the lobes 5, 1.5 × 1 mm; stamens 5, the filaments not seen in pins, 3–4 mm long in thrums, the anthers 1 mm long; style not seen in pins, 2–2.5 mm long in thrums, the branches linear. *Fruit* when dry spherical to ellipsoidal, 4–4.5 mm long, 3–4 mm diam., maturing red, drying black; calyx persistent, to 1.5 mm long, drying green; seed dorsal surface with 4 longitudinal furrows, the ventral surface with 2 longitudinal furrows.

Distribution (Fig. 17). Known from the Caribbean coast of Panama, just east and west of the Canal, collected near sea level in tropical moist to tropical wet forest with equatorial-tropical climate. It has been collected in flower February, April, May, and August; fruiting specimens date from April and August.

Additional specimens examined. PANAMA. CANAL AREA: Fort Sherman, from Piña to 3 mi. NE of Piña, 2 Apr. 1973 (fl), *Liesner 1386* (F, MO). COLÓN: Miguel de la Borda, along steep clay sea coast, 24 Apr. 1970 (fl, fr), *Croat 10023* (F, MO, NY); Isla Grande, 11 Apr. 1970 (fl), *D'Arcy 4020* (MO); María Chiquita, nr. beach, 10 Aug. 1967 (fl, fr), *Dwyer & Kirkbride 7783* (MO—3 sheets, NY); 4.5 km SW of Piña, Qda. Sta. Marta, 0–5 m, 17 May 1974 (fl), *Nee 11682* (MO); *Nee 11688* (MO). SAN BLAS: between Puerto Obaldía and Puerto Armila, coastal rocks, 0–100 m, 29 Apr. 1980 (fl), *D'Arcy 13676* (MO).

Psychotria fendleri may be recognized by its coriaceous, moderate-sized (7–9 cm long) leaves usually drying chalky yellow-green and with brochidodromous secondary venation suggestive of that of *P. horizontalis*. *Psychotria fendleri* is distinguished from *P. horizontalis*, from which it may be a localized derivative, by its coriaceous leaves and chalky color when dry.

The eight flowering specimens examined are all thrums, suggesting that the species is thrum-monomorphic.

11. Psychotria flava Oersted ex Standley, J. Wash. Acad. Sci. 17: 341. 1927. TYPE: Mexico. Veracruz: Misantla (fl), *Liebmann 11605* (holotype, C, n.v., photo, F neg. no. 22830). Figures 7b, 10j, 17.

Shrub or small tree, 2–10 m tall; young stems glabrous to puberulent, the bark pale, smooth; stipules ovate, the apex biaristate, 7–22 × 4–8 mm, the extensions 3–5 mm long, puberulent, fringed, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 1.5–3.5 cm long, glabrous, grooved above; blades membranous, elliptic, the apex acute to acuminate, the base attenuate, 16–40 × 6–13 cm, glabrous above, puberulent to sometimes glabrous below, drying chalky yellow-green to green-brown above, darker green-brown below; secondary veins 14–21 pairs, diverging 60°–70°, eucamptodromous to brochidodromous, straight to constantly arcuate, elevated below, puberulent or sometimes glabrous below, the axils lacking domatia or hairs; tertiary veins evident to conspicuous, orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of glomerules (Fig. 7b); panicle branched to 4 degrees; main axis (9–)13–26 cm long, the peduncle (5–)7–15 cm long; secondary axes in (3–)4 ranks, the first-rank axes 4 or 6, the longer pair 2.5–9.5 cm long, the medium pair 0.7–4 cm long, the shorter pair reduced or to 2 cm long, the second-rank axes 4 or 6, the longer pair (0.3–)1.5–5 cm long, the medium pair (0–)0.7–2 cm long, the shorter pair 0.4–0.5 cm long, the third-rank axes (2 or) 4 or 6, the longer pair (0–)0.3–2 cm long, the medium pair (0–)0.1–0.5 cm long, the shorter pair reduced, the fourth-rank axes 2 (or 4), the longer pair 0.2–0.3 cm long, the shorter pair reduced; bracts triangular to linear, 3–5 mm long, red-brown pubescent, fringed. *Flowers* sessile; calyx cup-shaped, the tube 1 mm long, the lobes 5, triangular to barely evident, to 0.3 × 0.8 mm, puberulent, fringed; corolla white, the tube campanulate, 2.5–3 × ca. 1.5 mm, white pubescent in throat, the lobes 5, linear, 2 × 1–1.2 mm; stamens 5, the filaments 2.5–3 mm long in pins, 4–5 mm long in thrums, the anthers 1 mm long; style 4.5–5 mm long in pins, 2.5–3.5 mm long in thrums, the branches linear. *Fruit* when dry ellipsoidal to slightly obovoid, 8–12(–13) mm long, 6–8(–9) mm diam., maturing red, drying black; calyx sometimes persistent as beak drying pale brown; seed dorsal surface with 6–10 irregular longitudinal furrows, the ventral surface with 1 often T-shaped longitudinal furrow (Fig. 10j).

Distribution (Fig. 17). Known from southern Mexico, primarily the Gulf coast, and Petén, Guatemala, occurring at elevations of 20–1,000 m, mostly under 200 m, in evergreen forest with equa-

torial-tropical to tropical-mountainous climate. *Psychotria flava* has been collected in flower almost exclusively February–May and in fruit throughout the year, primarily August–December.

Selected specimens examined. MEXICO. CHIAPAS: Mpio. Ocozocoautla de Espinosa, 46 km N of Ocozocoautla on rd. to Mal Paso, 700 m, 8 Oct. 1974 (fl, fr), *Breedlove 38672* (MEXU, MO); Palenque, Ruina, 10–12 July 1939 (early fr), *Matuda 3710* (A, F—2 sheets, MEXU); Mpio. Pichucalco, al NO de Pichucalco o a la Montaña del Carbón, 20–21 Aug. 1950 (fr), *Miranda 6594* (MEXU). OAXACA: Dto. Juchitán, a 23 km al SE de Lázaro Cárdenas, camino Juchitán a Sta. María Chimalapa, 330 m, 11 Mar. 1982 (fl), *Cedillo & Torres 1143* (MEXU, MO); Dto. Choapam (= Santiago Choapan), Yaveo, trail del Chorro, 460 m, 27 Mar. 1938 (fl), *Mexia 9221* (B, F, GH, K, MO, NY, US); Mpio. Matías Romero, 3–5 km al S del Aserradero La Floresta, 16–18 km al S de Esmeralda, 17°02′N, 94°47′W, 200 m, 8 Apr. 1981 (fl), *Wendt et al. 3163* (ENCB, MEXU). PUEBLA: Mpio. de Cuetzalan, Cuauhtapanaloyan, 21 Nov. 1980 (fr), *Basurto-Rafael 246* (MEXU). TABASCO: km 7 camino Tacotalpa–Tapijulapa, Cerro del Madrigal, 150 m, 5 Apr. 1980 (fl), *Cowan 2890* (ENCB); 32 km al SE de Emiliano Zapata, camino a Tenosique, Rancho La Ceiba, 60 m, 5 Mar. 1983 (fr), *R. Fernández N. & Guadarrama-Zamudio 1379* (MO—2 sheets); Mpio. Huimanguillo, 3 km W de Chontalpa, 20 m, 2 Mar. 1972 (fr), *Puig 669* (MEXU). VERACRUZ: cerca da la cima del Cerro Blanco al NW de Santiago Tuxtla, 6 June 1972 (early fr), *Beaman 6081* (F, MEXU, NY); Mpio. San Andres Tuxtla, cima de la Estación de Biología Tropical Los Tuxtlas, Feb. 1971 (fl), *Calzada 116* (F, MEXU); 2 Aug. 1972 (fr), *Villegas 30* (F, MEXU—2 sheets, NY); Mpio. Hidalgotitlán, km 0–3 camino Cedillo–La Laguna, 17°20′N, 94°35′W, 140 m, 10 May 1974 (fr), *B. Dorantes 3028* (ENCB, F, MEXU); Mpio. Pajapán, camino a Jicacal a Pajapán, 0–5 m, 20 Apr. 1980 (fr), *Gutiérrez & J. Dorantes L. 234* (MEXU); Mpio. Catemaco, Sontecomapan, arroyo basuras, 100 m, 25 Sep. 1971 (fr), *R. Hernández M. 1250* (ENCB, F, GH, MEXU); Mpio. Jesús Carranza, carret. de Palomares a Uxpanapa, Río Alegre, 150 m, 9 Dec. 1975 (fr), *Monsalvo 11* (MEXU); Mpio. Soteapan, cerca de San Fernando, Santa Martha, 18°22′N, 94°54′W, 1,123 m, 22 Dec. 1978 (fr), *Ortega et al. 1225* (ENCB); Mpio. Misantla, 500 m, 15 Dec. 1975 (fr), *Ventura 12258* (ENCB); Mpio. Tlapacoyán, El Limón, 300 m, 27 Jan. 1981 (fr), *Ventura 18139* (MEXU); Mpio. Minatitlán, 1 km al N de Poblada 13 en el camino a Uxpanapa (Pob. 12), 17°16′N, 94°09′W, 130 m, 16 May 1983 (fl), *Wendt et al. 4090* (MEXU). GUATEMALA. PETÉN: Remate, on Tikal Rd., ca. 8.5 km NE of the village, 13 May 1960 (fl), *Contreras 936* (MO); Dolores, in pineland on Old Machaquila Rd., ca. 1.8 km S, 16 May 1961 (fl), *Contreras 2304* (LL).

Psychotria flava may be recognized by its large elliptic leaves drying chalky yellow-green to green-brown and by its large panicles of glomerules with three unequal pairs of secondary axes per rank (Fig. 7b). It differs from *P. costivenia* in having much larger leaves, glomerules instead of cymes in the inflorescence, and 6–10 irregular (vs. 4–5 regular) longitudinal furrows on the seed dorsal surface and one T-shaped (vs. two) longitudinal furrows on the ventral surface (Fig. 10j).

12. Psychotria grandis Swartz, Prodr., 43. 1788. *Uragoga grandis* (Sw.) Kuntze, Revis. Gen. Pl. 2: 960. 1891. TYPE: Jamaica: Jamaicae interioris occidentalis (fl), *Swartz s.n.* (holotype, S, n.v., photo, A). Cf. also Swartz, Fl. Ind. Occid. 417. 1797. Figures 10i, 19.

Tree or shrub, (1–)4–10 m tall; young branches red-brown puberulent, the bark smooth; stipules ovate, the apex acuminate, often with central keel, usually diverging from stem, the margins usually reflexed, the center paler, 10–20(–25) × 6–14 (–20) mm, glabrous or sometimes red-brown puberulent in center, sometimes fringed, caducous, leaving a pale ridge with red-brown fringe, often persistent at terminal 3–6 nodes. *Leaves* petiolate; petioles 0.3–2 cm long, glabrous, flat above; blades membranous, obovate to sometimes oblanceolate, the apex acuminate, the base attenuate, (10–)17–32(–39) × (3.5–)7.5–11(–16) cm, glabrous above, glabrous or densely puberulent below, drying green-brown to red-brown; secondary veins 13–19 pairs, diverging (65°–)70°–85°, eucamptodromous to brochidodromous, constantly arcuate, slightly elevated, glabrous or densely pubescent below, the axils lacking domatia or hairs; tertiary veins evident, orthogonal reticulate to slightly percurrent, the intersecondaries often conspicuous. *Inflorescences* terminal or pseudoaxillary, robust panicles of cymes; panicle branched to 5 degrees; main axis 18–33 cm long, the peduncle 11–18 cm long; secondary axes in 4–5 ranks, the first-rank axes (2 or) 4 or 6, the longer pair 5–10 cm long, the medium pair 3.5–6 cm long, the shorter pair 2.5 cm long, the second-rank axes 2 or 4, the longer pair 2.5–6 cm long, the shorter pair 0.7–4 cm long, the third-rank axes 2 or 4, subequal, 0.7–2 cm long, the fourth-rank axes 4, equal, 0.3–1 cm long, the fifth-rank axes 2, 0.3–0.5 cm long; cymes branched to 2–3 degrees; bracts triangular, ca. 2 mm long, often tomentose within; bracteoles lanceolate, 0.5–1.5 mm long, red-brown puberulent. *Flowers* sessile to pedicellate, the pedicels to 1.5 mm long; calyx cup-shaped, the tube 0.5 mm long, the lobes 5, triangular to barely evident, to 0.3 × 0.5 mm, puberulent; corolla white, the tube cylindrical to campanulate, 2.5 × 1.5 mm, white pubescent in throat, the lobes 5, ovate, 1.5–2 × 1 mm; stamens 5, the filaments 2 mm long in pins, 3.5–4 mm long in thrums, the anthers 0.8 mm long; style 4 mm long in pins, 2.5 mm long in

thrums, the branches linear. *Fruit* when dry spherical to slightly ellipsoidal, 5–6.5(–8) mm long, 4.5–6(–7) mm diam., maturing red, drying black or sometimes red-brown; persistent calyx inconspicuous or a minute beak, drying pale brown; seed dorsal surface with 10–15 irregular longitudinal furrows, the ventral surface with 2 very deep longitudinal furrows (Fig. 10i).

Distribution (Fig. 19). Commonly collected from Belize, Guatemala, and adjacent Honduras near the Caribbean coast and also from Nicaragua–Panama, where it reaches the Pacific side. It occurs also in the Greater Antilles—Cuba, Jamaica, Hispañola, and Puerto Rico—and Colombia, Venezuela, and Ecuador. In Central America this species ranges in elevation 0–2,000 m, reaching over 500 m only occasionally, and is found in tropical moist to premontane rain forest with equatorial to tropical-equatorial climate. *Psychotria grandis* has been collected in flower almost exclusively March–July and in fruit throughout the year, especially August–January.

Selected specimens examined. GUATEMALA. ALTA VERAPAZ: region of Cocolá, NE of Carchá, 1,200 m, 2 Apr. 1939 (fl), *Standley 70305* (F); woods between Finca Cubilgüitz and Hda. Yaxcabanal, 300 m, 7 Mar. 1942 (fr), *Steyermark 44833* (F, US); along Río Sebol, downstream from Carrizal, 150–200 m, 19 Apr. 1942 (fr), *Steyermark 45800* (F—2 sheets, NY); Cobán, 1,350 m, Apr. 1908 (fl), *Türckheim II-1828* (F, GH, MO, NY, US). HUEHUETENANGO: ca. 27 km N of Barillas, vic. Maxbal, Sierra da los Cuchumatanes, 1,500 m, 15–16 July 1942 (early fr), *Steyermark 48850* (F–2 sheets); around Ixcan at "Patcushín," Sierra de los Cuchumatanes, 500 m, 22 July 1942 (early fr), *Steyermark 49197* (F). IZABAL: Puerto Méndez, 5 Aug. 1966 (fr), *Contreras 5907* (MO); vic. Puerto Barrios, 0 m, 2 June 1905 (fl), *Pittier 377* (NY, US); Jaqua trail to creek, Finca Murielago, 28 May 1966 (fl), *Snedaker D-127* (A, F); vic. Quiriguá, 75–225 m, 15–31 May 1922 (fl), *Standley 23866* (GH, NY, US); between Bananera and "La Presa" in Montaña de Mico, 40–300 m, 28 Mar. 1940 (st), *Steyermark 38103* (F). PETÉN: 47 km S of Poptún, 29 June 1970 (fl), *Harmon & Dwyer 2837* (MO, NY); San Luis, en orillando el camino para La Cumbre, a km 120, 3 Dec. 1970 (fr), *Ortíz 1447* (DUKE, F, GH, MO); Parque Nacional de Tikal, en orillando la aguada del Hotel Posada la Selva, lado SE, 1 June 1971 (fr), *Ortíz 1827* (F, NY, US); San Luis, 9 May 1976 (fl), *Ventur 267* (F). BELIZE. TOLEDO: Columbia Forest Station, nr. entrance, 11 June 1973 (fl), *Dwyer 11091* (GH, MO); Río Temash, 26 July 1979 (fr), *Dwyer 14793* (MO); vic. Columbia Forestry Station, N of San Antonio, 90–150 m, 11–12 June 1973 (fl), *Gentry 8076* (F, MO, NY); Sand Hill, Punta Gorda, 90 m, 1 Sep. 1932 (fr), *Schipp 1013* (A, F, GH, K, MO, NY). HONDURAS. ATLANTIDA: Cuyamel, 2 Jan. 1923 (fr), *Carleton 429a* (US); Corozal, orilla del Río Juana Leandra, 100 m, 1–3 May 1980 (fl), *C. Nelson 5534* (TEFH); E of Tela, nr. Yoro trail, 30 m, 9 Aug. 1934 (fr), *Yuncker 4975* (A, F, MO); 23 km E of La Ceiba, plains nr. Roma siding of S. F. Co. RR, 21 July 1938 (fr), *Yuncker et al. 8567* (F, GH, K, MO, NY, US). OLANCHO: Mata de Maíz, 30 km NE Culmí, 700 m, 1–4 May 1975 (fl), *C. Nelson & Vargas 2740* (MO). NICARAGUA. CHONTALES: 4 km al NO de Santo Domingo, 12°17′N, 85°06′W, 280 m, 12–13 May 1984 (fl), *Grijalva 3793* (MO). RÍO SAN JUAN: along Río San Juan between San Juan del Norte and Delta de San Juan, 0–50 m, 24–25 Mar. 1961 (fl), *Bunting & Licht 855* (F). RIVAS: Isla Ometepe, Volcán Maderas, Balgüe, 11°26′N, 85°30′W, 1,200–1,260 m, 1 May 1984 (fl), *Robleto 524* (MO). ZELAYA: Comarca del Cabo, San Mateo, 16 mi. al S de Tronquera cerca de Río Wawa, 35 m, 22 Aug. 1965 (fr), *A. Molina R. 15083* (F, NY); Río Punta Gorda, Atlanta, "La Richard," 11°32′N, 84°05′W, 20 m, 13 Nov. 1981 (fr), *P. P. Moreno & Sandino 13027b* (MO); 12 km NE of La Cruz de Río Grande, 10 m, 10 June 1978 (fl), *Neill 4375* (MO); Caño El Ocote, 13°38′N, 85°04′W, 340 m, Apr. 1983 (fl), *Ortíz 1388* (MO); Caño Serrano, 40 km E of Nueva Guinea, 1 Apr. 1984 (fl), *Sandino 4952* (MO); vic. El Recreo, on Río Mico, 30 m, 23 Apr.–14 May 1949 (bud), *Standley 19362* (F); new rd. to Mina Nueva America, more or less westward from ca. 14.3 km N of El Empalme on main rd. to Rosita, ca. 8.6 km from main rd., 27 Apr. 1978 (fl), *W. D. Stevens 8399* (MO); Monkey Point, 11°35′N, 83°39′W, 0–20 m, 7 Apr. 1981 (bud), *W. D. Stevens 20025* (MO). COSTA RICA. ALAJUELA: rd. between Cañas and Upala, 10 km N of Bijagua, 200 m, 26 June 1976 (early fr), *Croat 36465* (MO, US); 4 km SE of Fortuna, 10°29′N, 84°43′W, 29 Apr. 1983 (fl), *Liesner et al. 15222* (MO). CARTAGO: Río Reventazón, nr. Inter-American Institute of Agricultural Sciences, 3 km SE of Turrialba, 9°55′N, 83°41′W, 500–600 m, 20 June 1949 (early fr), *Holm & Iltis 22* (B, F, NY). HEREDIA: Finca La Selva, OTS field station on Río Puerto Viejo, 100 m, 4 Aug. 1980 (fr), *Hammel 9447* (DUKE); along Río Vueltas from old rd. to Carillo, 10°05′N, 84°05′W, 2,000 m, 6 May 1982 (fl), *Hufi & Barringer 2030* (CR, MO). LIMÓN: 1.6 km E of Guápiles, 200 m, 9 July 1949 (fr), *Holm & Iltis 355* (F); rd. from Moin to Puerto Limón, 10 m, 1 Sep. 1946 (fr), *Morley 811* (F, US); drenajes de los Ríos Parismina y Reventazón, 0 m, 3 Oct. 1951 (fr), *Shank & Molina 4154* (F, GH). PUNTARENAS: Corcovado National Park, nr. Sirena, 8°29′N, 83°36′W, 0–200 m, 5 July 1977 (early fr), *Liesner 2944* (CR, MO); Sto. Domingo de Golfo Dulce, Mar. 1896 (fl), *Tonduz 7053* (US). SAN JOSÉ: basin of El General, 675–900 m, May 1940 (fl), *Skutch 4949* (CR, F, US). PANAMA. BOCAS DEL TORO: Almirante region, 1927 (fl), *Cooper & Slater 33* (US); Súrsuba, 10 Sep. 1963 (fr), *Dwyer 4387* (US); Río Cricamola between Finca St. Louis and Konkintoë, 10–50 m, 12–16 Aug. 1938 (fr), *Woodson et al. 1918* (A, F, MO). CANAL AREA: Pipeline Rd. 5.6 mi. from gate, 6 Dec. 1970 (fr), *Croat 12757* (DUKE, F, MO, NY); Fort Sherman, 30 Nov. 1966 (fr), *Dwyer 7179* (GH, MO); Barro Colorado Island, 25 Feb. 1932 (fl), *Woodworth & Vestal 700* (A, F, MO). CHIRIQUÍ: Progreso, July–Aug. 1927 (fr), *Cooper & Slater 186* (F, US); Puerto Armuelles, 15 m, 15 Aug. 1938 (fr), *M. Davidson 1120* (F); vic. San Bartolomé, Peninsula de Burica, 0–50 m, 28 July–1 Aug. 1940 (fr), *Woodson & Schery 946* (F, MO). DARIÉN: vic. El Real, 15 m, 7 Oct. 1938 (fl, fr), *Allen 951* (GH, MO, NY, US); Río Chucunaque, between Río Membrillo and Río Subcutí, 22 Aug. 1966 (fr), *Duke 8597* (MO, US); Río Piña, 2 Mar. 1967 (fl), *Duke 10568* (MO, US); Serranía del Sapo, 7°40′N, 78°10′W, 450 m, 2 Jan. 1981 (fl, fr), *W. Hahn*

296 (MO); Manené to mouth of Río Cuasi, 28 Apr. 1968 (fl), *Kirkbride & Bristan 1460* (MO, NY); trail from Paya to Pucro, 12 June 1959 (early fr), *Stern et al. 426* (GH, MO, US); vic. Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, 5 July 1959 (early fr), *Stern et al. 935* (GH, MO, US). LOS SANTOS: Loma Prieta, 800–900 m, 8 June 1967 (fl), *Duke 11897* (MO); on rd. cut towards Veraguas from El Cortezo, 300–600 m, 26 Oct. 1978 (fr), *Hammel 5321* (MO). PANAMÁ: vic. Pacora, 35 m, 5 Nov. 1939 (fl), *Allen 2035* (GH, MO, NY, US); La Chorrera, frente a la fábrica Maribel, 20 Nov. 1971 (fr), *Atencio 11* (DUKE, MO); Río Pita, 1–3 mi. above confluence with Río La Maestra, 14 Oct. 1961 (early fr), *Duke 4759* (GH, MO); El Llano–Cartí rd., 1.4 km N of Panam. Hwy., 150 m, 8 Jan. 1974 (fr), *Nee & Dwyer 9235* (F, MO). SAN BLAS: headwaters of Río Cuadí, 100 m, 18 Dec. 1967 (fl), *Duke et al. 3652* (MO); mainland opposite Playón Chico, 0–3 mi. from Caribbean, 0–200 m, 4 Oct. 1972 (fr), *Gentry 6417* (F, MO); nr. Puerto Obaldía, 8°40′N, 77°25′W, 0 m, 16 Apr. 1982 (fl, fr), *Knapp & Mallet 4641* (MO—2 sheets). Veraguas: Isla de Coiba, 16 Aug. 1961 (early fr), *Dwyer 1540* (MO).

Psychotria grandis may be recognized by its large size (to 10 m tall), robust keeled stipules with margins reflexed and usually persistent at terminal 3–6 nodes, large (17–32 cm long) leaves with conspicuous intersecondary veins, large robust inflorescences, and fruit drying spherical and smooth, the latter due to the seed dorsal surface having many shallow irregular furrows instead of few deep furrows (Fig. 10i). The distinction between this species and *P. costivenia* is somewhat problematic, as it is based largely on quantitative characters, such as leaf and stipule and inflorescence size. Differences in seed cross section (10–15 irregular vs. 4–5 deep regular furrows on dorsal surface) support the distinction. The two species occur sympatrically only in northern Guatemala and southern Belize.

General puberulence is common only in Belize and Honduras. Material from Belize has the longest stipules; Guatemalan material has the largest inflorescences; and Nicaraguan fruit is generally larger than elsewhere.

13. Psychotria horizontalis Swartz, Prodr., 44. 1788. *Uragoga horizontalis* (Sw.) Kuntze, Revis. Gen. Pl. 1: 300. 1891. *Myrstiphyllum horizontalis* (Sw.) Millsp., Publ. Field Mus. Nat. Hist., Bot. Ser. 2: 102. 1900. TYPE: Hispaniola (fr), *Swartz s.n.* (holotype, S, n.v., photo, A; isotype, B—Willdenow 4087). Cf. also Swartz, Fl. Ind. Occid., 410. 1797. Figures 3b, 9e, 10b, 16.

Psychotria glaucescens Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 3: 358. 1819. *Uragoga glaucescens* (Kunth) Kuntze, Revis. Gen. Pl. 2: 960. 1891. *Psychotria horizontalis* Sw. var. *glaucescens* (Kunth) Steyerm., Mem. New York Bot. Gard. 23: 472. 1972. TYPE: Venezuela. In ripa Orinoci fluminis, June (fl, fr), *Bonpland s.n.* (holotype, P, n.v.).

Psychotria longicollis Bentham in Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 33. 1853. *Uragoga longicollis* (Benth.) Kuntze, Revis. Gen. Pl. 2: 961. 1891. TYPE: Costa Rica. Cartago: nr. Turrialba, ca. 900 m, May (fr), *Oersted s.n.* (holotype, C, n.v., photo, MO).

Psychotria bimea L. Riley, Kew Bull. 1927: 124. 1927. TYPE: Panama. Panamá: between Panamá and Sabanas, 14 June 1924 (fl), *Riley 112* (holotype, K, n.v.; isotype, MO).

Psychotria horizontalis Swartz subsp. *basicordata* Dwyer, Ann. Missouri Bot. Gard. 55: 42. 1968. TYPE: Panama. Veraguas: Isla de Coiba, Camp Aguja, 8 July 1962 (early fr), *Dwyer 2384a* (holotype, MO—2165270; isotype, MO).

Psychotria horizontalis Swartz var. *psilophylla* Steyermark, Mem. New York Bot. Gard. 23: 472. 1972. TYPE: Colombia. Magdalena: nr. Masinga Vieja, Sta. Marta, 300–450 m, May 1898–1899 (fl), *H. H. Smith 393* (holotype, NY; isotypes, F, GH).

Shrub 1–3 m tall; young stems glabrous or puberulent or ferrugineous-pubescent, the bark pale, smooth; stipules sheathing, ovate-acuminate, (2.5–)4–7 × 2–3.5 mm, puberulent to ferrugineous-pubescent, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles (1–)2–13 mm long, glabrous to puberulent to ferrugineous-pubescent, flat or grooved above; blades membranous, elliptic or rarely ovate, the apex acute to long-acuminate, the base cuneate to sometimes cordate, the margins often crenate, (6–)7.5–15 (–17) × 3–6.5(–8) cm, glabrous above, glabrous to puberulent on midvein to puberulent below, drying dull green or sometimes red-brown; secondary veins (6–)8–11(–14) pairs, diverging (45°–)60°–75°, brochidodromous, the secondary loops far from margin (Fig. 3b), increasingly arcuate toward margin, prominulous below, glabrous or sometimes puberulent below, the axils sometimes with minute domatia below; tertiary veins evident to conspicuous, orthogonal reticulate, the loops between secondary loops and margins evident. *Inflorescences* terminal or pseudoaxillary, globose panicles of cymes; panicle branched to 3 degrees; main axis (2.5–)4–10 cm long, the peduncle rarely lacking or (2–)3–7 cm long; secondary axes in (2–)3–4 ranks, the first-rank axes 4 or 6, the longer pair (0.7–)1–2 cm long, the medium pair 0.4–1.4 cm long, the shorter pair 0.3–0.6 cm long, the second-rank axes 2 or 4, the longer pair (0.2–)0.4–0.9 cm long, the shorter pair 0.3–0.6 cm long, the third-rank axes 2, 0.1–0.3 cm long, the fourth-rank axes 2, 0.1–0.2 cm long; cymes branched to 1(–2) degrees; bracts inconspicuous, linear to tri-

angular, to 5 mm long, puberulent to ferrugineous-pubescent; bracteoles linear, to 1 mm long, puberulent to ferrugineous-pubescent. *Flowers* pedicellate, the pedicels 0.5–1.5 mm long; calyx campanulate, the tube 0.5 mm long, the lobes 5, lanceolate, (0.5–)1–2 × 0.6 mm, puberulent; corolla white, the tube cylindrical, 2.5–3.5 × 1.3–1.5 mm, white pubescent in throat, the lobes 5, lanceolate, 1.5–2 × 0.6 mm; stamens 5, the filaments (2.5–)3–3.5 mm long in pins, 5–6 mm long in thrums, the anthers 0.8–1 mm long; style (4.5–)5–6 mm long in pins, 3–3.5 mm long in thrums, the branches linear, often recurved. *Fruit* when dry ellipsoidal, 3.5–4.5(–5) mm long, 2.5–3.5(–4) mm diam., maturing red, drying red-brown, sometimes sparsely puberulent; persistent calyx of conspicuous lanceolate lobes, 1–3(–5) mm long (Fig. 9e); seed dorsal surface with 3–5 longitudinal furrows, the ventral surface with 2 longitudinal furrows (Fig. 10b).

Distribution (Fig. 16). Known from Mexico, primarily the Pacific coast from Sinaloa eastward, through Panama, ubiquitous throughout its range at elevations of 0–1,300 m, mostly below 600 m, in tropical moist to premontane wet to sometimes tropical dry forest (deciduous forest in western Mexico) with equatorial or usually tropical or sometimes subtropical-tropical climate. *Psychotria horizontalis* occurs also in Cuba, Hispaniola, Colombia, Venezuela, the Guianas, Ecuador, and Brazil. It has been collected in flower June–August in Mexico and primarily March–July throughout the rest of its range; fruiting collections come from throughout the year, primarily August–March.

Selected specimens examined. MEXICO. CHIAPAS: Mpio. Frontera Comalapa, 6–8 km E of Frontera Comalapa along rd. to Ciudad Cuauhtemoc, 1,000 m, 15 Aug. 1972 (fr), *Breedlove 26989* (MEXU); Mpio. Arriaga, 6 km N of Arriaga, 250 m, 23 Aug. 1972 (fr), *Breedlove 27286* (ENCB); Mpio. Ocozocoautla de Espinosa, canyon at head of Río de la Venta at the chorreadero nr. Derna, 800–1,000 m, 1 Sep. 1976 (fr), *Breedlove 39816* (MEXU); Mpio. Ocosingo, ruins of Yaxchilan on banks of Río Usumacinta, 300 m, 20–21 Dec. 1976 (fr), *Breedlove 42841* (MEXU, MO); 4 mi. N of Tapachula along rd. to Nueva Alemania, 250 m, 20 Aug. 1977 (fr), *Croat 43779* (MO); Sierra de Tonala, Sep. 1913 (fr), *Purpus 7023* (F, GH, MO, NY, US). GUERRERO: Montes de Oca, Vallecitos, 500 m, 26 June 1937 (fl), *Hinton et al. 10368* (K, LL, NY, US); Mpio. Atoyac, 19 km NE of Atoyac, nr. Santiago La Unión, 770 m, 3 Nov. 1979 (fr), *Koch et al. 79294* (MEXU); Rincón Viejo, nr. Agua de Obispo, 710 m, 11 June 1960 (fl), 13 Aug. 1960 (fr), *Kruse 277* (ENCB). JALISCO: carret. Guadalajara–Colima, a la altura de Pihuamo, cerca del río, 750 m, 24 July 1966 (fl), *Puga 569* (ENCB); Mpio. La Huerta, Estación de Biología Chamela, selva baja caducifolia perturbada, 19°30′N, 105°03′W, 25 Sep. 1981 (fr), *Lott 575* (MEXU, MO); Mpio. La Huerta, Puerto Vallarta–Barra de Navidad, ca. 7 km al SE de la Estación de Biología Chamela, 27 Oct. 1981 (fr), *Lott & Magallanes 625* (MEXU). MICHOACÁN: Coalcomán, Villa Victoria, 700 m, 11 July 1939 (fl), *Hinton 13912* (F, GH, MO, NY, US). NAYARIT: Old San Blas, on hill, 6 Oct. 1925 (fr), *Ferris 5417* (US—2 sheets). OAXACA: deep ravine along stream nr. Hwy. 185 ca. 5 km N of junction with rd. to Matías Romero, 200–300 m, 20 Aug. 1974 (fr), *J. Conrad & R. Conrad 3006* (MO); 2 km E of Zanatepec, Route 190, 50 m or less, 21 July 1959 (early fr), *King 1955* (US); Mpio. Juquila, 1 km al S de Charco Redondo en el Parque Nacional "Lagunas de Chacahua," 3–5 m, 4 Aug. 1979 (fr), *Loera et al. C-3* (MEXU); Jamiltepec, 1.5 km al N del Rosario y 13 km al N de Jamiltepec, 22 Oct. 1982 (fr), *Torres et al. 1646* (ENCB, MEXU, MO). SINALOA: Mazatlán, San Ignacio, San Juan, 200 m (fl), *J. González Ortega 4013* (MEXU, US); Mazatlán, San Ignacio, Arroya del Palmarito, 220 m, 25 Sep. 1918 (fr), *Montes & Salazar 614* (US). TABASCO: Mpio. Tenosique, a ca. 15 km arriba de La Palma por río, a 0.5 km del rancho Punta de Montaña del Sr. Angel Zubieta, 4 July 1981 (fl), *Cowan & Niño 3385* (MEXU, MO); Balancán, ejido el Soberano a 7 km del ejido El Palmar, 10 Dec. 1975 (fr), *Novelo et al. 204* (MO). GUATEMALA. CHIQUIMULA: moist thickets of Esquipulas River, 1,100 m, 26 Sep. 1971 (fr), *A. Molina R. & A. Molina 26735* (ENCB, F). ESCUINTLA: jct. of CA-2 and Río Coyolate, 300 m, 26 May 1970 (fl), *Harmon & Fuentes 2375* (ENCB, MO—2 sheets). HUEHUETENANGO: canyon tributary to Río Trapichillo, between Democracia and canyon of Chamushú, 1,000–1,100 m, 24 Aug. 1942 (early fr), *Steyermark 51230* (A, F). IZABAL: Quiriguá, 75–225 m, 15–31 May 1922 (fl), *Standley 24701* (GH, US). PETÉN: La Libertad and vicinity, 3 June 1934 (fl), *M. Aguilar H: 260* (F, GH, K, MO, NY); ca. 1.5 km S of Lacandón, 5 Mar 1962 (fr), *Contreras 3466* (MO); bordering Lake Petén Itza, between San José and Chachaclum, low forest, 25 Jan. 1971 (fr), *Contreras 10396* (MO); Santa Elena, en orillando el camino para La Libertad, a km 20, 13 Dec. 1970 (fr), *Ortíz 1500* (ENCB, F, MO, NY); en el camino que conduce a Arroyo Pucte, km 40 S saliente de Sayaxché, 15 June 1973 (fl), *Ortíz 2698* (F, US); Cerro Ceibal (Sierra Mojada), between mouth of Río Santa Mónica and mouth of Río San Martín, on W side of Río Cancuen, 75–150 m, 30 Apr. 1942 (st), *Steyermark 46101* (F). SANTA ROSA: Santa Rosa, 900 m, May 1903 (fl), *Heyde & Lux 4494* (F, US—2 sheets); nr. Oratorio, 1,200 m, 21 Dec. 1938 (st), *Standley 60657* (F); nr. Cuilapa, 895 m, 20–27 Nov. 1940 (fr), *Standley 77925* (A, F). SUCHITEPÉQUEZ: 6 km W of Cuyotenango, rubber finca of government experiment station Los Brillantes, 300 m, 16 May 1970 (fl), *Harmon 2340* (MO); vic. Tiquisate, 100 m, 17 June 1942 (fr), *Steyermark 47694* (F, GH). BELIZE. BELIZE: Gracie Rock, 1.5 mi. S of mile 22 on Western Hwy., 4–5 June 1973 (fl), *Croat 23838* (F, MO, NY). CAYO: Cocquericot, 16 Mar. 1931 (fl), *Bartlett 12043a* (F); Spanish Lookout Crossing E of Belize River along rd., 17 Mar. 1967 (st), *Dwyer et al. 167* (MO); vic. Blancaneaux Lodge, 26 km S of Georgeville, Mt. Pine ridge, 600 m, 24 Jan. 1974 (fr), *Liesner & Dwyer 1598* (GH, MO); Caves Branch, Mountain Cow hill, 25 July 1976 (fl), *Whitefoord 1119* (MO). ORANGE WALK: Indian Church, 27 June 1976 (fl, fr), *Arnason & Lambert 17081* (MO). HONDURAS. COMAYAGUA: Qda. Las Mercedes, Valle Comayagua, 650 m, 28 June 1964 (fl), *A. Molina R. 14378* (F, NY); Río Hondo, 5 km to La Libertad,

500 m, 17 Oct. 1971 (fr), *A. Molina R. & A. Molina 26857* (F). COPÁN: Copán Ruins on rd. to Sta. Rita, Qda. Seca, 500 m, 19 Nov. 1969 (fr), *A. Molina R. & A. Molina 24627* (F, NY). CORTÉS: Ocote Arrancado, 50 km N Lago de Yojoa, 600 m, Nov. 1980 (fr), *C. Nelson et al. 5574* (TEFH). EL PARAISO: matorrales del Río Teupasenti cerca del pueblo de Teupasenti, 600 m, 26–27 Apr. 1963 (fl), *A. Molina R. 11910* (F); Las Mesas region nr. Yuscarán, Aug. 1960 (early fr), *Pfeifer 1511* (US). FRANCISCO MORAZÁN: 5 km O de Cedros, orillas de riachuelo Chimbo, 900–1,000 m, 28–30 May 1976 (fl), *C. Nelson & Vargas 3473* (MO); Sabana Grande, 1,100 m, 26 Aug. 1945 (early fr), *J. V. Rodríguez 3271* (F); drainage of Río Yeguare, between Las Mesas and Sta. Clara, 14°N, 87°W, 900 m, 3 Sep. 1949 (early fr), *L. O. Williams 15953* (F, GH). ISLAS DE LA BAHIA: Island of Roatán, nr. town of Roatán, 16 Aug. 1970 (early fr), *Harmon & Dwyer 3945* (ENCB, F, MO, NY, US). OCOTEPEQUE: nr. San Antonio, forest El Cerro, 1,300 m, 30 Aug. 1968 (fr), *A. Molina R. 22447* (F, NY—2 sheets). SANTA BARBARA: W side Lago de Yojoa, 850 m, 16 May 1972 (fl), *Burch 6091* (MO, NY); Los Dragos, on Río Chamelecón SW of Quimistán, 265–360 m, 16–17 Apr. 1947 (st), *Standley & Lindelie 7454* (F). VALLE: Planada del Puerto de San Lorenzo, 0 m, 7 Aug. 1955 (early fr), *A. Molina R. 5404* (F). EL SALVADOR. AHUACHAPÁN: 0–3 km NE of San Francisco, rd. to Tacuba, 200–450 m, 28 July 1977 (fr), *Croat 42072* (MO). CHALATENANGO: rd. to Chalatenango, 3 km E of Hwy. 4, 200 m, 10 June 1970 (fl), *Davidse & Pohl 2070* (F, MO, NY). SAN SALVADOR: camino al Cerro El Voladero, 5 km al oriente de Panchimalco, 22 May 1968 (fl), *A. Pérez & J. González 39* (MEXU). NICARAGUA. BOACO: N slope of Cerro Mombachito, between Cerro and main Boaco–Camoapa rd., 12°25′N, 85°33′W, 500–900 m, 8 Oct. 1979 (fr), *W. D. Stevens 14709* (MO). CARAZO: El Crucero, 1,000 m, 21 June 1981 (fl), *R. López 17* (HNMN). CHINANDEGA: 3–4 km al SE de San Pedro de Potrero Grande, "Los Laureles," 13°15′N, 86°53′W, 340–400 m, 28 Sep. 1981 (fr), *P. P. Moreno 11692* (MO). CHONTALES: bridge over Qda. Niscala along rd. between Acoyapa and Río Oyate, 11°47′N, 85°01′W, 50 m, 7 June 1981 (fl), *Henrich & Stevens 167* (MO); Juigalpa, km 118 carret. al Rama, "Cerro Grande," 12°09′N, 85°31′W, 200–230 m, 20 Aug. 1982 (fr), *P. P. Moreno 16953* (MO); vic. La Libertad, 500–700 m, 29 May–1 June 1947 (fl), *Standley 9124* (F); 2.8 km N of Cuapa, 12°17′N, 85°23′W, 400–500 m, 30 Dec. 1983 (fr), *W. D. Stevens 22698* (MO). ESTELÍ: Salto de Estanzuela, Río Estanzuela ca. 6 km S of Estelí, 13°01′N, 86°20′W, 920–1,020 m, 1 Oct. 1979 (fr), *W. D. Stevens et al. 14473* (MO). LEÓN: carret. a León, Hda. "El Chanal," a 2 km hacia León del empalme León–La Paz Centro, 26 Sep. 1982 (fr), *Grijalva & Grijalva 1282* (MO). MANAGUA: km 24 on Hwy. 12 (carret. vieja a León), 7 km WSW of summit of Sierra de Managua, 12°04′N, 86°26′W, 200 m, 7 July 1977 (fl), *W. D. Stevens 2653* (MO). MASAYA: Parque Nacional Volcán Masaya, 350 m, 6 Aug. 1982 (fr), *Grijalva 999* (MO). MATAGALPA: Río Tuma at El Tuma 40 km E of Matagalpa, 400 m, 25 May 1977 (fl), *Neill 1994* (MO); N de Matagalpa, carret. San Ramón–Pancasán, 12°55′N, 85°49′W, 700–800 m, 16 June 1982 (fl), *Sandino & Sáenz 3074* (MO). RÍO SAN JUAN: along rd. to San Carlos 5 km SE of Río Oyate, 11°42′N, 84°57′W, 40 m, 28 Aug. 1983 (fr), *J. Miller & Nee 1370* (MO); Archipelago Solentiname, Isla San Fernando, 11°11′N, 84°59′W, 30 m, 18 Sep. 1982 (fr), *Sandino 3629* (MO). ZELAYA: Caño Calcamo, ca. 5 km al SE de Siuna, carret. Siuna–Empalme, 13°40′N, 84°45′W, 26 Oct. 1982 (fr), *Grijalva & Burgos 1522* (MO); nr. Río Yaoya, 4 km S of crossing of Siuna–Rosita hwy., 100 m, 2 May 1978 (fl), *Neill 3791* (MO); Cerro Waylawás, E slope of northern range, 13°39′N, 84°49′W, 80 m, 11 Mar. 1979 (fr), *Pipoly 4396* (MO); Ibo Tingni, drainage of Caño Sung Sung, N of rd. between Puerto Cabezas and Río Wawa, 14°10′N, 83°30′W, 0–10 m, 6 Oct. 1978 (fr), *W. D. Stevens 10634* (MO). COSTA RICA. ALAJUELA: Río Jesús, San Ramón, 700 m, 20 May 1982 (fl), *Carvajal 260* (MO). GUANACASTE: Bebedero, 40–50 m, 19 June 1930 (fl), *Brenes 12603* (CR, F, NY); nr. 27 Abril, along rd. to Playa Tamarindo, 10°16′N, 85°46′W, 20–80 m, 9 Nov. 1975 (fr), *Burger & Baker 9894* (CR, F, MO); 5 mi. N of Bagaces, 14 July 1965 (fl), *Croat 632* (MO); Santa Rosa National Park, 30 km NW of Liberia, 10°50′N, 85°35′W, 0–300 m, 1 Dec. 1976 (fr), *Janzen 10426* (MO); 19 June 1978 (fl), *Janzen 10979* (MO); 10–20 km NE of Liberia on Camino Sta. María, 300–650 m, 20 Sep. 1975 (fr), *Utley & Utley 3134* (DUKE). PUNTARENAS: Cerro Punta Gorda, 3 km NW of Punta de Burica, 200 m, 5 Mar. 1973 (fl), *Busey 770* (CR, MO); Corovado National Park, Sirena, 8°29′N, 83°36′W, 0–5 m, 6 July 1977 (fr), *Liesner 2975* (CR, MO). SAN JOSÉ: vic. El General, 640 m, June 1939 (fl), *Skutch 4318* (F, GH, K, NY, US). PANAMA. CANAL AREA: vic. Madden Dam, 80 m, 22 May 1941 (fl), *Allen 2563* (F, GH, NY); nr. beach at Fort Kobbe, 3 Oct. 1961 (fr), *Duke 4197* (GH, MO); Barro Colorado Island, 5 Nov. 1969 (fr), *Foster 1365* (DUKE, F); Apr. 1983 (fl), *Hamilton 3681* (MO); Curundu, 9°00′N, 79°35′W, 50 m, 10 Aug. 1982 (early fr), *Hamilton 567* (CR, MO); Fort Sherman and nearby, 9°20′N, 80°00′W, 0–100 m, 16 June 1983 (early fr), *Hamilton & Stockwell 3706* (MO). COCLÉ: El Valle, 26 May 1970 (fl), *I. Aguilar 21* (F, MO); nr. El Copé, 27 Oct. 1967 (fr), *Garner 40* (DUKE, MO). COLÓN: path from sea to ridge behind Garrote, 4 Nov. 1975 (fr), *D'Arcy 9316* (MO, NY); nr. Peluca, km 25.6 from Transisthmian Hwy. on rd. to Nombre de Dios, 25 Feb. 1973 (fl), *Kennedy 2671* (GH, MO, NY). DARIÉN: Río Mortí, ca. 250 m, 18 Sep. 1967 (fr), *Duke 14178* (F, MO); S of El Real on slopes of Cerro Pirre, 500–1,000 m, 26 Sep. 1969 (fr), *Foster & Kennedy 1274* (DUKE); Enseñada del Guayabo, 18 km SE of Jaqué, 1–12 Apr. 1978 (fl), *Garwood 772* (F); Canglón, N of Panamerican Hwy., 8°20′N, 77°45′W, 100 m, 17 July 1982 (early fr), *Hamilton et al. 513* (MO); Río San Antonia, 2 hours upstream from Garachiné, 150 m, 10 May 1979 (fl), *Hammel 7323* (MO); Patiño, cliffs along beach, June 1914 (fl), *Pittier 6969* (US); vic. Yaviza, along Río Chucunaque, nr. El Punteadero, 7 June 1959 (early fr), *Stern et al. 164* (GH, MO, US). HERRERA: Ocú, 27 Aug. 1960 (early fr), *Ebinger 1058* (ENCB, F, MO). LOS SANTOS: 10 km SW of El Cortezo, 810 m, 27 Oct. 1978 (fr), *Hammel 5371* (MO); N of Guaniquito, ca. 10 mi. N of Tonosí along Río Tonosí, 100–200 m, 17 July 1970 (early fr), *Luteyn & Foster 1382* (DUKE, F, MO). PANAMÁ: La Ermita–San Carlos, 5 Nov. 1972 (fr), *Bernal 11* (ENCB); Isla del Rey, trail to landing strip, 20 July 1967 (early fr), *M. Correa A. 111* (A, DUKE, MO); Río Pita, 1–3 mi. above confluence with Río Maestra, 14 Oct. 1961 (fr), *Duke 4764* (GH—2 sheets, MO, US); San José Island, 28 May 1945 (fl), *Erlanson 236* (GH, NY, US); Majé, 5 mi. up Río Majé, 200 m, 18 Nov. 1970 (fr), *Foster & Kennedy 2013* (DUKE); Taboga Island, 15 Aug. 1972 (fr), *Gentry 5736*

(MO); between Chepo and El Llano, 1 Sep. 1971 (fr), *Gentry & Tyson 1693* (MO, NY); Alcalde Díaz, 11 Nov. 1974 (fr), *J. Gómez 22* (DUKE, MO); Cañitas, just S of Panamerican Hwy., 9°10′N, 78°52′W, ca. 150 m, 19 Sep. 1982 (fr), *Hamilton & D'Arcy 1411* (MO); Punta Paitilla, Nov. 1921 (fr), *Heriberto 207* (GH, NY, US); Chimán, 3–4 mi. up Río Pasiga, 28 Oct. 1971 (fr), *Kennedy 1216* (DUKE); 1–2 mi. S of Panam. Hwy., 3 mi. E of Cañazas checkpoint, 8°52′N, 78°15′W, 0–50 m, 27 Feb. 1982 (fl), *Knapp 3882* (MO); Pearl Islands, Trapiche Island, 15 Mar. 1937 (fl), *G. Miller 1900* (US); camino a Burunda–Arraiján, 12 Apr. 1970 (fl), *Sandoval 26* (DUKE, MO); swamp E of Río Tocumen, 11 Dec. 1923 (fr), *Standley 26586* (US). SAN BLAS: Ailigandí, Aug. 1965 (fr), *Dwyer 6820* (MO). VERAGUAS: Islas Contreras, Isla Uva, 8°48′N, 81°45′W, 50 m, 18 July 1984 (fr), *Churchill 5688* (MO—2 sheets); Cerro Tute, 8 Aug. 1963 (early fr), *Dwyer 4286* (MO); vic. Ponuga, 31 July 1967 (early fr), *Dwyer & Kirkbride 7440* (DUKE, MO); 2 mi. W of Santiago on Panamerican Hwy., 6 Aug. 1967 (early fr), *Dwyer et al. 7558* (GH, MO, US); Coiba Island, Enseñada Sta. Cruz, 27 Aug. 1970 (fr), *Foster 1622* (DUKE, F, MO); 18 km W of Las Minas, N slope of Alto Higo, cutover areas, 720–900 m, 8 Aug. 1978 (fr), *Hammel 4332* (MO).

All the species in synonymy have been properly synonymized before (cf. Dwyer, 1980). Infraspecific categories are not recognized herein because they have been defined in terms of variation seen within almost any population, such as the basicordate leaf blades on which *P. horizontalis* subsp. *basicordata* was based.

Psychotria horizontalis may be recognized by its leaves drying usually dull pale green, with secondary veins brochidodromous and making connecting arches far from the margin (Fig. 3b), and by its fruit with conspicuous persistent calyx of long, linear lobes (Fig. 9e).

Material from Guatemala, Belize, and Nicaragua is generally more pubescent than elsewhere in Central America. The calyx lobes, prominently persistent in fruit, are often much shorter in central Panama than elsewhere.

14. Psychotria papantlensis (Oersted) Hemsley, Biol. Cent. Amer. Bot. 50. 1881. Based on *Mapouria papantlensis* Oersted, Amér. Centr. p. 17, t. 14, fig. 5. 1863. *Uragoga papantlensis* (Oerst.) Kuntze, Revis. Gen. Pl. 2: 962. 1891. TYPE: Mexico. Veracruz: Papantla, *Liebmann s.n.* (holotype, C, n.v.). Figures 9b, 16.

Shrub or tree, 1–4 m tall; young stems glabrous, the bark pale, smooth; stipules sheathing, ovate, the apex usually biaristate, 4–9 × 2.5–6 mm, often paler in the central triangle, the margin often ciliate, often persistent at terminal 2–4 nodes, leaving a pale ridge with short red-brown fringe. *Leaves* petiolate; petioles (0.5–)1–3(–4) cm long, often diverging at right angles to stem, glabrous, flat above; blades very thin membranous, elliptic to oblanceolate, the apex acuminate, the base attenuate, (6.5–)9–14(–17) × (1.5–)2.5–5(–6) cm, glabrous above and below, drying usually pale green to sometimes pale red-brown; secondary veins 9–11 pairs, diverging 65°–75°, eucamptodromous to brochidodromous, constantly arcuate, prominulous below, glabrous, the axils lacking domatia or hairs; tertiary veins evident, orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of cymes; panicle branched to 3 degrees; main axis 3.5–14.5 cm long, the peduncle 2.5–11 cm long; secondary axes in 3(–4) ranks, the first-rank axes 4, the longer pair 0.6–1.7 cm long, the shorter pair 0.4–1 cm long, the second-rank axes 4, subequal, 0.3–0.8 cm long, the third-rank axes 2 or 4, subequal, 0.2–0.4 cm long, the fourth-rank axes 2, 0.1 cm long; cymes branched to 1–2(–3) degrees; bracts and bracteoles lanceolate, ca. 1 mm long, fringed, caducous. *Flowers* sessile to pedicellate, the pedicels to 0.7 mm long; calyx drying pale brown against darker petiole and receptacle, cup-shaped, the tube to 0.5 mm long, the lobes 5, triangular, 0.5 × 0.5 mm, glabrous to minutely ciliate; corolla white, the tube cylindrical, 4–5 × 1 mm, sparsely white pubescent in throat, the lobes 5, lanceolate, 1.5–2.5 × 0.8–1 mm; stamens 5, the filaments 3 mm long in pins, 6–7.5 mm long in thrums, the anthers 1.3–2 mm long; style 6 mm long in pins, 4–5 mm long in thrums, the branches linear. *Fruit* when dry ellipsoidal, (6–)7–7.5 mm long, (4–)4.5–5 mm diam., maturing red, drying black; persistent calyx a tubular beak, drying pale green, 0.5–1 mm long (Fig. 9b); seed dorsal surface with 4 shallow longitudinal furrows, the ventral surface with 2 deep incompletely divided longitudinal furrows.

Distribution (Fig. 16). Common in southern Mexico through Petén, Guatemala, into southwestern Belize, at 0–400 m elevation in evergreen forest with usually equatorial-tropical climate. *Psychotria papantlensis* has been collected in flower March–June and in fruit in March and July–December.

Selected specimens examined. MEXICO. CHIAPAS: 60 mi. SE of Palenque, gravel rd. from Palenque to Bonampak, 400 m, 5 July 1977 (fr), *Croat 40180* (MO); La Gloria, 29 Apr. 1952 (fl), *Miranda 7584* (MEXU); 41 km NW of Ocozocoautla, rd. to Mal Paso, 17°12′N, 93°40′W, 350 m, 4–5 Aug. 1965 (fr), *Roe et al. 903* (ENCB); ruinas de Palenque, 24 Mar. 1911 (fl), *Seler & Seler 5502* (F, GH). TABASCO: Río Zanapa, 50 km W of Huimanguillo, 6 Apr. 1963 (fl), *Barlow 10/5* (GH); June

1964 (fl), *Barlow 10/5B* (MEXU); Mpio. Heróica Cárdenas, km 21 de la carret. Cárdenas–Coatzacoalcos, 30 Apr. 1981 (fl), *Magaña & Curiel 189* (ENCB, MEXU). VERACRUZ: Estación de Biología Tropical Los Tuxtlas, 400 m, 4 Apr. 1972 (fl), *Cedillo 155* (ENCB—2 sheets, K, MEXU); camino Catemaco–Montepio, llegando a Montepio, 50 m, 27 July 1977 (fr), *Horvitz 206* (MEXU—2 sheets, NY); Estación de Biología Tropical Los Tuxtlas, 200 m, 17 Nov. 1968 (fr), *G. Martínez C. 1790* (A, ENCB—3 sheets, K, MEXU, MO); Santa Lucrecia, 20 m, 1923 (fl), *Reko 4623* (MEXU); Mpio. Minatitlán, lomas al S del Poblado 11 y al S de la brecha 105, hasta 500 m, 2 Oct. 1980 (fr), *Wendt et al. 2821* (MEXU); Fortuño, Coatzacoalcos River, 30–50 m, Mar. 1937 (fl, fr), *L. O. Williams 8798* (F, US). GUATEMALA. ALTA VERAPAZ: Chahal, bordering Cluiju River, in zapotal, 28 Sep. 1968 (fr), *Contreras 7749* (MO). IZABAL: Cadenas/Puerto Méndez, New Cadenas Rd., 3.5 km from village, 19 Aug. 1969 (fr), *Contreras 8988* (MO); along Río Bonita, 30–150 m, 21 Dec. 1941 (fr), *Steyermark 41678* (F). PETÉN: on Sebol rd. ca. 8 km from San Luis Rd., 20 Nov. 1966 (fr), *Contreras 6618* (MO); forest between Finca Yalpemech along Río San Diego and San Diego on Río Cancuen, 50–150 m, 25 Mar. 1942 (fl), *Steyermark 45346a* (F, NY); lowland forest W & NW of Chinajá between Río Chinajá and 6 mi. W of Río San Román, 50–70 m, 29 Mar. 1942 (fl), *Steyermark 45492* (F). BELIZE. TOLEDO: San José Maya Indian village, 10 km N of Columbia Forest Station, 13 June 1973 (early fr), *Croat 24378* (F, GH, MO); *Dwyer 11152a* (DUKE, F, MO, NY, US).

Psychotria papantlensis may be recognized by its elliptic long-petiolate leaves drying pale green and by its calyx drying conspicuously pale in flower and in fruit, when it contrasts markedly with the black-drying ellipsoidal fruit (Fig. 9b).

As in several species, the corolla tube of the thrum flower morph is longer than that of the pin morph (5 mm vs. 4 mm); but the species appears otherwise normally distylous.

15. Psychotria pleuropoda Donnell-Smith, Bot. Gaz. (Crawfordsville) 40: 5. 1905. TYPE: Guatemala. Alta Verapaz: Cubilgüitz, 350 m, Aug. 1903 (fr), *H. von Tuerckheim 8529* (lectotype designated herein, GH; isolectotypes, US—2 sheets, fragments, F, US). Figure 17.

Shrub 0.5–5 m tall; young stems glabrous, the bark pale, furrowed longitudinally; stipules ovate, the apex biacuminate, the central triangle drying pale green, 10–17 × 4–6 mm, fringed, persistent at terminal 3–5 nodes, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles (0.2–)0.5–1 cm long, glabrous, terete; blades membranous, narrow-oblanceolate, the apex long-acuminate, the base attenuate, (7–)12–21 × (1–)1.3–2.7 cm, glabrous above and below, drying dull pale green-brown to sometimes red-brown; secondary veins 15–18 pairs, diverging 60°–75°, eucamptodromous to brochidodromous, constantly arcuate, prominulous below, glabrous, the axils lacking domatia or hairs; tertiary veins evident, percurrent, the intersecondaries especially evident. *Inflorescences* terminal or pseudoaxillary, panicles of cymes; panicle branched to 3 degrees; main axis (1.5–)2.5–12 cm long, the peduncle (1–)2–9.5 cm long; secondary axes in 1–2 ranks, the first-rank axes 4, the longer pair 0.3–1.3 cm long, the shorter pair 0.2–1 cm long, the second-rank axes 2 or 4, subequal, 0.2–0.5 cm long; cymes branched to 1–2 degrees; bracts linear, to 5 mm long, ciliate; bracteoles irregular, ca. 1 mm long, ciliate. *Flowers* sessile to pedicellate, the pedicels to 1 mm long; calyx drying pale brown against darker petiole and receptacle, cylindrical, the tube 1 mm long, the lobes 5, triangular, barely evident, minutely ciliate; corolla white, the tube cylindrical, 2.5–3 × 1.5 mm, white pubescent in throat, the lobes 5, lanceolate, 2.5 × 1 mm; stamens 5, the filaments 3 mm long in pins, 3.5–4 mm long in thrums, the anthers 0.8–1 mm long; style 5 mm long in pins, 2.5–3 mm long in thrums, the branches clublike in pins and linear in thrums. *Fruit* when dry ellipsoidal, (5.5–)6 mm long, (4.5–)5 mm diam., maturing red, drying black or green-brown; persistent calyx a tubular beak ca. 1 mm long; seed dorsal surface with 4–5 deep longitudinal furrows, the ventral surface with 2 deep sometimes incompletely divided longitudinal furrows.

Distribution (Fig. 17). Known from Tabasco, Mexico, northern Guatemala, and southern Belize, at 50–500 m elevation in evergreen forest with equatorial-tropical to equatorial-mountainous climate. This species has been collected in flower February–June and in fruit August–February.

Selected specimens examined. MEXICO. TABASCO: Mpio. Tacotalpa, 3 km a pie a E del ejido Lázaro Cárdenas, 50 m, 10 May 1979 (fl), *Cowan 2069* (NY). GUATEMALA. ALTA VERAPAZ: Montaña Yxocubvain, 4 km W of Cubilgüitz, 300–500 m, 12 Mar. 1942 (fl), *Steyermark 44990* (F—2 sheets, GH, NY). IZABAL: damp forested slopes and barrancos, 300–900 m, 25 Dec. 1941 (fr), *Steyermark 41882* (F—3 sheets, NY). PETÉN: Sayaxché, Laguna Petex-Batun, 1 km S of wharf, 30 Mar. 1964 (fl), *Contreras 4130* (MEXU, MO); La Cumbre, Las Cañas, E of km 142 of the Petén–Izabal rd., 20 Sep. 1966 (fr), *Contreras 6166* (MO); 6 Mar. 1975 (fl), *Lundell & Contreras 19063* (MO); lowland forest W & NW of Chinajá, between Río Chinajá and 6 mi. W of Río San Román, 50–70 m, 29 Mar. 1942 (fl), *Steyermark 45488* (F, NY). BELIZE. TOLEDO: San Benito Poite, nr. Otoxha, 200 m, Feb. 1973 (st), *Boster s.n.* (ECON); trail from Columbia Forest Station to Esperanza, 3–6 km W of San José rd., 180–330 m, 13 June 1973 (fl), *Gentry 8172a*

(F, NY); Deep River Forest Reserve, limestone-derived soil, Feb. 1945 (fl), *Lamb 54, 62* (F).

Psychotria pleuropoda may be recognized readily by its narrow-oblanceolate (length/width = 8–10) leaves unique in subg. *Psychotria* in Mesoamerica. It differs from *P. costivenia* by having very narrow leaf blades and inflorescences with relatively short secondary axes in only 1–2 (vs. ca. 4) ranks. The persistent calyx tube in fruit is also distinctive.

16. Psychotria sylvivaga Standley, J. Wash. Acad. Sci. 18: 274. 1928. TYPE: Costa Rica. Heredia: Yerba Buena, NE of San Isidro, 2,000 m, 28 Feb. 1926 (fr), *Standley & Valerio 49989* (holotype, US). Figure 17.

Shrub 2–3 m tall; young stems sparsely red-brown puberulent, the bark pale, furrowed longitudinally; stipules broadly ovate, 9–12 × 5–6 mm, glabrous, sometimes ciliate near base, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 1–2 cm long, glabrous, flat above; blades membranous to sometimes subcoriaceous, elliptic to oblanceolate, the apex acuminate to caudate, the base attenuate, (8.5–)10–17 × (2.5–)3–4.5(–5) cm, glabrous above and below, drying green-brown to red-brown; secondary veins 11–14 pairs, diverging (60°–)65°–75°(–80°), brochidodromous, constantly arcuate, elevated below, glabrous, the axils sometimes with minute tufts of red-brown hairs; tertiary veins evident to inconspicuous, orthogonal reticulate, the intersecondaries often evident. *Inflorescences* terminal or pseudoaxillary, sparse panicles of cymes; panicle branched to 4 degrees; main axis 9.5–14 cm long, the peduncle 6–7.5 cm long; secondary axes in (3–)4 ranks, the first-rank axes 2, 2–3.2 cm long, the second-rank axes 2, 0.8–1.2 cm long, the third-rank axes 2, 0.4–0.8 cm long, the fourth-rank axes 2, 0.2–0.5 cm long; cymes branched to 1 degree; bracts lanceolate, 3 mm long, glabrous; bracteoles triangular, to 1 mm long, red-brown ciliate. *Flowers* pedicellate, the pedicels to 1 mm long; calyx cup-shaped, the tube 0.5 mm long, the lobes 5, triangular, 0.5 mm long, puberulent; mature corolla, stamens, and style not seen. *Fruit* when dry spherical, 4.5–5 mm long, 4–5 mm diam., maturing red, drying red-black; persistent calyx 1 mm long, drying pale brown; seed dorsal surface with 6–8 often irregular longitudinal furrows, the ventral surface with 2 medium-deep often plus ca. 4 irregular longitudinal furrows.

Distribution (Fig. 17). Known from southern Alajuela and San José, Costa Rica, at 2,000–2,200 m elevation in a region of premontane to low montane rain forest with equatorial-mountainous climate. *Psychotria sylvivaga* has been collected in flower in December and in fruit in December and February.

Additional specimens examined. COSTA RICA. SAN JOSÉ: nr. Laguna de la Escuadra, NE of El Copey, 2,000–2,200 m, 16 Dec. 1925 (fr), *Standley 41924* (A, US), *41974* (F, US); Laguna de la Chonta, NE of Sta. María de Dota, 2,000–2,100 m, 18 Dec. 1925 (fl, early fr), *Standley 42212* (K, US).

Psychotria sylvivaga may be recognized by its elliptic to oblanceolate leaves drying green-brown to red-brown with brochidodromous secondary veins and evident intersecondaries and by its fruit with persistent calyx a conspicuous tube.

Standley described a mature flower with corolla tube 5 × 1.2 mm, the lobes triangular-ovate, 1.5 mm long, in his original description, but I was unable to find a mature flower.

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DIANTHOVEUS: A NEW GENUS OF CYCLANTHACEAE[1]

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Abstract

Dianthoveus cremnophilus, a terrestrial Cyclanthaceae from southwestern Colombia to northern Ecuador, is described as a new genus and species. The cupules at the base of the stamens and the long, narrow, moderately flattened seeds are unique. Cladistic analysis supports the hypothesis that leaf idioblasts with randomly oriented styloids (leaves scabrous when dry), root styloids, sessile anthers, and inaperturate pollen are synapomorphies with the widespread, monospecific *Evodianthus*. The new genus differs fundamentally from *Evodianthus* by having a uniseriate staminate perianth and in seed shape and seed coat structure. *Dianthoveus* shares additional uncommon characters with *Evodianthus* (e.g., separate fruits, terminal inflorescences, symmetrical flowers) that are not unique in the family. With *Schultesiophytum* it shares some of these uncommon characters but uniquely shares only laminar anther appendages. Although *Dianthoveus* and *Dicranopygium* subgenus *Gleasonianthus* uniquely share staminate flowers with eglandular tepals, no other characters suggest a close relationship between them.

Exploration of tropical wet forests in southern Central America and northwestern South America in recent years has greatly increased the number of collections and species known from these areas. This was especially predictable for the Cyclanthaceae, which are restricted to the wettest, often least-explored habitats (Grayum & Hammel, 1982). Since the time of Harling's (1958) monograph, which included 178 species in 11 genera, 29 new species have been added to this predominantly epiphytic family. More than 30 additional new species are now known from Central America and the Chocó region of South America alone (Hammel, unpubl.). However, only one new subgenus (Wilder, 1978) and no other supraspecific taxa have been described. In fact, in recent years only 10 genera have been recognized; *Pseudoludovia* is thought to be a mixed collection: a spadix, perhaps of a *Sphaeradenia*, and leaves of *Ludovia* (Wilder, 1978). Harling suggested that on further study it might be possible and logical to subdivide the three largest genera into additional genera, and for *Sphaeradenia* this reclassification is imminent (R. Eriksson, in press). *Dianthoveus*, the name an anagram of "Evodianthus," is a totally novel, monotypic genus.

This plant was first described and illustrated, as a short-stemmed terrestrial, in *The Flora of the Río Palenque Science Center* (Dodson & Gentry, 1978), where it was identified as *Asplundia vagans* Harl., a common root-climbing epiphyte of Central and South America. Examination of specimens of Cyclanthaceae in the herbarium at the Marie Selby Botanical Gardens, where vouchers for the Río Palenque florula are deposited, revealed that the plant was neither poorly illustrated nor a terrestrial form of *A. vagans*, but rather something problematic, exhibiting unusual characters of several genera. This stimulated two field trips to Ecuador, which, along with laboratory studies, convinced us that the plant is an undescribed genus.

Materials and Methods

In total, well over 200 individuals in seven populations were examined in the field. Plants at various stages—from early anthesis through ripe infructescences to peduncle remains—were fixed in FAA for anatomical and morphological studies. Twenty-eight fluid-preserved collections at these stages were made, and numerous herbarium vouchers and live plants were collected. In the field, live specimens were examined to determine inflorescence position, presence/absence of latex, drying qualities of wounded and air-dried leaves, and features of leaf color and texture.

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Plants preserved in the field in FAA were drained of fluid and transported in sealed plastic bags within a large plastic container. Subsequently they were washed in water for several days and then stored in an aqueous solution of 5% glycerin and 50% ethanol. All measurements were taken from live or fluid-preserved plants at populations along the Río Pilatón (*Hammel & Wilder 16058, 16059, 16066, 16067* & *16074*). Leaf measurements were taken from a total of 17 adult leaves from three individuals. Inflorescence measurements were taken from four individuals, and flower measurements come from ten flowers in each inflorescence. Infructescence measurements were from ten individuals, and fruit measurements from ten fruits in each of four individuals. For anatomical studies, material of laminae, roots, and stems was prepared according to the methods of Wilder (1985). Seeds were taken from mature preserved infructescences embedded in Tissue Tek OTC polysaccharide compound, frozen, and sectioned in a cryostat. Sections were mounted, stained with toluidine blue, and viewed with a bright field microscope. Pollen was prepared with and without acetolysis and with and without critical point drying, coated with gold, and viewed with a Hitachi S45D scanning electron microscope. Detailed studies on the morphology and development of vegetative parts and inflorescences, and the anatomy of laminae, first-order roots, and rhizomes are in progress (Wilder, unpubl.).

In order to test our initial hypothesis of relationship of the new genus to *Evodianthus* we selected 22 characters for the 11 genera of Cyclanthaceae (Table 1), developed a character-by-taxon matrix (Table 2), and analyzed the data using PAUP for microcomputer, a maximum parsimony technique (Swofford, 1985). All characters were unweighted, but the four character states of "habit" were restricted to a specific order (Table 1 and discussion below). Since no logical basis was apparent for restricting the order of character transformations of other multistate characters, all other characters were treated as unordered. Characters with variable states for a particular genus were coded as missing (Pimentel & Riggins, 1987). Autapomorphies for each of the genera were not included in the analysis.

Collections made in December 1988 were added in proof and not considered in the counts and measurements.

TABLE 1. Characters and character states for the genera of Cyclanthaceae. Characters found only in one genus (autapomorphies) are not included.

A = Placentation: 0 = parietal, 1 = apical
B = Fruit fusion: 0 = some, 1 = none
C = Fruit type: 0 = other, 1 = succulent pixis
D = Seed shape: 0 = terete, 1 = moderately flattened, 2 = strongly flattened
E = Orientation of cells of testa: 0 = horizontal, 1 = vertical
F = Outer layer of testa with enlarged, dark cells: 0 = no, 1 = yes
G = Spinules on wall of inner layer of testa integument: 0 = no, 1 = yes
H = Inner tangential and radial walls of inner layer of integument equally much thickened: 0 = yes, 1 = no
I = Inflorescence position: 0 = terminal, 1 = lateral
J = Anther appendages: 0 = none, 1 = laminar-apiculate, 2 = globular
K = Phyllotaxis: 0 = distichous, 1 = spiral
L = Glands on staminate tepals: 0 = absent, 1 = present
M = Staminate flower symmetrical: 0 = yes, 1 = no
N = Staminate flower funnel-shaped: 0 = yes, 1 = no
O = Pollen: 0 = aperturate, 1 = inaperturate
P = Leaf styloids: 0 = unidirectional, 1 = omni, 2 = absent
Q = Birefringent cells in leaves: 0 = absent, 1 = present
R = Anthers: 0 = not sessile, 1 = sessile (no basal bulb or filament)
S = Habit:
0 = terrestrial
a: 1 = epiphyte
b: 1 = on rocks
c: 1 = climber
T = Root styloids: 0 = absent, 1 = present
U = Circumstelar sclerenchymatous ring: 0 = absent, 1 = U-shaped, 2 = evenly thickened
V = Root stele nonperipheral phloem: 0 = in fascicles, 1 = dispersed
W = Spathe arrangement: 0 = dispersed, 1 = clustered

TAXONOMY

Dianthoveus cremnophilus Hammel & Wilder, gen. et sp. nov. TYPE: Ecuador. Pichincha: Quito to Santo Domingo de los Colorados, Río Pilatón valley, 44 km E of Santo Domingo, on steep wet slope along highway, 0°23'S, 78°50'W, 1,200 m, 18 June 1987 (infr), *B. Hammel & G. Wilder 16058* (holotype, MO; isotypes, COL, DUKE, F, GB, NY, QCA, US).

Evodianthi funiferi affinis sed habitu terrestre, statura majore, periantho floris masculini uniseriato, tepalis acuminatis eglandulosisque, receptaculo plano, connectivo antherarum laminare apiculatoque, seminibus modice applanatis vel quasi teretis, perlongioribus quam latioribus differt. Ob receptaculi papillas multicellulares, formantes basibus staminorum cupulas, inter omnes Cyclanthaceas peculiaris.

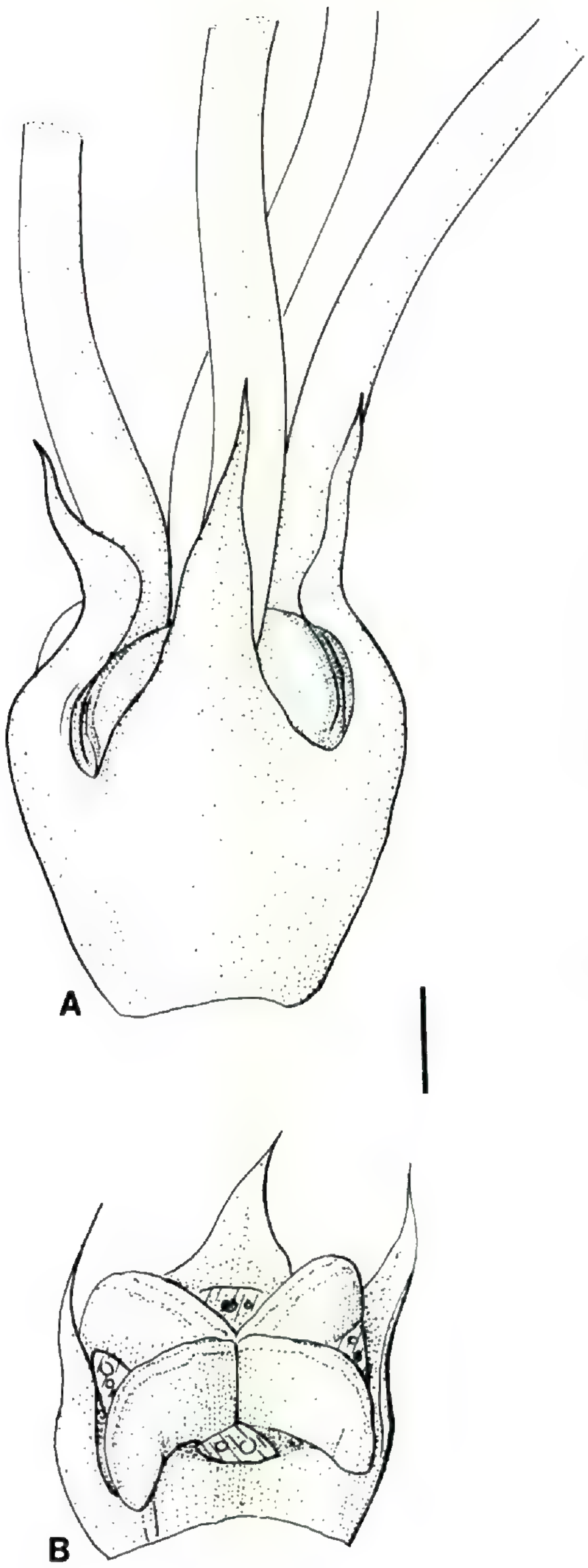
TABLE 2. Data matrix for the 10 genera of subfamily Carludovicoideae with *Cyclanthus* as hypothetical ancestor. Characters coded ? were inapplicable or variable characters.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S a	S b	S c	T	U	V	W
Cyclanthus	0	?	0	0	0	0	0	0	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0
Asplundia	0	0	1	2	?	0	0	1	1	0	1	1	?	?	0	0	0	0	0	0	?	0	1	0	0
Carludovica	0	0	0	1	1	0	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1
Dicranopygium	0	0	0	0	0	0	0	0	1	0	1	?	1	1	0	0	0	0	0	1	0	0	1	0	1
Evodianthus	0	1	0	2	1	0	0	1	0	0	1	1	0	0	1	1	0	1	0	0	1	1	2	1	1
Ludovia	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	2	1	0	?	0	?	0	1	0	0
Sphaeradenia	1	1	0	0	?	1	0	0	1	2	0	1	1	1	0	0	1	0	1	0	0	0	1	1	0
Stelestylis	1	0	1	0	?	1	0	0	1	2	0	1	1	1	0	0	1	0	1	0	0	0	1	1	0
Thoracocarpus	0	0	1	2	0	0	1	1	1	0	1	1	0	0	0	2	0	0	0	0	1	0	2	0	0
Dianthoveus	0	1	0	1	1	0	1	1	0	1	1	0	0	1	1	1	0	1	0	0	0	1	1	0	1
Schultesiophytum	0	1	0	1	1	1	0	0	1	1	1	1	0	1	0	2	0	0	0	0	0	0	0	0	1

Terrestrial herbaceous plant, often forming clumps by vegetative branching; the rhizomes 7–53 cm long, to about 6 cm diam. in mature specimens, often exposed and held erect by numerous stout, monomorphic, adventitious roots up to 75 cm long and 0.85 cm diam. Foliage leaves of adult plants 145–271.5 cm long, with spiral (dispersed, sensu Harling) phyllotaxy, crowded on the rhizome at internodes mostly less than 1 cm apart, eventually detaching and leaving the naked rhizome with well-defined leaf scars; sheaths 52–101 cm long, dull green and remaining intact; petioles 21–77 cm long; lamina unicostate or rarely and inconspicuously subtricostate, bifid to ½ or slightly less, 72–107 cm long, 16.5–30 cm wide at the base of the median sinus, the segments 9–16 cm wide; each half of the lamina with 19–26 folds, lanceolate with a short-acuminate tip, dark satiny green above, dull and paler below, scabrous when dry. Inflorescences solitary and terminal but becoming laterally displaced by the subtending, precociously expanding renewal bud. Peduncles 25–34 cm long at anthesis, becoming 41–61 cm long and curving down in mature fruiting stage, 1.4–1.8 cm diam. Spathes of two kinds, both persisting until very late flowering stage: 3 conspicuous spathes, thick, green and fleshy, differentiated into sheath, lamina, and sometimes petiole, 9.5–25.8 cm long, ca. 5–6 cm wide, ± clustered and inserted no more than 3 cm below the spadix, collectively surrounding the spadix, the lowermost much larger than the upper 2 and unusual in bearing petiolate and often bifid lamina; up to 6 inconspicuous spathes, comprising membranous greenish white scale leaves, up to 4.7 cm long and 1 cm wide, inserted above the conspicuous spathes and all ± at one level, usually subtending flowers and often inserted above the base of the spadix, arising only from one side of the inflorescence. Spadices cylindrical, at anthesis 7.8–9.5 cm long, 2.6–3.1 cm diam., sordid white, in ripe fruiting stage becoming 11–14.8 cm long, 4–6 cm diam., green. Staminate flowers ± obpyramidal, 3.3–5.5 mm long; receptacle approximately triangular in top view, ca. 2–3.3 mm wide, adorned with numerous multicellular papillae forming a cupule around the base of each anther; perianth lobes 10–18, thin and narrowly triangular-acuminate, (1–)1.3–2.7 mm long, eglandular, distributed ± evenly on the receptacle margin; stamens 19–32, the anthers ± elliptic but often widest above the middle, 0.7–1.1 mm long, 0.4–0.8 mm wide, the thecae occupying the lower ½–⅔ of the anther and separated by the broad upper portion of connective, this terminating in a laminar apiculate tip; filaments minute, 0.1–0.2 mm long or lacking; basal bulbs lacking. Pollen grains mostly ovoid but varying to nearly globose, 15–21.5 μm long, 14–15.5 μm wide, psilate, inaperturate. Pistillate flowers free to base, narrowly turbinate, at anthesis 3–3.5 mm long (from base

→

FIGURE 1. Flowers and fruits of *Dianthoveus cremnophilus*.—A, B. Young pistillate flowers, B with one tepal and all staminodia removed. Bar = 1 mm; *Hammel & Wilder 16066*.—C, D. Mature fruits, C viewed from side parallel to axis of spadix, D viewed from side perpendicular to axis of spadix. Bar = 5 mm; *Hammel & Wilder 16058*.—E. Mature fruit, top view. Bar = 5 mm; *Hammel & Wilder 16058*.—F. Staminate flower. Bar = 1 mm; *Hammel & Wilder 16067*.—G, H. Anthers, front view (G) and side view (H). Bar = 0.5 mm; *Hammel & Wilder 16067*.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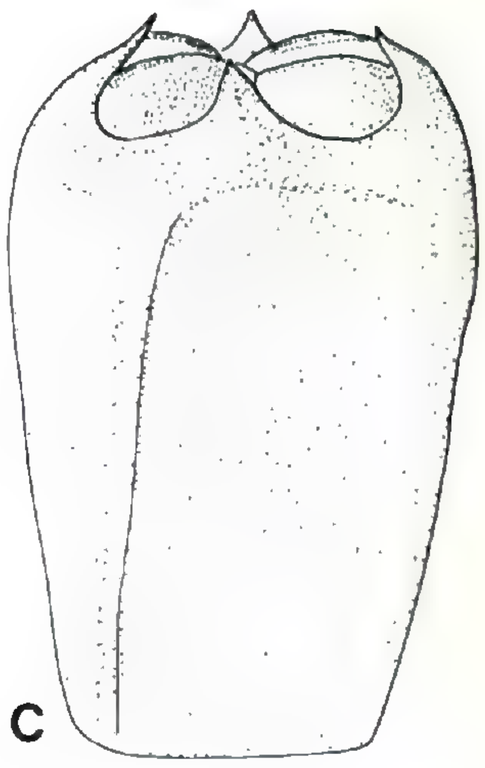
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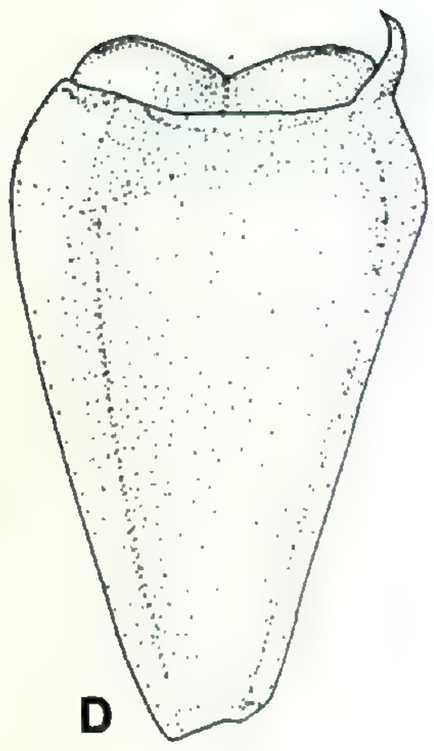
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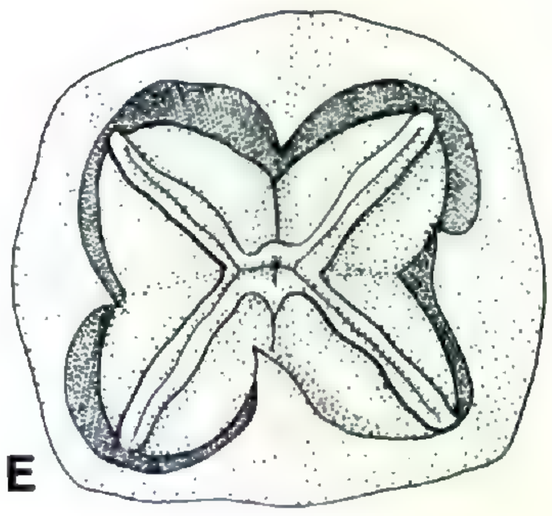
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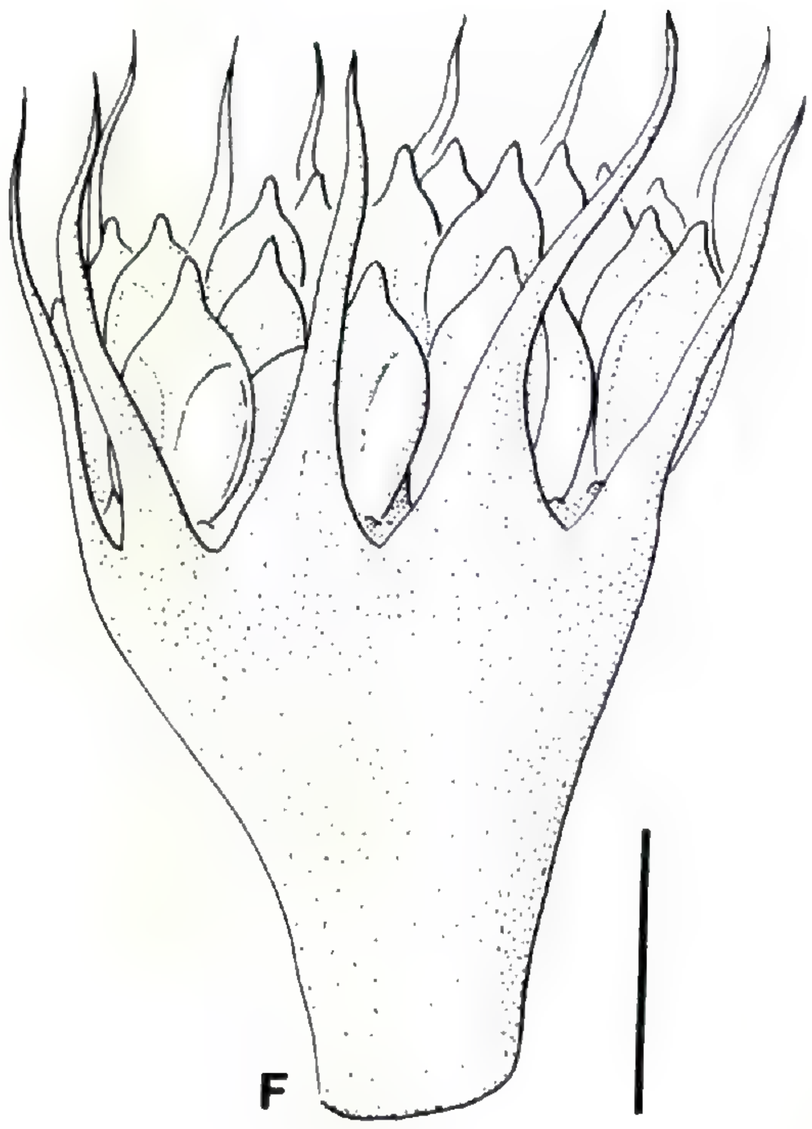
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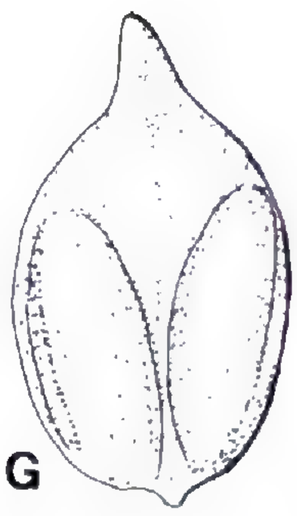
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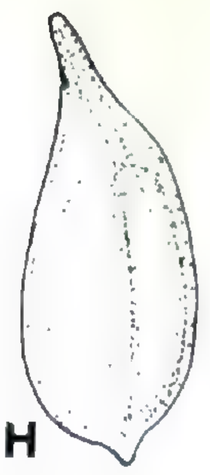
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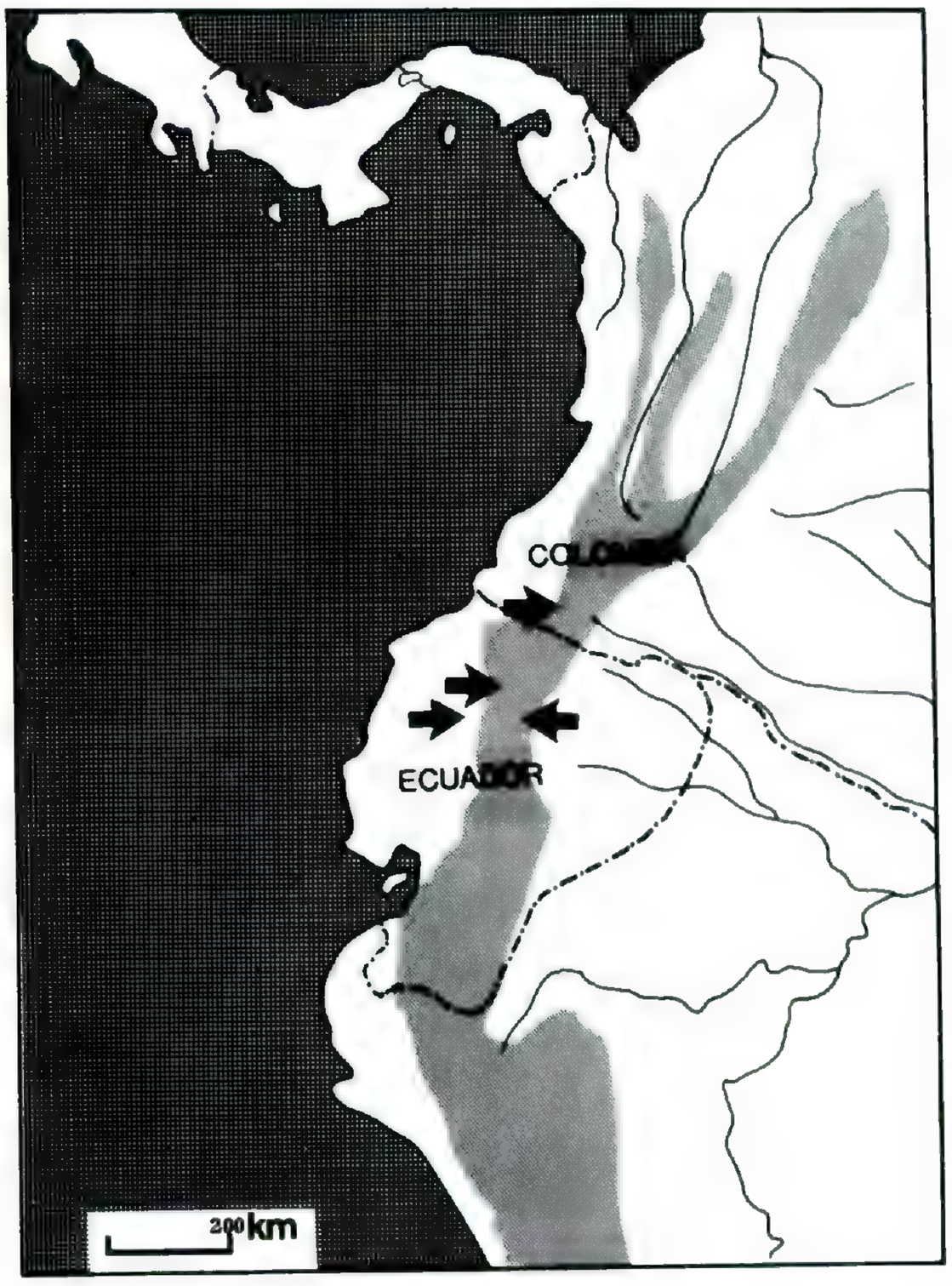


FIGURE 2. Distribution of *Dianthoveus cremnophilus*.

to top of stigma), 3.8–4.1 mm wide, at ripe fruiting stage becoming 2.1–2.4 cm long, 1.5–1.7 cm wide, green at maturity; tepals free to base (partially connate in age), arising from the top of the inferior ovary, long-acuminate, the tips folding over the stigmas and then curving out, at anthesis 2–4.3 mm long, 2–4.3 mm wide, in fruiting stages the tips often breaking off, becoming acute to rounded, 1.5–3.2 mm long, 4.5–9.5 mm wide; staminodia white, to ca. 9.5 cm long, ca. 1.5 mm diam., the distal ends apiculate, relatively flattened and attenuated but otherwise identical to an anther; styles at anthesis 0.9–2 mm tall, in fruiting stages 1–2.5 mm tall; stigmas convex in side view and slightly uncinate, extending between the tepals, at anthesis 1.2–3 mm long, 0.7–2 mm wide, in mature fruiting stages 3.5–4.2 mm long, 2–3.7 mm wide; stigmatic crest seen from above linear, papillate and sometimes sulcate; placentae 4, parietal. Seeds fusiform but moderately flattened, 1.4–2.45 mm long, 0.3–0.6 mm wide, dark amber-colored; seed coat with tannin and mucus; embryo lacking starch. Figure 1.

Distribution and habitat. Known only from wet forest in the Andean foothills of southwestern Colombia and northern Ecuador. In Colombia the species has been found only on the Pacific slope at mid elevations, but in Ecuador it is known from between 150 to 1,200 m elevation and occurs on both sides of the Andes.

Paratypes. COLOMBIA. NARIÑO: road from El Espino to Tumaco, ca. 16 km W of Ricaurte, 850 m, 18 Nov. 1986 (sterile), *B. Hammel & R. Bernal 15735* (MO); 7 Dec. 1988 (infr), *B. Hammel 17135* (COL, MO). ECUADOR. LOS RÍOS: between Santo Domingo and Quevedo, Centinela ridge, 13 km E of Patricia Pilar, 300 m, 1 Dec. 1986 (infr), *B. Hammel & J. Trainer 15846* (MO); Río Palenque Science Center, 2 km S of Patricia Pilar, common plant on creek bank, 150–220 m, 5–14 Mar. 1977 (young infr), *C. Dodson 6645* (SEL); 19 July–11 Aug. 1977 (old infl and young infr), *C. & H. Dodson 6730* (SEL); 30 Nov. 1986 (infr), *B. Hammel & C. Dodson 15845* (MO); 18 Nov. 1979 (sterile), *Schupp 50* (SEL). NAPO: new road to Loreto, 18 km E of junction with Baeza-Tena Road, 1,200 m, 21 Dec. 1988 (infr), *B. Hammel & G. Wilder 17272* (COL, MO, QCA, NY); Baeza to Tena, ca. 58 km S of Baeza, ca. 1,200 m, 17 Dec. 1986 (sterile), *B. Hammel 15971* (MO); Tena to Puyo, 3 km S of Tena, 500 m (sterile), *B. Hammel 16017* (MO). PICHINCHA: Reserva ENDESA, km 113 on Quito to Puerto Quito road, 450 m, 16 Dec. 1988 (infr), *B. Hammel & G. Wilder 17234* (GB, MO, PSO, QCA); Santo Domingo de los Colorados to Quito, Río Pilatón valley, 13 km E of Santo Domingo, Tinalandia resort, on steep slope along stream in forest, 800 m, 30 Nov. 1986 (old infl and young infr), *B. Hammel & J. Trainer 15820* (CAS, K, MO, US); 20 June 1987 (infl), *B. Hammel & G. Wilder 16066* (MO); (infl and infr), *B. Hammel & G. Wilder 16067* (COL, F, MO, QCA); 18 km E of Santo Domingo, on vertical slope just behind CEPE gas station, 750 m, 22 June 1987 (infl), *B. Hammel & G. Wilder 16080* (MO, US); 32 km E of Santo Domingo, N of highway and Río Pilatón, 850 m, 19 June 1987 (infl), *B. Hammel & G. Wilder 16059* (MO); 34.5 km E of Santo Domingo, on steep slopes S of highway, 1,100 m, 21 June 1987 (infl and infr), *B. Hammel & G. Wilder 16074* (COL, GB, GH, MO, QCA); same locality as type, 6 Dec. 1986 (infr), *B. Hammel & J. Trainer 15890* (MO, SEL).

Dianthoveus cremnophilus is robust, short-stemmed, and terrestrial (Fig. 3) but, as indicated by its epithet, it is a "cliff-loving" plant (Fig. 4). At many of the sites along the Río Pilatón we were able to collect plants only by pulling ourselves up nearly vertical slopes, using roots and stems as hand holds. Several large populations, including the type, were growing on dripping and mossy rock walls. All of the sites were along small streams or gullies or on wet, shaded slopes in isolated patches of relatively undisturbed forest. Even at Río Palenque, where the terrain is essentially a rolling plain, plants occur only on steep banks along small streams in the forest. Plants at two of the sites had been exposed by recent felling of forest cover and showed signs of sun damage.

Although *Dianthoveus* is locally abundant and probably formerly occurred throughout the wet lowlands and foothills of the Andes in northern

FIGURES 3, 4. Habit and habitat of *Dianthoveus cremnophilus*, at type locality.—3. Habit; divisions on tape are 10 cm each.—4. Habitat; plants were often abundant on wet, vertical slopes.

Ecuador, it seems not to occur outside of that area. Attempts to find it have failed on the Amazonian side of the Andes in southern Colombia near Mocoa in Putumayo Province, and in the Pacific lowlands of southern Colombia (near Barbacoas) in habitat similar to that of the adjacent Ecuadorian localities.

Phenology. Nearly all of the collections of *Dianthoveus* have been made from June through December, which spans the primary dry season for humid areas of northwestern Ecuador (Dodson & Gentry, 1978). Our search of numerous large populations at five different localities during June revealed four phenological classes: (1) most plants bore no outward sign of fertile structures (N = ca. 200) except for some with old peduncle stubs; (2) next most abundant were plants with remnants of old infructescences, primarily long-rotten peduncles (N = ca. 30); (3) we saw and collected only 12 individuals with young to mature infructescences, and (4) five individuals with immature to old inflorescences. At the type locality, only fruiting plants were observed in December of 1986 and in June of 1987. The single mid wet season collection has a young infructescence. Individuals apparently bear a single inflorescence per rhizome at one time. Our studies suggest that *Dianthoveus* flowers and fruits sporadically throughout the year. From the relatively frequent plants with peduncle remnants during June, we infer a somewhat higher flowering frequency during January through March, i.e., in the middle of the rainy season, a common pattern in other Cyclanthaceae.

Development and morphology of fertile structures. The peduncles are most flexible at the base and are held erect at anthesis by the tightly overlapping leaf sheaths. Later, as the infructescence becomes heavier, the elongating peduncle bends so that the mature infructescence is held either horizontally or nearly pendent. The peduncle is persistent long after the fruits have been shed, and plants are often found with the fibrous remains of peduncle firmly attached to the rhizome. Both conspicuous and inconspicuous spathes persist into very late flowering stage with the largest, lowermost spathe persisting longest. Spathe scars are indistinct.

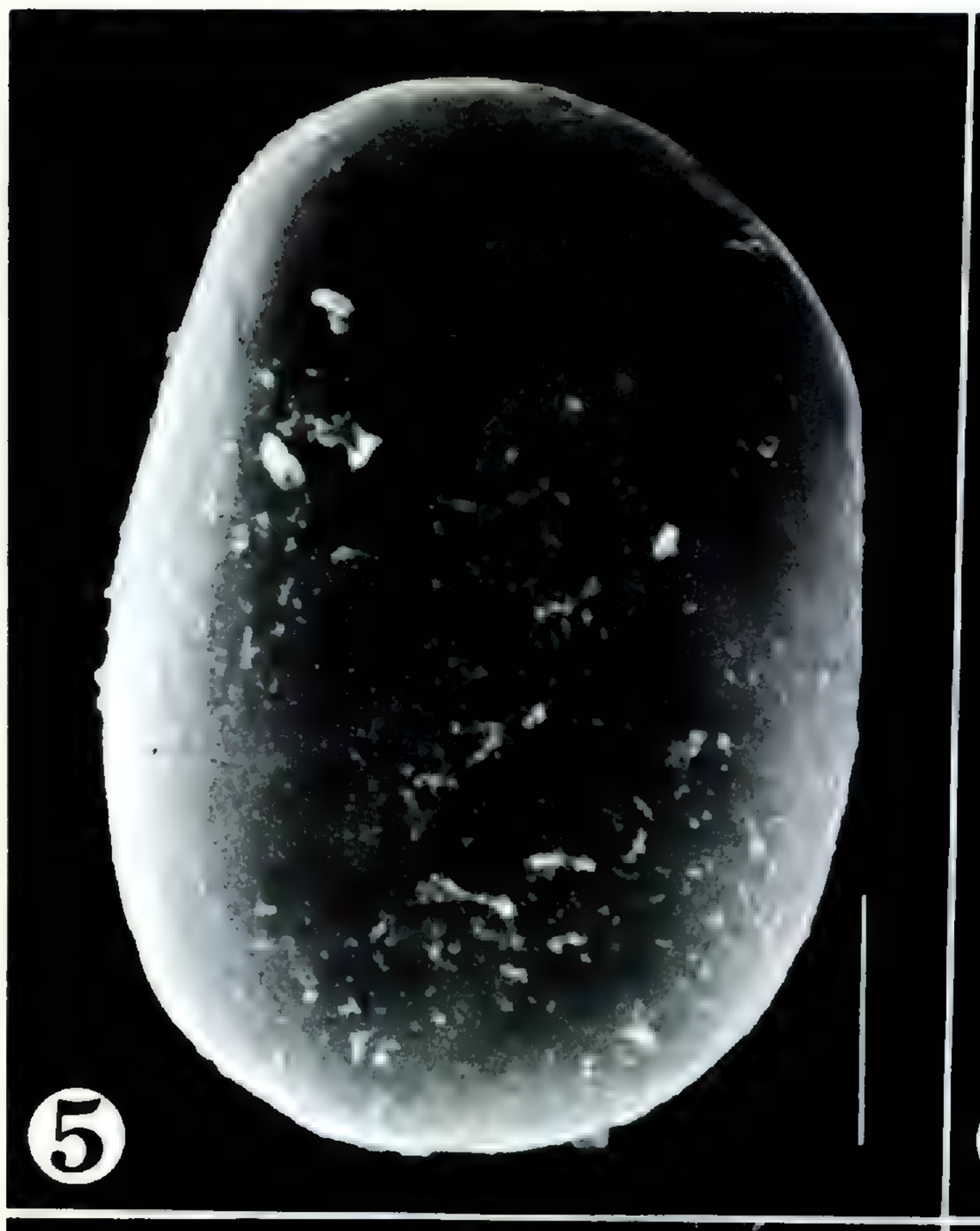
The fruits of *Dianthoveus* remain green or become light brown at maturity and apparently offer little attraction to dispersers; they are neither fragrant nor very juicy. We found seeds germinating in the debris of an old infructescence at the base of a plant, and often seedlings were found on wet rock walls below the mother plants. Such gravity or "flush dispersal" is probably usual for the genus; however, we found several fruits on one infructescence with the distinctive prints of bat teeth. In *Evodianthus* the berries become bright pale orange and very juicy at maturity and are undoubtedly dispersed by birds or bats.

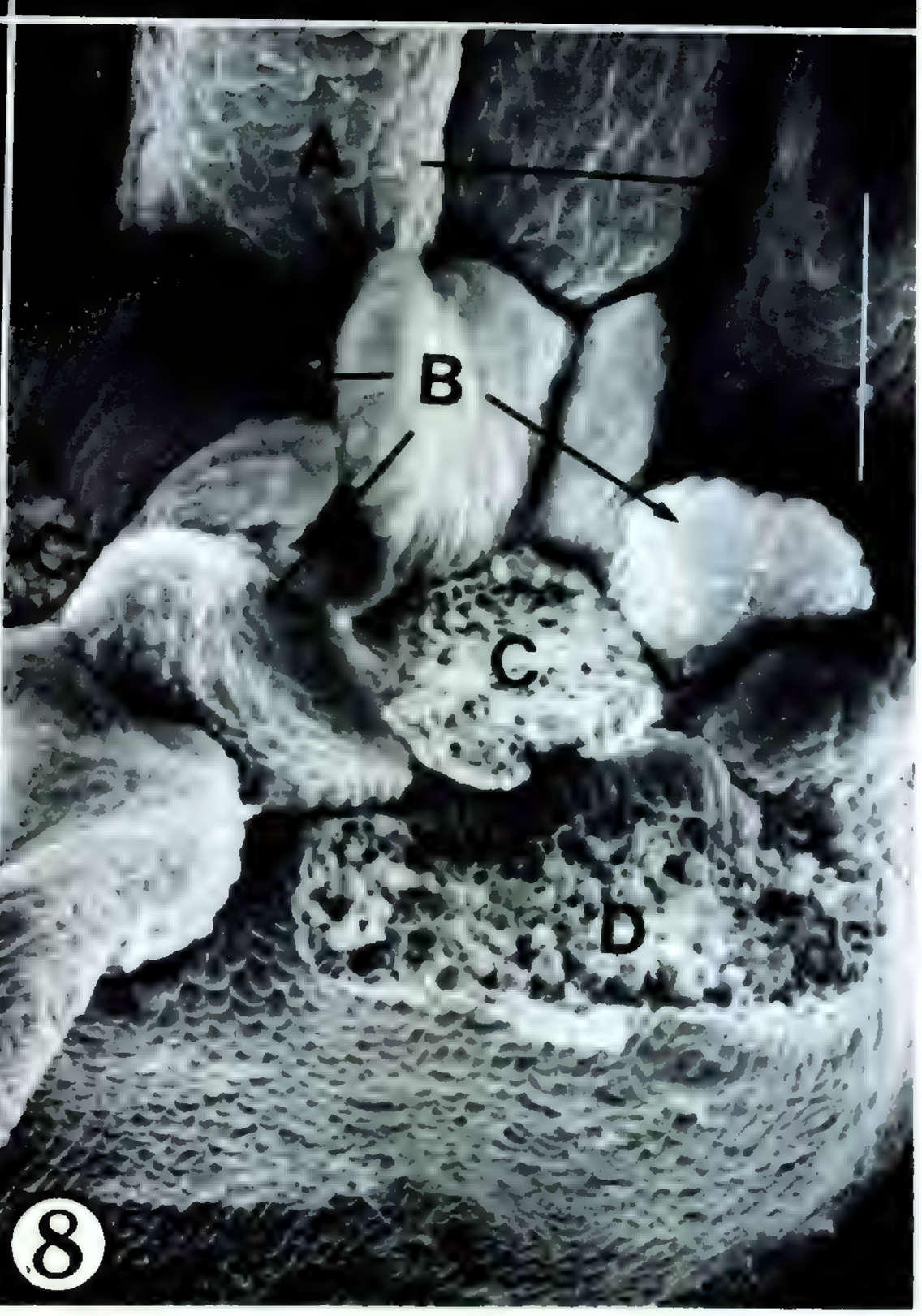
Staminate flowers are tightly crowded among the pistillate flowers throughout development and persist into the early stages of fruiting; remains of the pedicels can be found even among mature fruits. Tepals often vary in length within one flower and usually with a tendency for the longest tepals to be together, making the flower slightly asymmetrical. This asymmetry, however, appears to be random with respect to the associated pistillate flower; the longest tepals, for example, may or may not face the pistillate flower. The tepals are thin and become brown at anthesis. They are always without resin glandules.

Tepals of the pistillate flowers are quite similar in shape and texture to those of the staminate flowers, an unusual condition for the family. Their apices are thin, nearly filamentous, and at first lie closely appressed to the stigmas and to the staminodia. In fruiting stages the tepals become much broader—only acute to rounded—and the tips often break off, leaving an irregular ridge around the stigmas, which no longer protrude and are often turned upward rather than uncinate. The sides of the fruit converge basally towards the long axis of the spadix into a narrow, vertical, lenticular shape.

Relationships. A simple comparison of the new genus with others in the family suggests that it is closely related to *Evodianthus*. Most notably, both genera and no others have leaves that are scabrous when dry. Anatomically, this translates into "styloid sacs [which] are normally elongated in all directions within the mesophyll, routinely crossing cell layers" (Wilder, 1985). All other Cyclanthaceae with styloid sacs have them elongated only parallel to the longitudinal files of parenchyma cells and confined to one layer. Only *Evodianthus* and *Dianthoveus* have styloid sacs in roots. Pollen of both genera is the smallest in the family and inaperturate (Figs. 5, 6), in contrast to the aperturate pollen of all other genera. Both genera have very short or no filaments and lack basal bulbs. Both have unicostate or cryptically subtricostate leaves, separate fruits, symmetrical staminate flowers, and terminal inflorescences, characters unusual in the family but shared with other genera (Table 3).

Features of staminate flowers and seeds have been especially important for delimiting suprageneric taxa within the Cyclanthaceae (Gleason,





FIGURES 5–8.—5. Pollen of *Dianthoveus cremnophilus*. Bar = 5 μm; *Hammel & Wilder 16067*.—6. Pollen of *Evodianthus funifer*. Bar = 5 μm.—7. Seed of *Dianthoveus cremnophilus*. Bar = 0.5 mm; *Hammel & Wilder 16058*.—8. Receptacle of staminate flower of *Dianthoveus cremnophilus*. A = base of anthers; B = cupule-forming papillae; C = point of attachment of stamen; D = point of attachment of tepal. Bar = 0.2 mm; *Hammel & Wilder 16067*.

TABLE 3. Hierarchy of unusual characters of *Dianthoveus* and the genera sharing them.

Character	Shared with
Papillate receptacles	none
Long-acuminate tepals	none
Inconspicuous spathes	*Cyclanthus*
Eglandular staminate tepals	*Dicranopygium* subg. *Gleasonianthus*
Apiculate anther appendages	*Schultesiophytum*
Scabrous leaves	*Evodianthus*
Styloids in roots	*Evodianthus*
Inaperturate pollen grains	*Evodianthus*
Sessile anthers	*Evodianthus*
Spinules on wall of seed coat	*Carludovica*, *Thoracocarpus*
Moderately flattened seeds	*Carludovica*, *Schultesiophytum*
Separate fruits	*Evodianthus*, *Schultesiophytum*, *Sphaeradenia*
Terminal inflorescences	*Evodianthus*, *Carludovica*, *Cyclanthus*
Clustered spathes	*Evodianthus*, *Carludovica*, *Schultesiophytum*, *Dicranopygium*

1929; Harling, 1958; Wilder, 1978). In the new genus, characters of both these structures differ markedly from those of *Evodianthus*, from which the former differs by its lack of a biseriate perianth (unique to *Evodianthus*), its lack of a funnelform receptacle in the staminate flowers (found in *Evodianthus* and several other genera), and by its only moderately flattened and narrowly elliptic seeds (Fig. 7). *Evodianthus*, as well as *Asplundia* and *Thoracocarpus*, have broadly elliptic, strongly flattened seeds. The seed coat structure also differs markedly from that of *Evodianthus* (see below). The new genus is further distinguished by the eglandular, acuminate tepals of the staminate flowers (which are similar only to those of *Dicranopygium* subgenus *Gleasonianthus*), the apiculate laminar appendages of the anthers (shared only with *Schultesiophytum*), and especially the peculiar papillate receptacle of the staminate flowers (Fig. 8).

Seed coat structure is variable among genera of Cyclanthaceae and was an important consideration in Harling's delimitation of genera in the family. We have interpreted the wall layers by focusing on the inner and outer cuticles, described by Harling and present in all genera. The seed coat of *Dianthoveus* (Fig. 9) is similar to those of *Carludovica* and *Thoracocarpus*; the innermost layer of the outer integument in all three genera has relatively large thin-walled cells with spinulose wall ingrowths on the inner tangential walls, whereas *Evodianthus* lacks these spinules (Harling, 1958: 38–43).

Evodianthus occurs rarely as a terrestrial plant and rarely with leaf blades nearly as large as those of the new genus. With fresh material, the less glossy (more satiny) aspect of the upper leaf surface, the larger size, and constantly terrestrial and short-stemmed habit of *Dianthoveus* distinguish it vegetatively from *Evodianthus*. Due to the similarity of these two genera, *Evodianthus* specimens (and all other Cyclanthaceae) at COL, F, MO, QCA, and SEL were examined to see if the new genus was included among them; it was not.

PHYLOGENETIC ANALYSIS

The Cyclanthaceae are widely considered to be monophyletic (Dahlgren et al., 1985; French et al., 1983), and for the most part each of the 11 genera also has at least one clear apomorphy supporting its monophyly. Within Cyclanthaceae, *Cyclanthus* possesses many unique and highly derived features (Dahlgren et al., 1985; Harling, 1958; Wilder & Harris, 1982) and apparently shares only ancestral characters with other genera. The similarity of seeds of *Cyclanthus* to those of Pan-

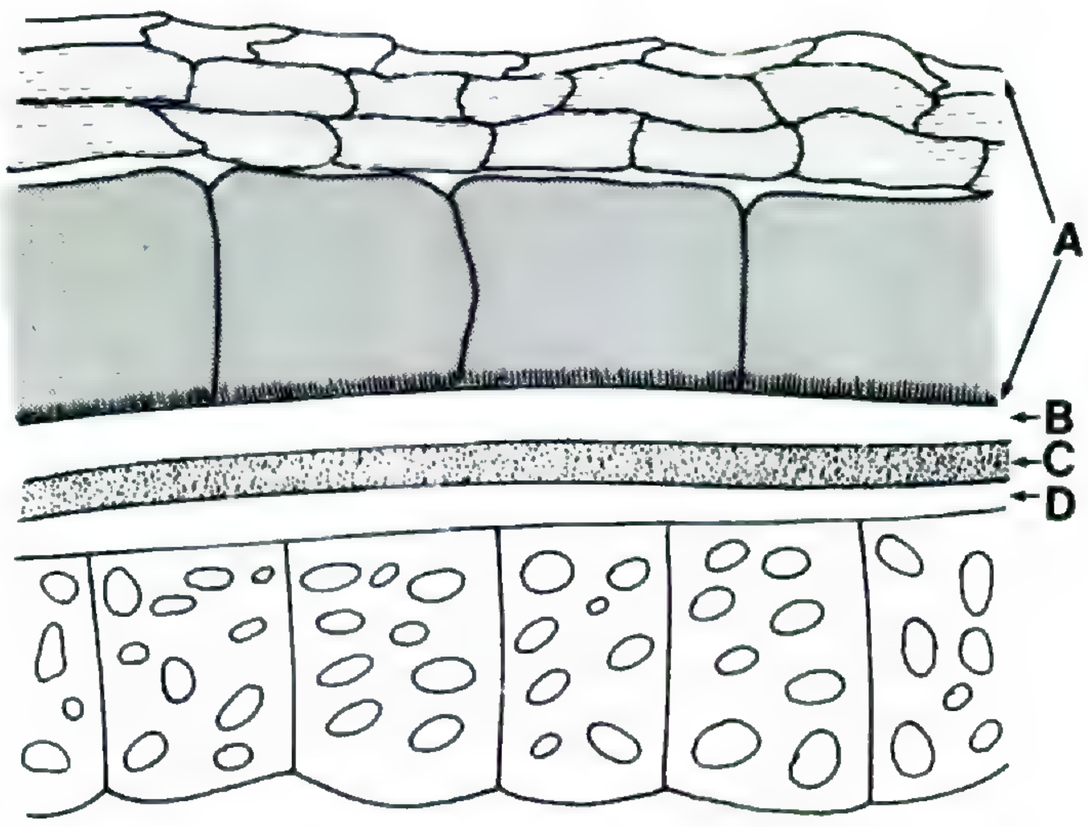


FIGURE 9. Seed coat of *Dianthoveus cremnophilus*.—A. Outer integument; lower arrow points to spinulose wall ingrowths.—B. Outer cuticle.—C. Inner integument.—D. Inner cuticle; *Hammel & Wilder 16058*.

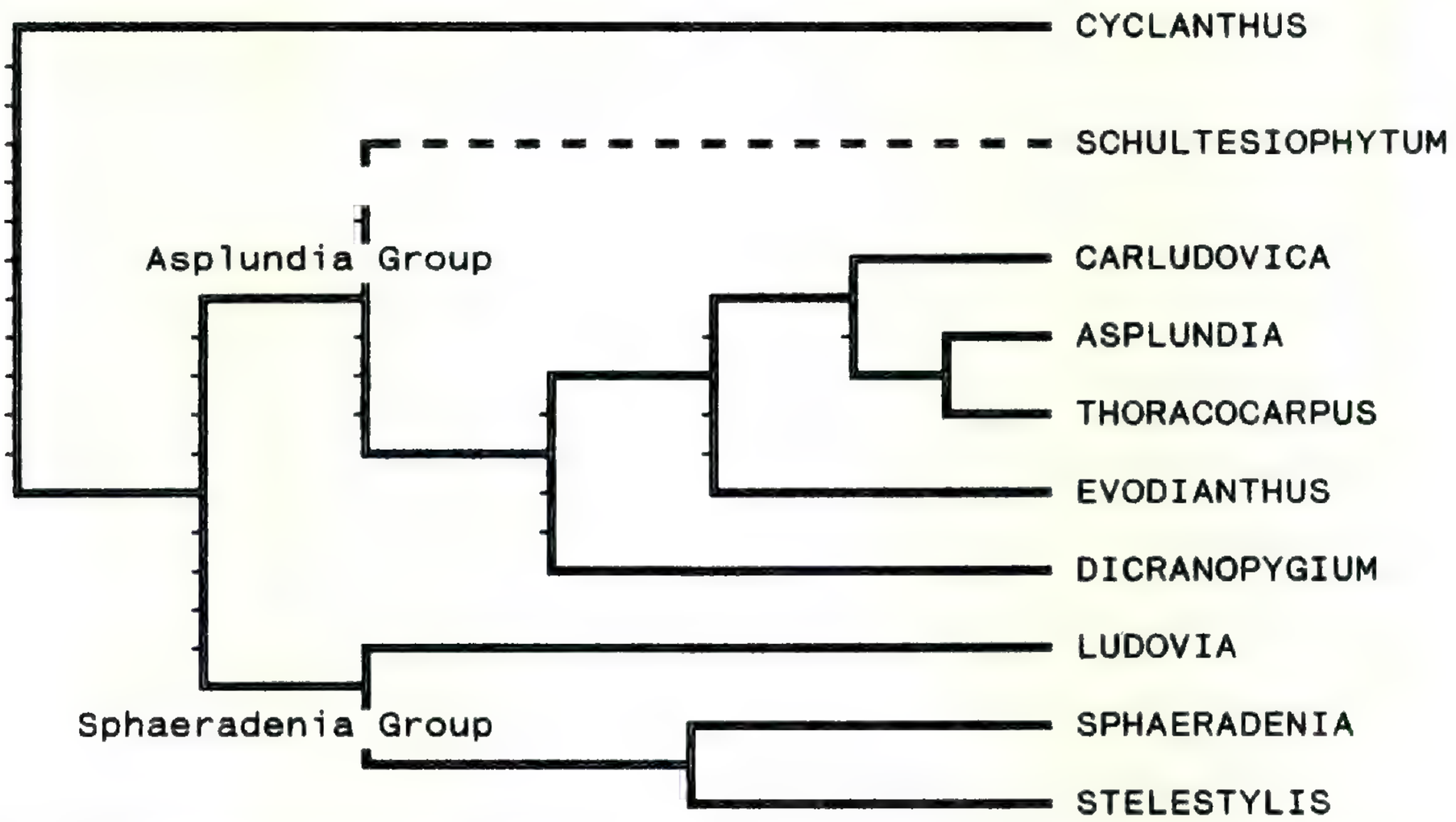


FIGURE 10. Phylogenetic scheme of Cyclanthaceae. Dashed line is Harling's convention for indicating highly uncertain position of *Schultesiophytum*—staminate flowers were unknown. Adapted from Harling (1958).

danaceae, especially in the genus *Freycinetia*, figured strongly in Harling's "geneological tree" (1958) for the genera of Cyclanthaceae (Fig. 10), including division of the family into two subfamilies. Furthermore, a preliminary analysis using *Freycinetia* (Pandanaceae) as the outgroup resulted in three trees, all of which supported the Cyclanthoideae/Carludovicoideae subdivision of the family (Hammel, unpubl.).

Thus, as a starting point we accepted a sister group relationship for the two subfamilies of Cyclanthaceae and postulated hypothetical ancestor for the Carludovicoideae based on the presumably ancestral characters of *Cyclanthus*, the only genus in the Cyclanthoideae. *Cyclanthus* contains only two species and is monomorphic for the characters analyzed; variability within the hypothetical ancestor was therefore not a problem. Characters not obviously comparable between the two subfamilies, e.g., floral symmetry (*Cyclanthus* lacks distinct, meristic floral units at maturity) were coded either by looking outside the family to the Araceae, Arecaceae, and Pandanaceae, where Harling and others have indicated the most likely affinity with the Cyclanthaceae, or by designating them as missing characters for *Cyclanthus*.

Harling's (1958) proposed relationships among genera in his "*Asplundia* group," which would include the new genus, by his own admission were quite tentative (Fig. 10). The main purpose of our analysis was to make an explicit statement as to the placement of *Dianthoveus* within the family, using characters from Harling and new characters. Discussion of those aspects of the character analysis not directly pertinent to the new genus and comparison of the phylogeny produced with these methods to that of Harling will be presented elsewhere (Hammel, unpubl.).

Character coding. Several characters were coded as missing in *Cyclanthus*, the hypothetical ancestor for this analysis. For example, although the pistillate "units" seem to demonstrate a remarkable extreme of fusion among parts, they readily dehisce from each other at maturity. Furthermore, it is difficult to judge an immediate ancestral state for this character from outgroup comparison; fruits are commonly fused in Pandanaceae, rarely in Araceae, and sometimes in Arecaceae. Note also that whereas Dahlgren & Rasmussen (1983) cited "indehiscent fruits" as a possible synapomorphy for their Areciflorae complex (Arecaceae, Cyclanthaceae, Pandanaceae), the berries in most species of Cyclanthaceae are dehiscent by apical caps (*Thoracocarpus*, all but one species of *Asplundia*, and most species of the *Sphaeradenia* group; Hammel, unpubl.). Live, mature infructescences of Pandanaceae, especially *Freycinetia*, need to be examined for comparison.

Characters of the staminate flowers were likewise difficult to polarize with reference to *Cyclanthus*, which at maturity has only amerous rows of stamens. Pandanaceae also have amerous and apetalous staminate inflorescences. Flowers were coded as primitively symmetrical by reference to Araceae and Arecaceae. Presence/absence of glands on tepals and shape of perianth were coded as missing data.

The phyllotaxy in *Cyclanthus* is spirodistichous (Wilder, 1981), making the coding of this char-

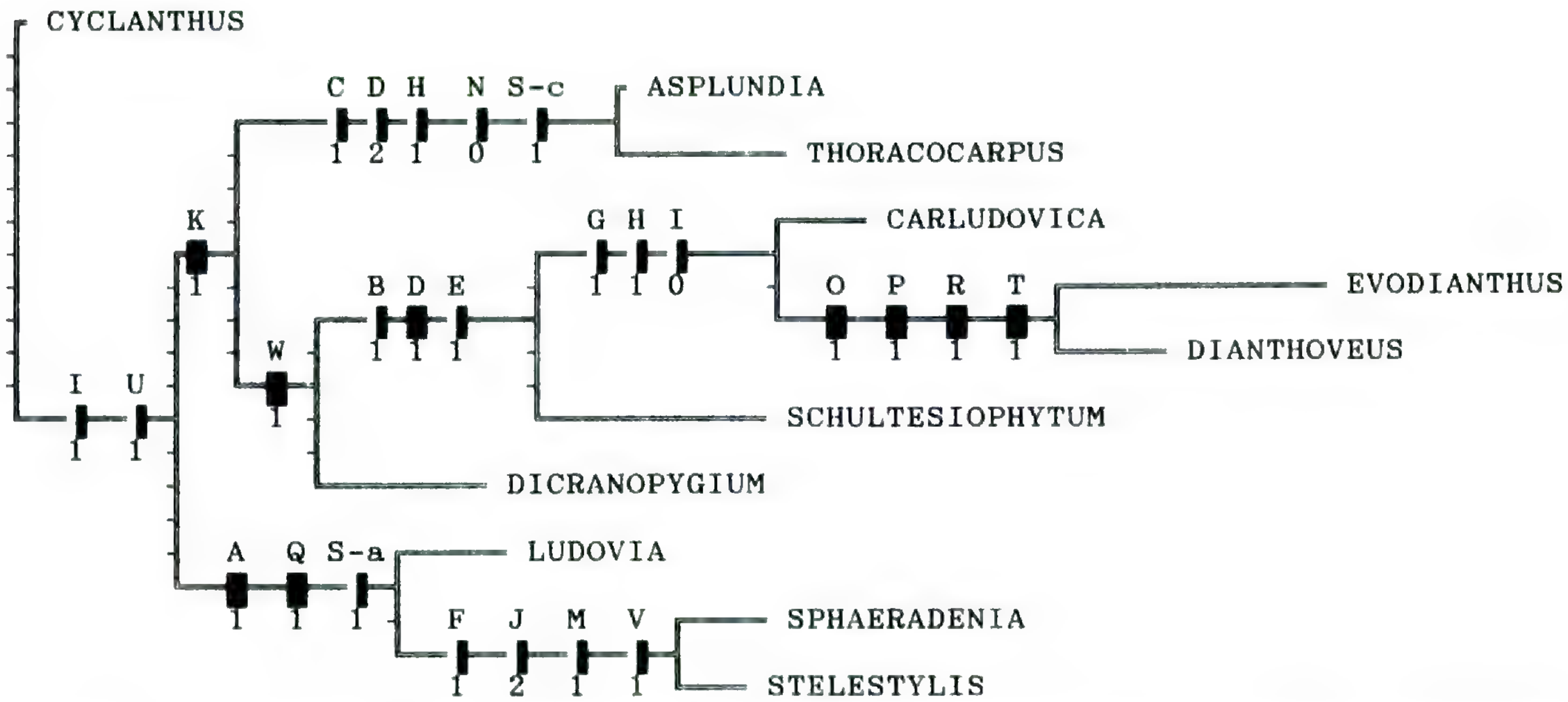


FIGURE 11. Cladogram of the Cyclanthaceae. Wide bars are uniquely derived and consistent synapomorphies; half-bars are synapomorphies of character states found elsewhere in the family or reversed within the defined group. Letters above bars refer to characters (Table 1), numbers below to character states. Length of terminal clade is directly related to number of apomorphies discovered by analysis. Length = 48; consistency index = 0.604; originally known autapomorphies not included in analysis.

acter problematic; genera of the Carludovicoideae have either orthodistichous (in a few species spirodistichous) or spiral phyllotaxy. The Pandanaceae have tristichous phyllotaxy. For this analysis spiro- and orthodistichy were both subsumed under the category "distichous," and phyllotaxy was coded as having only two states. The terminal inflorescences of *Cyclanthus* seem well supported as ancestral; terminal inflorescences are the rule in Araceae (Ray, 1987 and pers. comm.) and in Pandanaceae (Tomlinson & Wilder, 1984) and are characteristic of the "primitive" coryphoid palms. In palms, however, terminal inflorescences are never evicted by axillary shoots (Tomlinson & Wilder, 1984). States for seed characters were coded directly from *Cyclanthus* as ancestral; the similarity of seeds of *Cyclanthus*, *Dicranopygium*, and *Ludovia* with those of some members of the Pandanaceae is one of the main features that Harling (1958) saw as indicating a close relationship between Pandanaceae and Cyclanthaceae.

The branched order of character states for "habit" (Table 1) is rationalized by the observation that variable taxa almost always include terrestrial members. It then seems unlikely that any nonterrestrial form was derived one from another.

RESULTS AND DISCUSSION

From our data matrix (Table 2), PAUP found five trees with 49 steps and a single most parsimonious cladogram with 48 steps (Fig. 11). A sister-group relationship between *Dianthoveus* and *Evodianthus* is supported by all of these analyses. Furthermore, when the data matrix is changed to accommodate different possibilities for states coded as "missing" or different interpretations of problematic characters for the hypothetical ancestor, such as fruit fusion and phyllotaxy, this relationship remains unchanged even when the overall topology changes.

The highly corroborated sister-group relationship between *Evodianthus* and *Dianthoveus* allows a rational discussion of homologies of the unusual staminate flowers in the new genus. On the basis of our hypothesis (Fig. 11), *Dianthoveus* appears to retain more relatively primitive character states than *Evodianthus*, such as the terrestrial (vs. climbing) habit. The moderately flattened seeds are also relatively primitive as compared with the strongly flattened seeds of *Evodianthus*. The laminar-apiculate anther appendages of *Dianthoveus* could be symplesiomorphous with those of *Schultesiophytum*, but that assumption would require an additional step; it is more parsimonious to assume that this kind of anther evolved independently in the two genera. The biseriate perianth of *Evodianthus*—an apomorphy for *Evodianthus* not included in the analysis—appears to be derived within the family.

From this basis we can argue that the inner cycle of the biseriate perianth of *Evodianthus* might be an elaboration of the unusual papillate receptacle of *Dianthoveus*. By this hypothesis, the lobes of the inner perianth of *Evodianthus* are not appendicular organs (leaf homologues), but rather

emergences, equivalent developmentally to the papillae, which compose cupules in *Dianthoveus*.

In all cases, regardless of coding, eglandular staminate tepals appear to have arisen twice within the Carludovicoideae—in *Dicranopygium* subgenus *Gleasonianthus* and in *Dianthoveus*. However, according to Harling (1958; see also Wilder, 1978), the eglandular tepals of subgenus *Gleasonianthus* are not "real perianths," but rather are homologous with stamen filaments; he found that lobes of this "false perianth" sometimes bear reduced anthers. In addition, the filaments of anthers in subgenus *Gleasonianthus* are somewhat flattened and acute, resembling the lobes of the false perianth. In *Dianthoveus* we see no equivalent basis for hypothesizing a staminodial nature for the eglandular tepals. We found none with reduced anthers, and they certainly bear no resemblance to filaments of stamens (*Dianthoveus* lacks filaments). Based on their position, they appear simply to be homologous with the glandular outer whorl of the biseriate perianth of *Evodianthus* and the "real perianth" of other Cyclanthaceae. Under this reasoning, the eglandular tepals of *Dianthoveus* are similar to those of *Dicranopygium* subgenus *Gleasonianthus* only by convergence.

Conclusion

Before our cladogram or any other is presented as a phylogeny for the family, several of the characters and character states need to be re-evaluated and the hypothesis tested with additional characters. For example, the character of spathe position, crucial for placing *Dicranopygium* in the clade definied by clustered spathes, is somewhat subjective. The spathes of *Carludovica*, *Schultesiophytum*, and *Dianthoveus* are not much closer together than many species outside the clade. Which other, if any, multistate characters (e.g., seed shape) might logically be ordered? One also wonders if characters such as inflorescence position and phyllotaxy, which seem to encompass a large suite of characters, should be given extra weight or broken into several characters. All of this needs to be evaluated within the context of a hypothetical ancestor postulated on the basis of taxa outside the Cyclanthaceae.

Although a close relationship between *Dianthoveus* and *Evodianthus* was suggested initially by the observation that only these two have scabrous leaves, a phylogenetic analysis using parsimony demonstrates the hypothesis as supported by numerous characters. It also provides a logical basis for suggesting the evolutionary homologies of the unusual floral features of the new genus, in particular, the papillate receptacle (possibly homologous with the inner perianth of *Evodianthus*), the laminar apiculate anthers (evolved in parallel to those of *Schultesiophytum*), and the eglandular tepals (convergent with those of *Dicranopygium* subgenus *Gleasonianthus*).

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ANATOMIA REPRODUCTIVA DE *LACANDONIA SCHISMATICA* (LACANDONIACEAE)[1]

J. Márquez-Guzmán,[2] *M. Engleman,*[3] *A. Martínez-Mena,*[2] *E. Martínez*[4] *y C. Ramos*[2]

Resumen

Lacandonia schismatica es una familia, género, y especie nuevos para la ciencia. El carácter más conspicuo lo constituye la posición del androceo en el centro de la flor, rodeado por el gineceo apocárpico. Tal disposición no había sido mencionada antes para angiospermas. El androceo está formado por tres anteras (a veces cuatro) biloculares con dehiscencia introrsa. El gineceo es apocárpico. Cada carpelo contiene un solo óvulo sésil, basal, anátropo, y bitégmico; el tegumento interno forma el micrópilo. El endospermo es de tipo nuclear. El embrión en la semilla madura es poco desarrollado. El fruto es indehiscente.

Abstract

Lacandonia schismatica comprises a new family, genus, and species. Its most conspicuous character is the central position of the androecium, surrounded by the apocarpous gynoecium. This arrangement has not been recorded before for angiosperms. The androecium consists of three (sometimes four) bilocular anthers with introrse dehiscence. The gynoecium is apocarpic. Each carpel contains a single ovule that is sessile, basal, anatropous and bitegmic; the inner integument forms the micropyle. The position of the style on the ovary changes during development. The endosperm is of the nuclear type. The embryo of the mature seed is poorly developed. The fruit is indehiscent.

La nueva familia Lacandoniaceae del orden Triuridales (Martínez y Ramos, 1989) es afín a Triuridaceae Gardner (Maas y Rübsamen, 1986) pero se diferencia por el gineceo que rodea al androceo y la dehiscencia introrsa de las anteras.

La inversión de posición de los órganos reproductores fue lo suficientemente interesante para iniciar los estudios estructurales. A continuación se presentan los primeros resultados al respecto.

Materiales y Metodos

Se estudió material de dos colectas (E. Martínez M. *19310* y *21822*) de *Lacandonia schismatica* E. Martínez y C. H. Ramos. Se fijaron muestras de botones florales, flores, y frutos en diversas etapas de desarrollo en el sitio mismo de colecta (selva Lacandona, Chiapas, México), y las muestras se trasladaron al laboratorio para su procesamiento posterior.

Se usaron tres fijadores diferentes: a) FAA (formalina, ácido acético, etanol al 70%; 5 : 5 : 90); b) glutaraldehido al 5% en amortiguador de fosfatos 0.1 M pH 6.8 con sacarosa al 0.25 M; c) glutaraldehido al 5% + paraformaldehido al 4% en amortiguador de S colidina 0.1 M pH 7.2.

Después de la fijación algunas muestras fueron deshidratadas en series graduales de alcohol etílico

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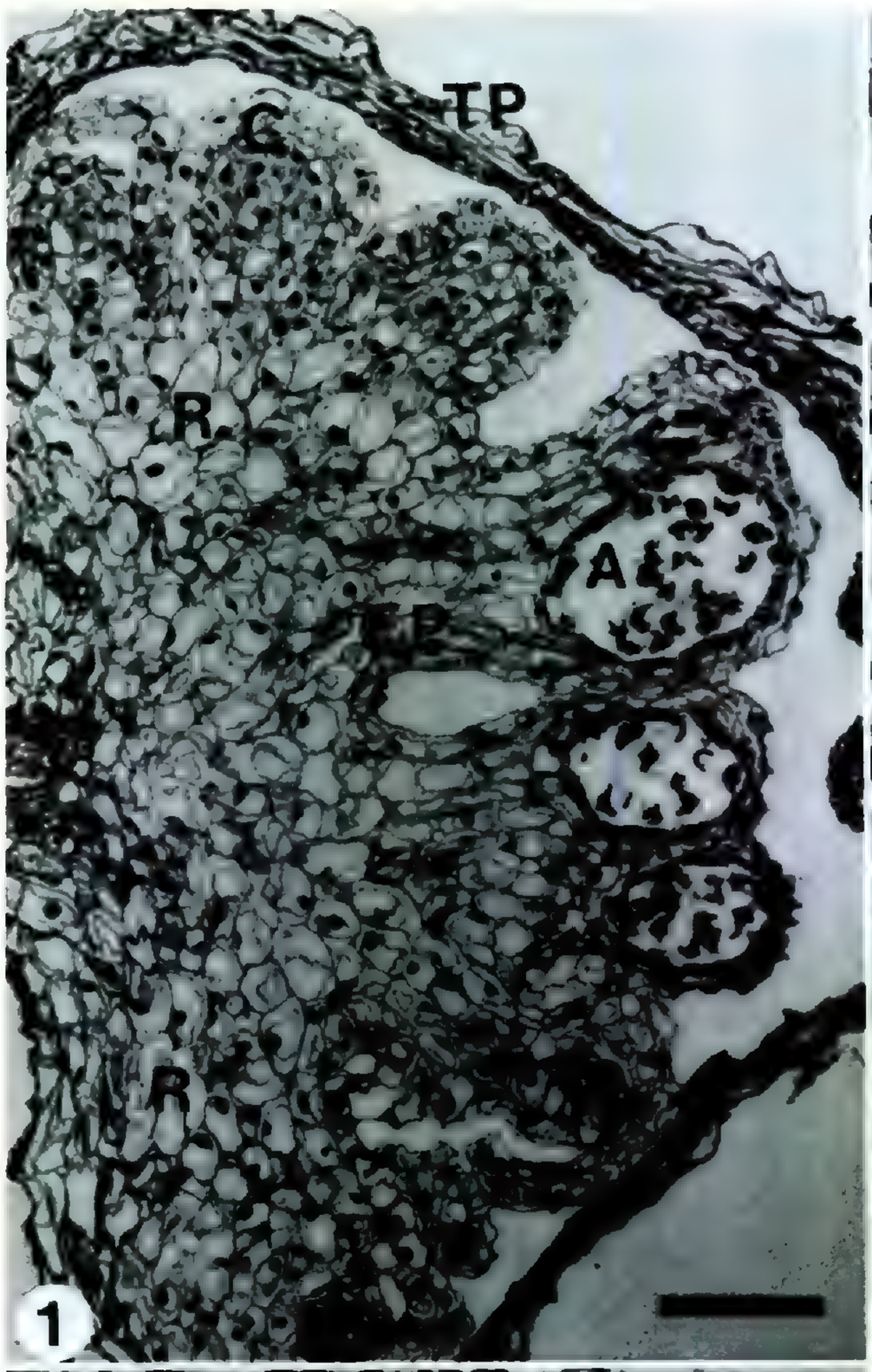
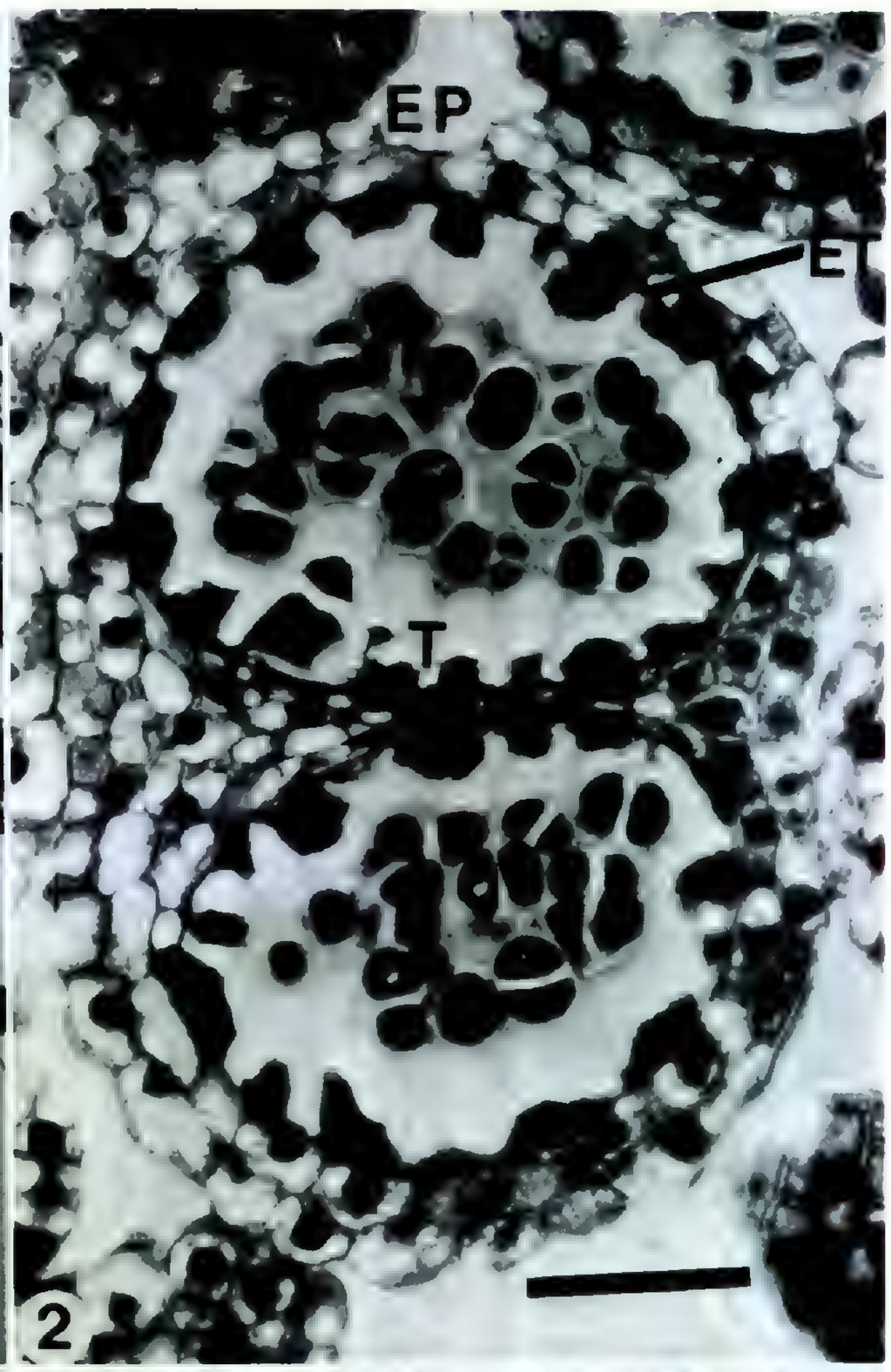
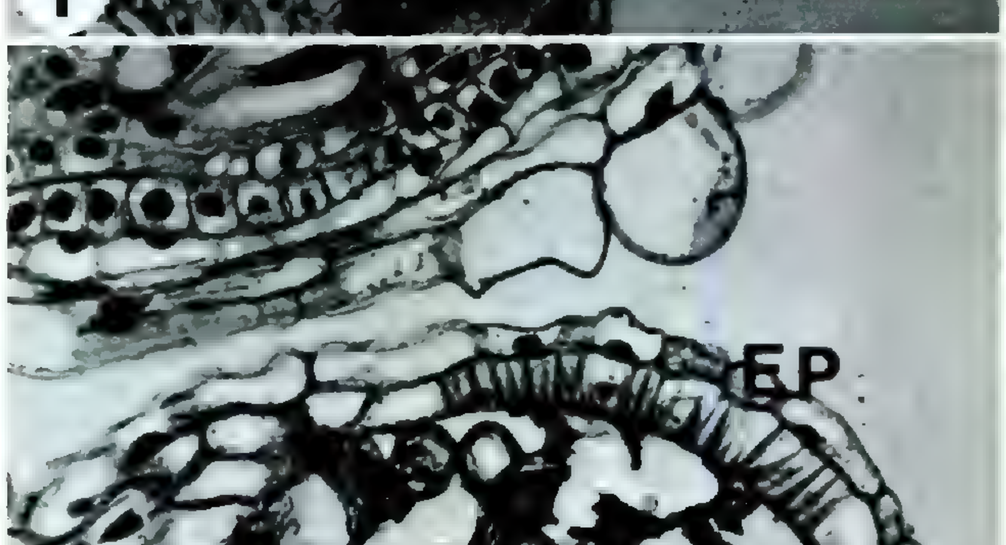
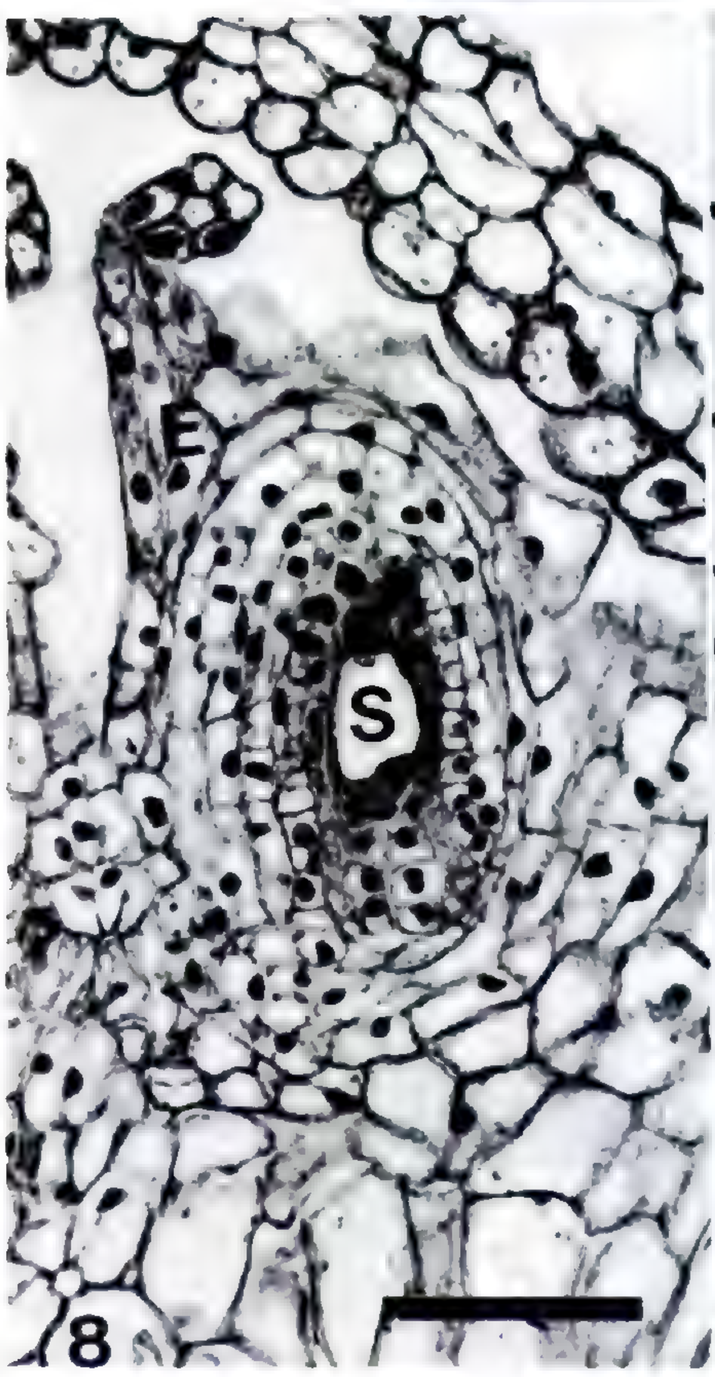
Figuras 1–4.—1. Corte longitudinal de botón floral con el pedicelo a la izquierda. Las anteras (A) ocupan la posición central. La epidermis (EP) se continúa con los tejidos del receptáculo (R). Los carpelos (C) ocupan una posición externa al androceo. Tépalos (TP).—2. Corte transversal de antera joven. La pared formada por epidermis

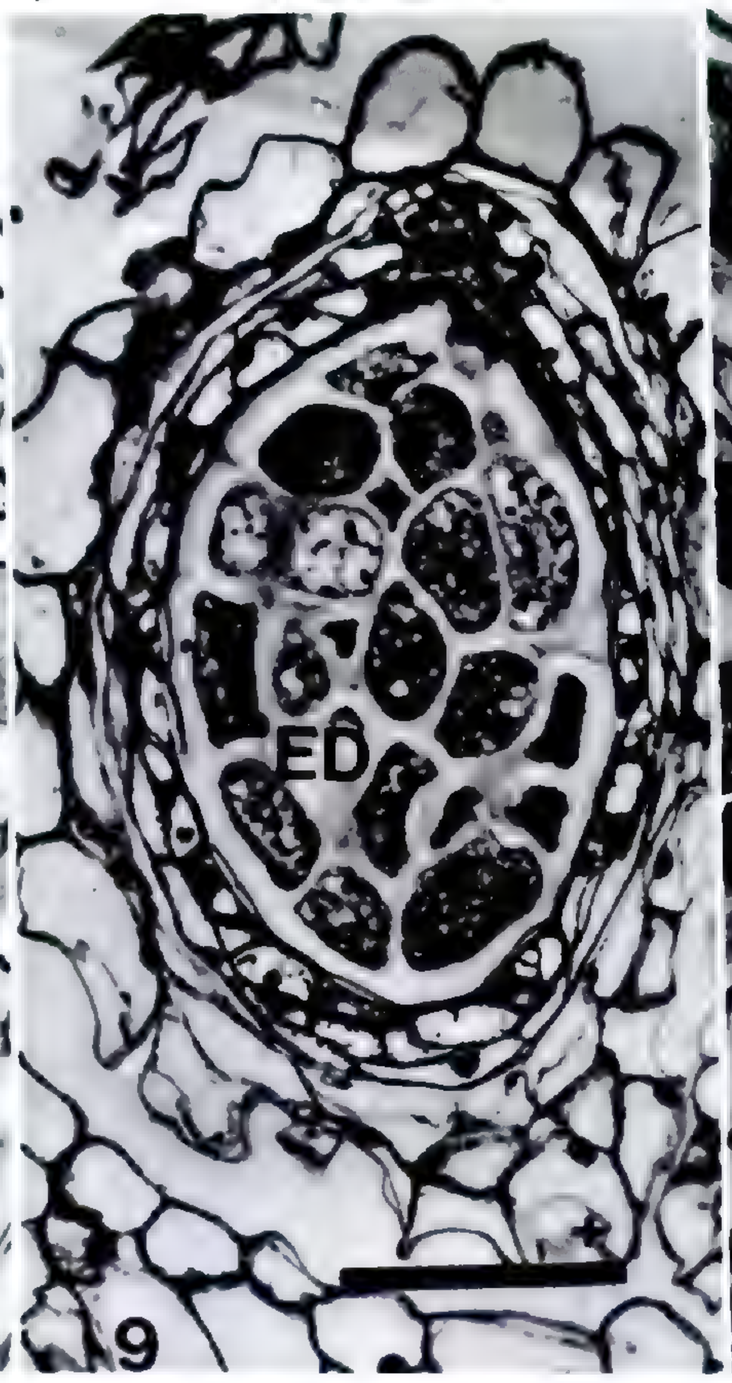


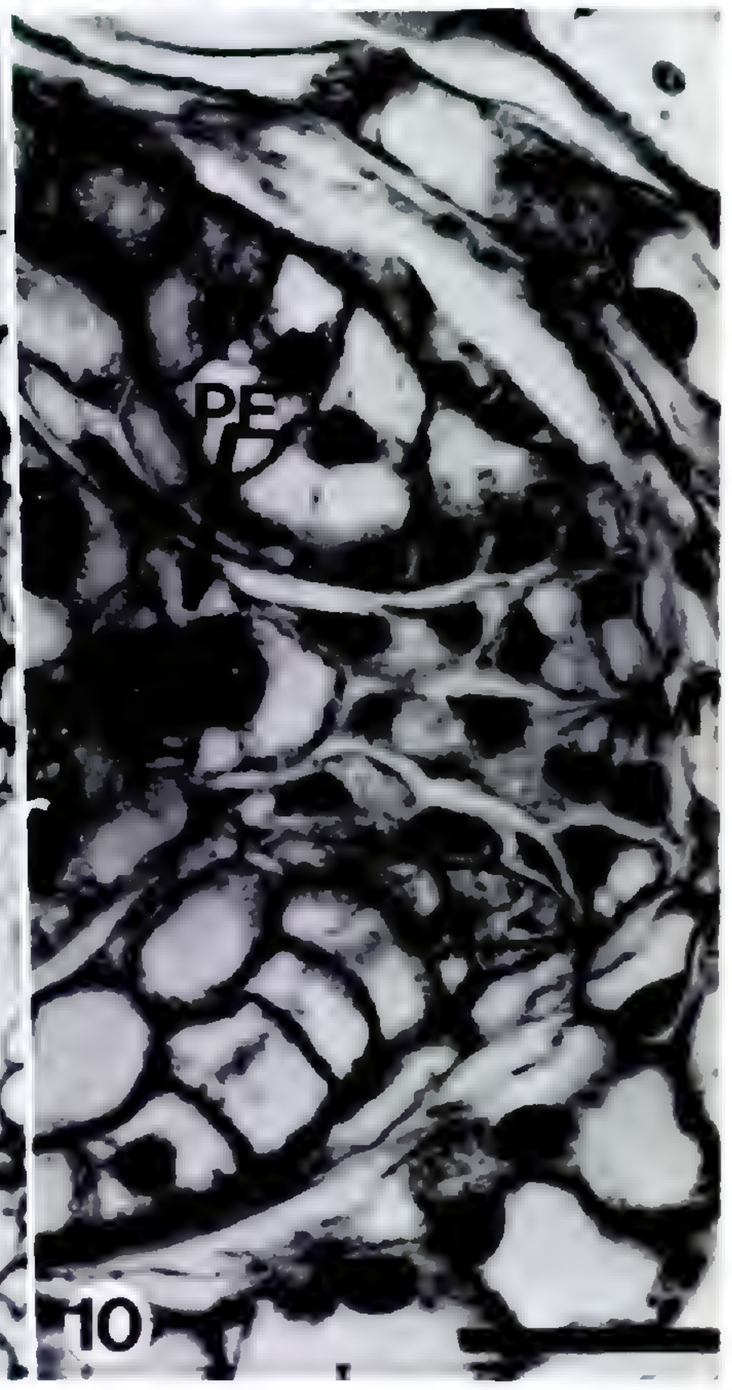




(EP), endotecio (ET), y tapete (T).—3. Corte longitudinal de antera madura. La pared está formada por la epidermis (EP) y el endotecio fibroso (ET). El septo separa los lóculos (L).—4. Corte transversal de antera madura. Epidermis (EP), endotecio (ET), y restos del tapete. La punta de un tépalo (TP) se ha metido entre las anteras. Escalas = 100 μm.







FIGURAS 5–10.—5. El grano de polen (G) está formado por tres células. Escala = 10 μm.—6. Corte transversal de antera. La flecha señala la posible zona de dehiscencia donde el endotecio (ET) queda interrumpido. Escala = 100 μm.—7. Corte longitudinal de un carpelo. El óvulo posee dos tegumentos (TG). El interno forma el micrópilo (M). Saco embrionario (S). Escala = 50 μm.—8. Corte longitudinal de un carpelo. El estilo (E) está en posición subapical. Escala = 100 μm.—9. Corte longitudinal del fruto. El endospermo (ED) con células de paredes gruesas. Escala = 100 μm.—10. Corte longitudinal de un proembrión (PE) de dos células. La división del cigoto ha sido transversal. El micrópilo (M) se dirige hacia la derecha. Escala = 50 μm.

y otras en acetona, y se incluyeron en parafina, plástico de JB4 o metacrilatos.

Para seccionar las muestras incluídas en parafina se utilizó un micrótomo rotatorio, y para las incluídas en resinas sintéticas un ultramicrótomo con navajas de vidrio. Los cortes de 1 a 2 μm se tiñeron con safranina/verde rápido o con azul de toluidina.

Resultados

Posición de los verticilos florales. El verticilo más externo está constituído por seis tépalos papilosos. La posición del androceo en el centro de la flor con el gineceo apocárpico alrededor se muestra claramente en cortes longitudinales de botones florales (Fig. 1). La continuidad de la epidermis que se observa desde la base de las anteras hasta el receptáculo no deja dudas sobre su posición central.

Androceo. Se observó que las anteras se desarrollan y maduran antes que los carpelos y persisten, sin caerse, después de que los frutos se han dispersado.

El androceo está formado por tres anteras (una flor entre cincuenta y cuatro observadas poseía cuatro anteras). Las anteras son biloculares, y la pared de la antera inmadura está formada por tres capas: la epidermis, el endotecio, y el tapetum (Fig. 2). El tapetum desaparece en la antera madura (Figs. 3, 4). Los estambres no poseen vascularización. El grano de polen maduro posee tres células (Fig. 5). La dehiscencia de las anteras es introrsa (Fig. 6).

Gineceo. El gineceo es apocárpico. La orientación de los carpelos es variable, de tal manera que la mayoría de ellos no tiene el estilo en el lado orientado hacia los estambres, en el centro del receptáculo. El estilo parte de la región superior del carpelo en el mismo lado que corresponde al hilo de la semilla (Fig. 8).

Cada carpelo contiene un solo óvulo sésil, basal, anátropo (Fig. 7), y bitégmico; ambos tegumentos son biestratificados, y el interno forma el micrópilo. El desarrollo del endospermo es de tipo nuclear, y el endospermo maduro posee células de paredes gruesas (Fig. 9). El embrión más desarrollado que se ha observado posee dos células; el cigoto se dividió transversalmente (Fig. 10). La cubierta seminal tiene una capa con inclusiones en forma de partículas.

El fruto es indehiscente. La epidermis del fruto posee células globosas cuando está en antesis.

Discusion

Las estructuras reproductoras de *Lacandonia schismatica* son comparables a las mencionadas por Tomlinson (1982) y por Maas y Rübsamen (1986) para la familia Triuridaceae.

La dehiscencia introrsa de las anteras es una característica que define esta especie. Sin embargo, el hecho más conspicuo, y nunca antes mencionado para Triuridaceae u otras angiospermas, es la posición central del androceo con respecto al gineceo (Cronquist, 1981). Esta disposición se observa más claramente en cortes medianos de botones florales inmaduros.

La continuidad celular, en especial la epidérmica, que se observa con los tejidos del centro del receptáculo es la prueba más fehaciente de su posición. Sin embargo muchos detalles de la formación del óvulo y la semilla se desconocen y aun no se sabe que tipo de embrión representan. La germinación no ha sido observada. Se pone de manifiesto la necesidad de realizar estudios embriológicos, además de estudios anatómicos comparativos de especies de la familia Triuridaceae. Tales resultados contribuirán a ubicar filogenéticamente a esta familia y dar luz sobre el significado evolutivo de la inversión en la posición de los órganos reproductores.

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LACANDONIACEAE (TRIURIDALES): UNA NUEVA FAMILIA DE MEXICO[1]

Esteban Martínez[2]
y Clara Hilda Ramos[3]

Resumen

Se describen una familia, un género y una especie de Triuridales nuevos para la ciencia. La nueva familia es afín a Triuridaceae Gardner, de la cual se diferencia por el gineceo rodeando al androceo; posición insólita que se describe por primera vez, y la dehiscencia introrsa de las anteras. Este es el primer registro del orden para México.

Abstract

A new family, genus, and species are described. The new family is placed in Triuridales. It differs from Triuridaceae by the unexpected and unknown elsewhere position of the gynoecium, which surrounds the androecium, and by the introrsely dehiscent anthers. This is the first record of the order for Mexico.

Entre las plantas colectadas para el proyecto Flora Mesoamericana (CONACyT PCECBEU-001109), se encontraron plantas del orden Triuridales que consideramos son familia, género, y especie nuevos para la ciencia y se describen a continuación:

Lacandoniaceae E. Martínez et C. H. Ramos, fam. nov. ordinis Triuridalium.

Flores hermaphroditi gynoecio apocarpo androecium cingenti, tribus staminibus centralibus antheris biloculatibus dehiscentia introrsa, apertura singularis.

Flores hermafroditas; gineceo apocárpico rodeando al androceo, tres estambres centrales y anteras biloculares con una sola línea de dehiscencia introrsa.

Lacandonia E. Martínez et C. H. Ramos, gen. nov.

Herbae saprophyticae, albidae, aphyllae. Caules simplices. Rhizoma glabrum horizontale radicibus pubescentibus. Inflorescentia racemosa. Flores hermaphroditi. Tepala (4–)6, apicibus caudatis, dense papillosa. Gynoecium apocarpum, carpellis 60–80. Styli subapicales. Stamina (2–)3(–4), centralia, marcescentia, gynoecium propinqua, antherae bilocularia introrsa, lobis 2(–3) confluentibus longitudinaliter dehiscentibus. Fructus aggregatus e multis acheniis constatus.

Hierbas saprofíticas, afilas, blanquecinas. Rizoma horizontal de crecimiento indefinido, con raíces fibrosas y esparcidamente pubescentes. Tallos aéreos simples, glabros. Inflorescencia racemosa, bracteada, de crecimiento simpodial; pedicelos ascendentes. Flores perfectas; tépalos (4–)6, densamente papilosos cuando frescos, cada uno con una cauda linear-laminar en el ápice. Gineceo y androceo sobre un receptáculo deprimido centralmente, con los carpelos rodeando al androceo. Gineceo con 60–80 carpelos papilosos; estilo subapical. Estambres (2–)3(–4), centrales, persistentes, insertos en el borde de la depresión del receptáculo; anteras biloculares con 2(–3) lóbulos, introrsas, una sola línea de dehiscencia longitudinal, polen intectado, inaperturado, verrugado. Fruto poliaquenio.

[1] Agradecemos a F. Chiang C. la ayuda solícita que nos brindó durante el desarrollo de este trabajo, así como la revisión crítica del manuscrito y las descripciones latinas; a G. Davidse y a M. Sousa S. el apoyo brindado en todo momento; a E. Martínez H. los datos de polen; a M. Veith por producir las preparaciones de SEM; a Mahinda Martínez la traducción del alemán; a R. Medina la elaboración del dibujo y sus valiosas sugerencias; a M. Sousa P. la mecanografía del texto; al Sr. Gabriel Aguilar su inapreciable ayuda en el trabajo de campo; a F. González Medrano, D. Lorence, R. Riba, J. L. Villaseñor, T. Wendt, y R. Weber sus valiosas sugerencias; a G. Andrade, B. Hammel, y P. Ramírez la bibliografía.

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Ann. Missouri Bot. Gard. 76: 128–135. 1989.

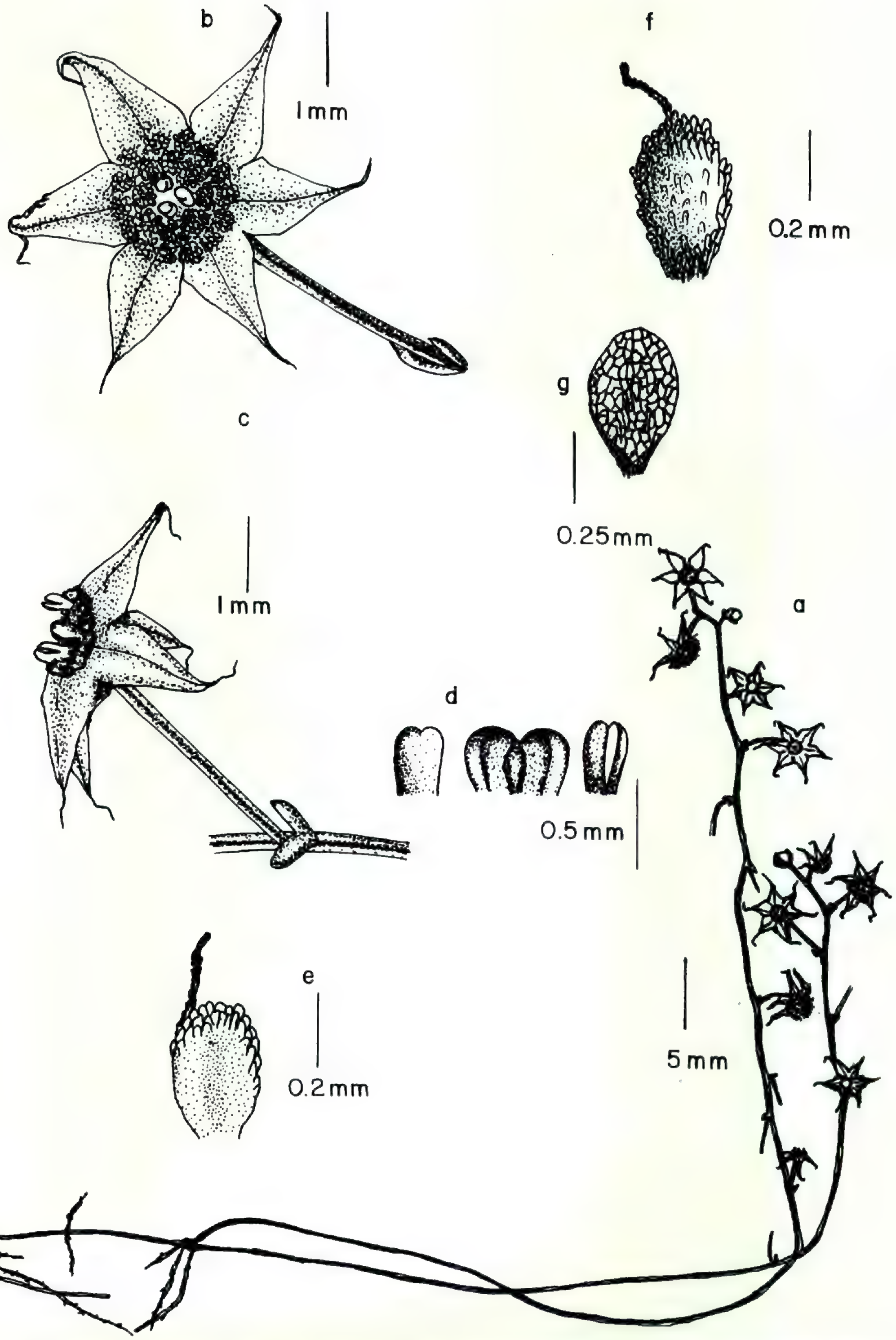
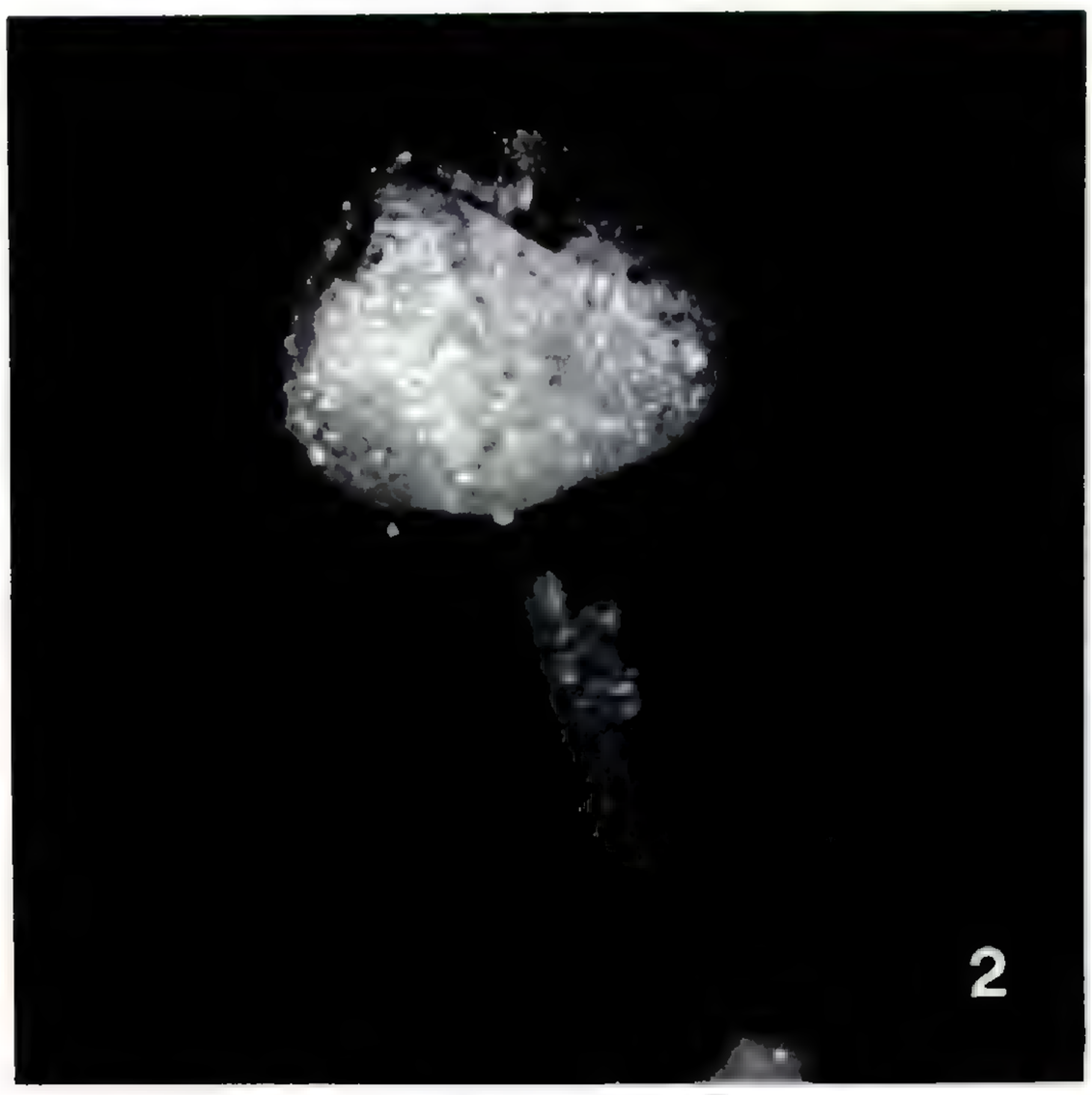
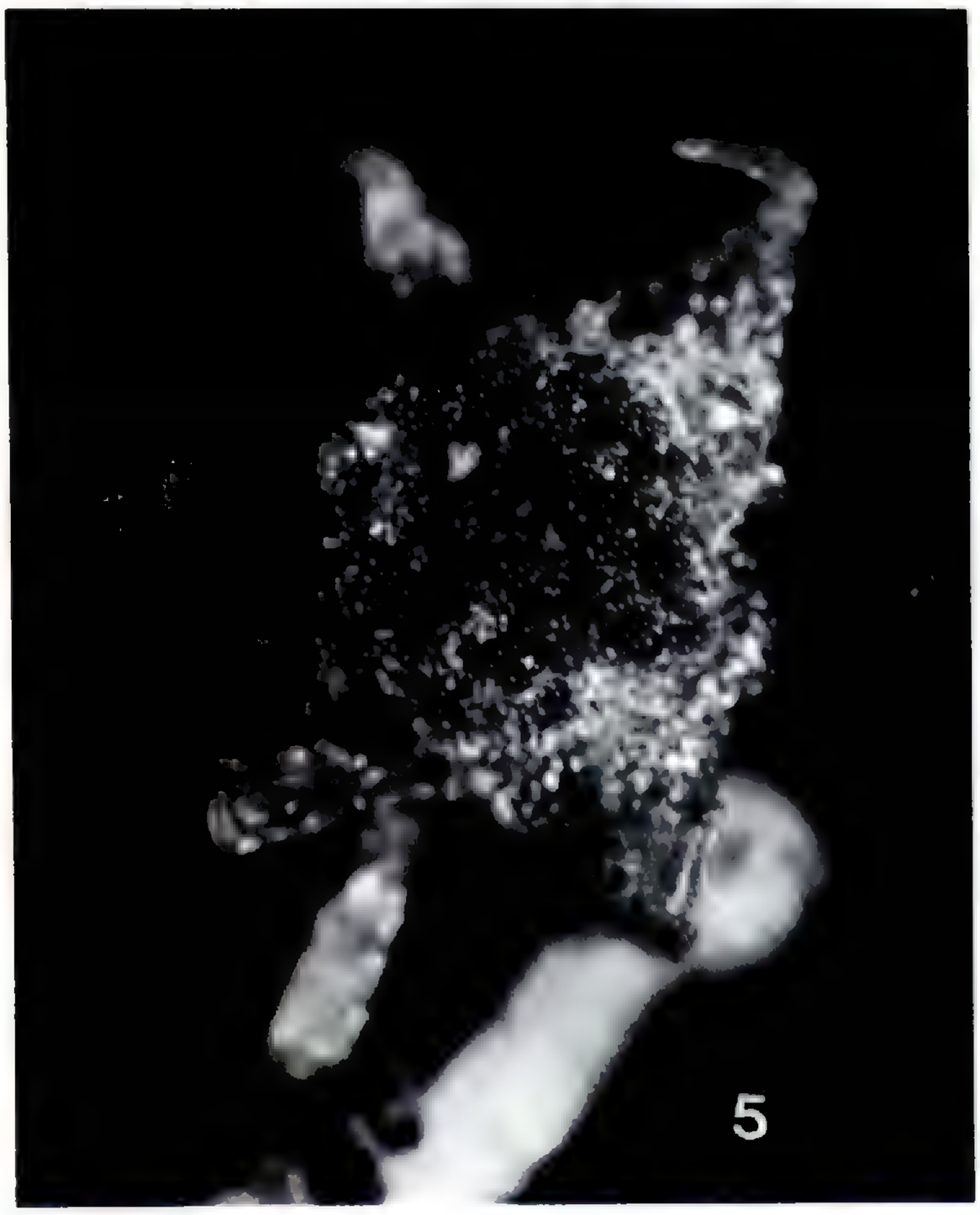
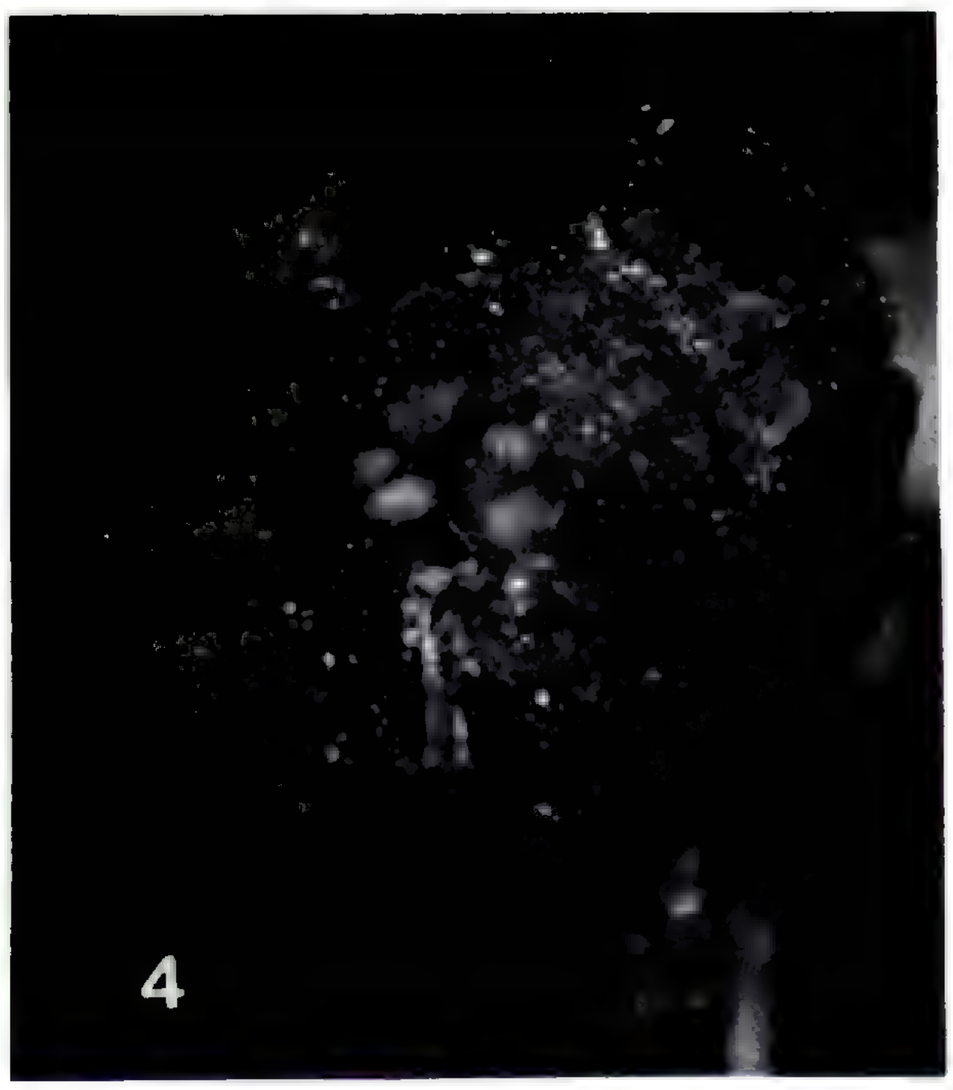


FIGURA 1.—a. Hábito.—b. Flor, pedicelo, y bráctea.—c. Flor vieja mostrando los estambres persistentes sobre el disco.—d. Estambre en vista dorsal; ventral (abierto con 2 lóculos y un septo); ventral, mostrando la línea de dehiscencia.—e. Ovario.—f. Fruto.—g. Semilla.





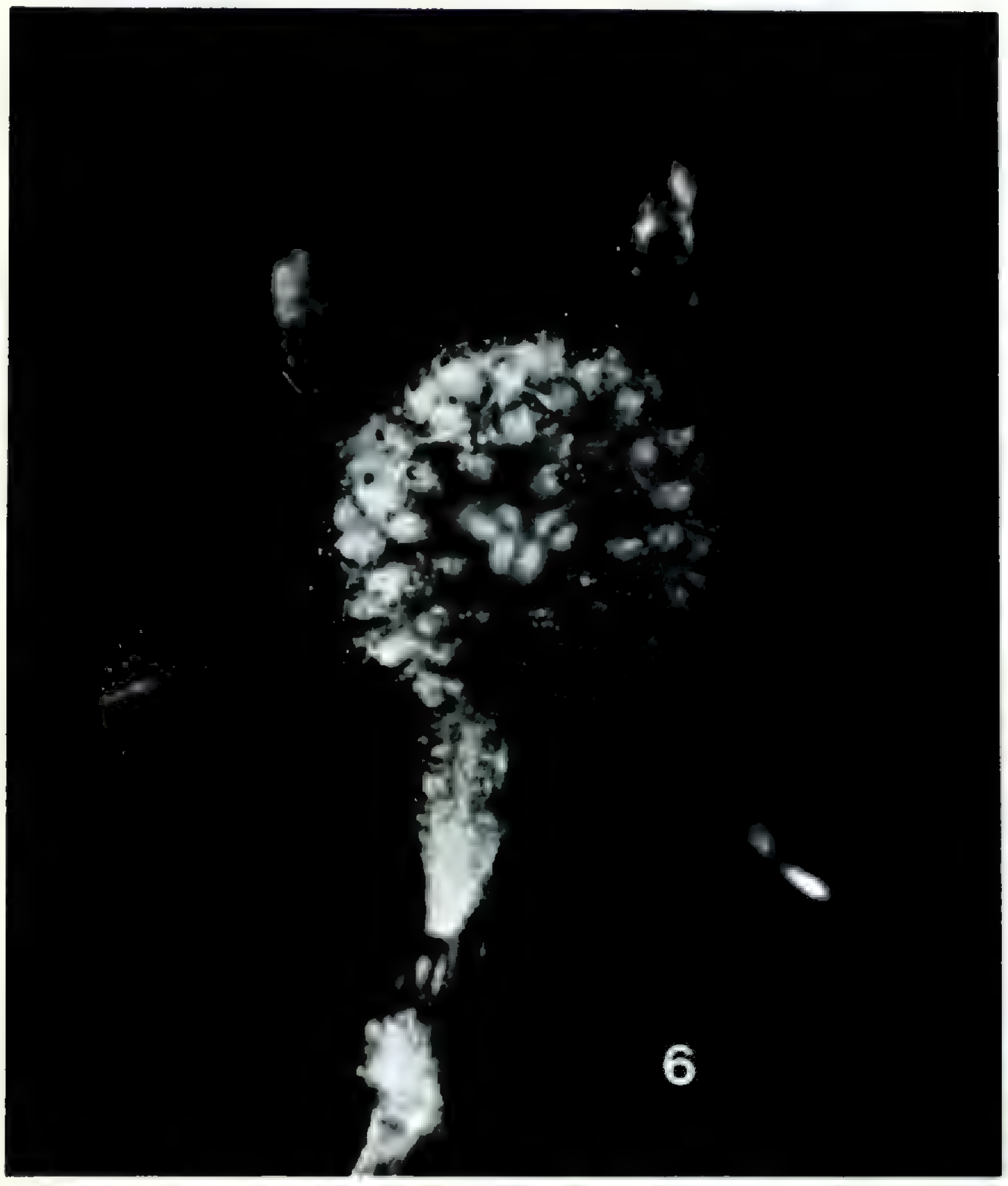


FIGURAS 2–5.—2. Botón floral con los tépalos en proceso de antesis.—3. Botones florales en diferentes etapas de desarrollo.—4. Flor recién abierta en la cual se distinguen tres estambres centrales rodeados por los ovarios inmaduros. Se ve el proceso de desenrrollamiento de las caudas.—5. Flor abierta con las caudas de los tépalos erectas y los ovarios bien desarrollados que ocultan los estambres. Fotografías de Alejandro Martínez Mena.

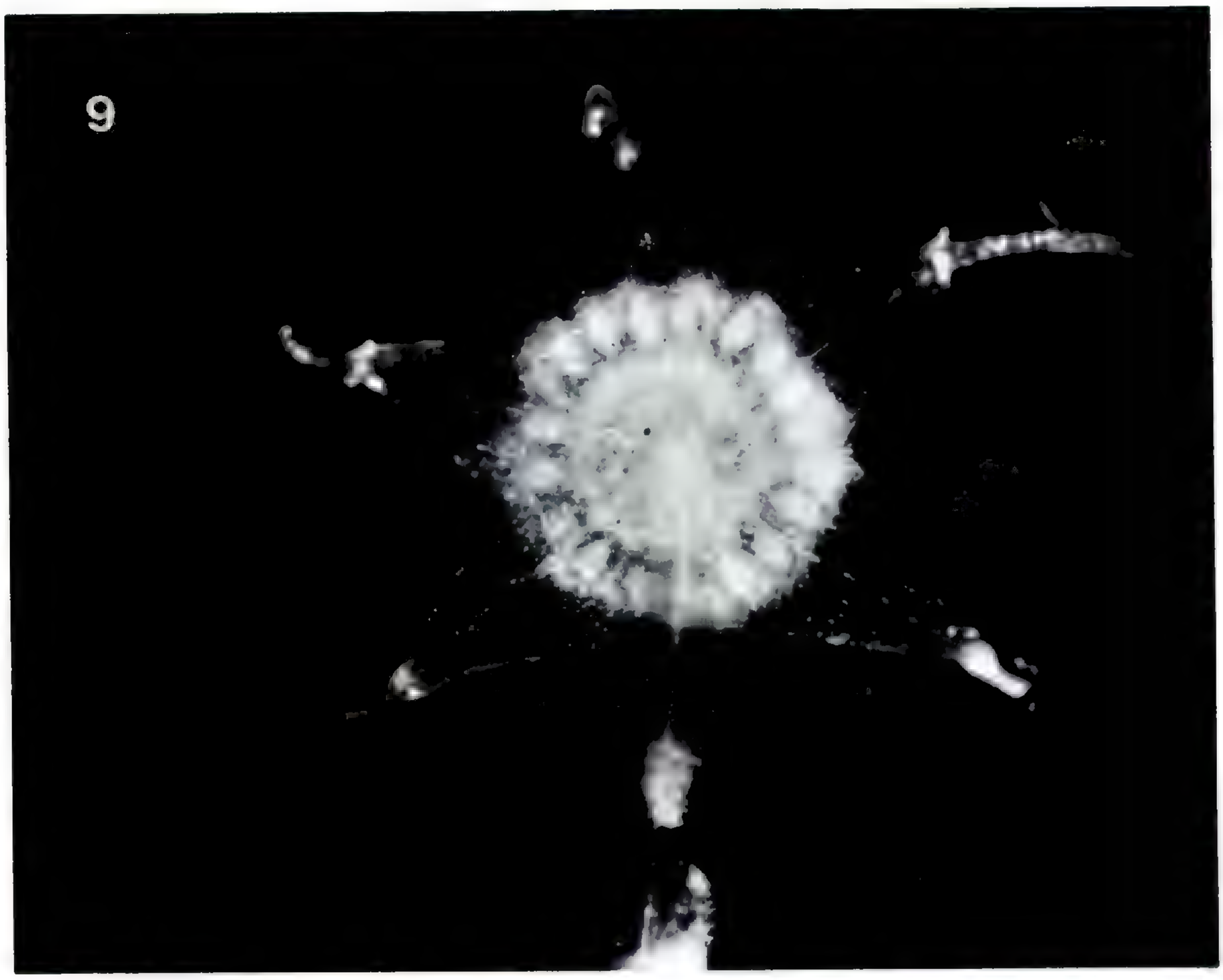
Semilla elipsoide con ornamentación reticulada, engrosada distalmente y con una corta proyección basal.

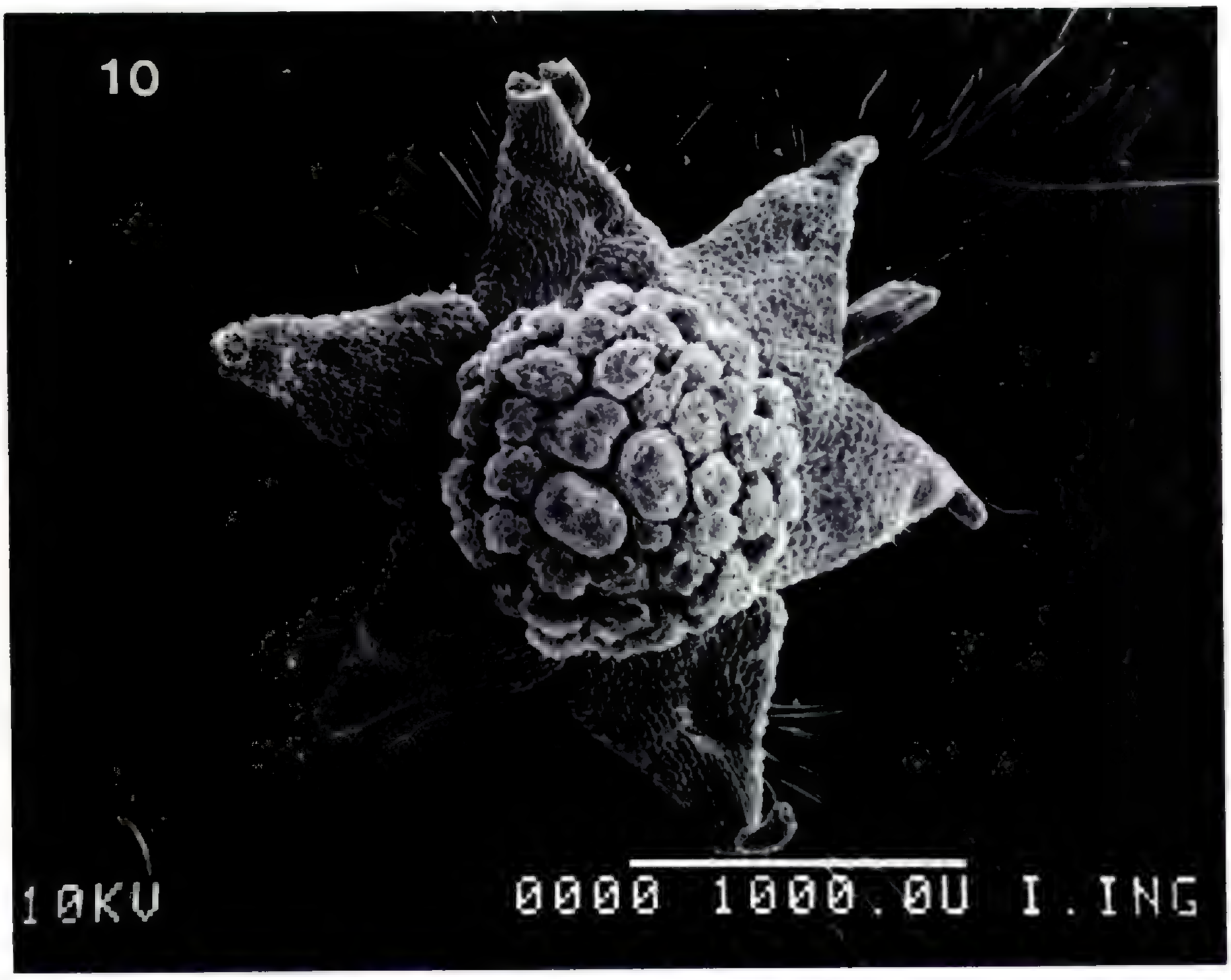
Lacandonia schismatica E. Martínez et C. H. Ramos, sp. nov. TIPO: México. Chiapas: Mpio. Ocosingo, Crucero Corozal, 170 km al SE de Palenque, camino a Boca Lacantum, sobre la carretera fronteriza del sur, 30 enero 1987, *E. Martínez S. 19310* (holotipo, MEXU; isotipos, CR, ENCB, K, LE, MO). Figuras 1–12.

Herbae tenues, usque ad 9 cm. Inflorescentia usque ad 4 cm longa, bracteis trilobatis, ca. 0.6–1.0 mm longis et 0.4–0.8 mm latis. Flores (1–)3–7(–13), pedicelli 3–4(–7) mm longi; tepala 6, deltata, ca. 1 mm longa et lata;

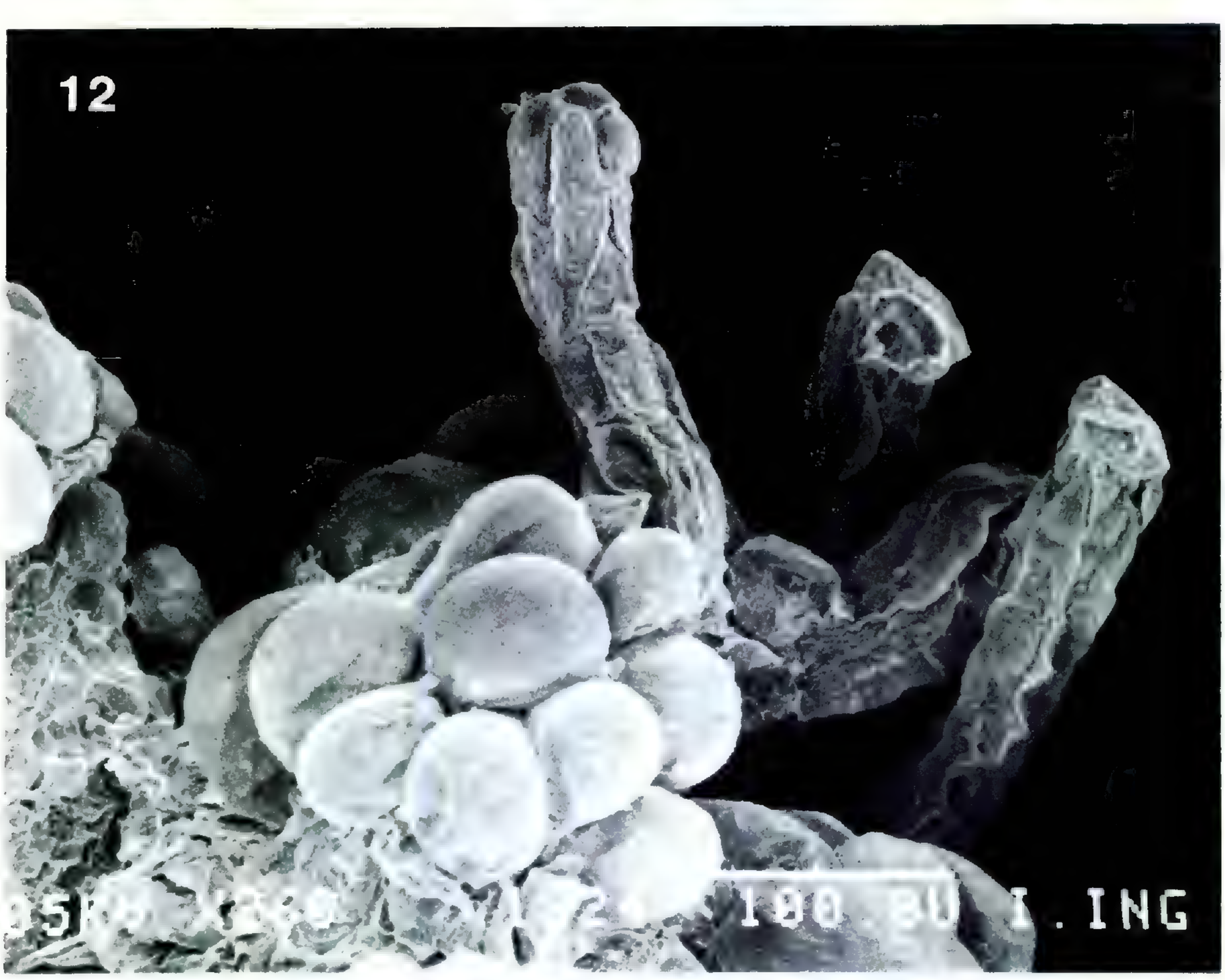


FIGURAS 6–8.—6. Flor con los frutículos bien desarrollados y las anteras centrales (material fijado).—7. Flor vieja mostrando los estambres marcescentes.—8. Rizoma con raíces saliendo de dos nudos. Fotografías de Alejandro Martínez Mena.





FIGURAS 9, 10.—9. Vista posterior de la flor en la que se observan los haces vasculares que divergen del pedicelo hacia los tépalos. A contraluz se distinguen los frutículos (material fijado). Fotografía de Alejandro Martínez Mena.—10. Vista de la flor. Se observan la apariencia papilada y los tres estambres centrales rodeados por los ovarios. Fotografía de Ricardo Peralta y Fabi.



FIGURAS 11, 12.—11. Apice de un tépalo con la cauda erecta. Se distinguen las papilas.—12. Frutículo. Se ven las papilas y el estilo persistente. Fotografías de Ricardo Peralta y Fabi.

cauda 1(–2) mm longa et 0.1 mm lata. Gynoecium carpellis obovoideis, dense papillosis. Stamina 3, filamentis 0.1 mm longis, antheris circa 0.3 mm longis, 0.1 mm latis. Achenia obovata, 0.45–0.6 mm longa, 0.28–0.35 mm lata, dense papilloso.

Hierbas hasta de 9 cm de alto. Rizoma glabro, 0.2–0.3 mm de diámetro, con raíces filiformes, 1.0–3.5 cm de largo, ca. 0.1 mm de diámetro. Tallos rollizos, usualmente 3–5 cm de largo, 0.4–0.5 mm

de diámetro. Inflorescencia hasta de 4 cm de largo con brácteas trilobadas, 0.6–1.0 mm de largo, 0.4–0.8 mm de ancho en la base, subamplexicaules; pedicelo 3–4(–7) mm de largo. Flores (1–)3–7(–13), en espiral, 3.8–4.1 mm de diámetro; tépalos 6, deltoides, fusionados desde la base hasta la parte media, ca. 1 mm de largo, 0.9–1.1 mm de ancho, las caudas ca. 1(–2) mm de largo y 0.1 mm de ancho. Carpelos obovoides, 0.48–0.6 mm de largo, 0.2–0.25 mm de ancho; estilo papilado 0.2–0.25 mm de largo; estigma de color oscuro, ca. 0.04 mm de largo y ancho. Estambres 3, con los filamentos de 0.1 mm de largo; anteras sub-basifijas, ca. 0.3 mm de largo y 0.1 mm de ancho. Aquenios obovoides 0.45–0.6 mm de largo, 0.28–0.35 mm de ancho, con el estilo persistente, papilosos, ligeramente esponjosos; semilla 0.4–0.5 mm de largo, 0.2–0.25 mm de ancho, pardo oscura.

Distribución y hábitat. Sólo conocida de la localidad tipo, en selva alta subperennifolia inundable de *Calophyllum brasiliense* Camb. con *Terminalia amazonia* (J. Gmelin) Exell y *Cryosophila argentea* Bartlett. Muchos de los elementos de esa zona son de nuevo registro para la región, como *Chionanthus domingensis* Lam., *Guettarda tikalana* Lundell, *Schizaea poeppigiana* Sturm, *Actinostachys germanii* Fée, y *Guzmania lingulata* (L.) Mez var. *minor* (Mez) L. B. Smith & Pittend, entre otros. Vive sobre substratos de materia orgánica muy húmedos, pero no inundados, en lugares muy sombreados con poca oscilación de temperatura. La localidad tipo se sitúa en el exterior del borde de la reserva de Montes Azules, área que se talará para crear potreros.

Fenología. Florece todo el año si las condiciones de humedad son adecuadas. Muy abundante en noviembre y diciembre, después de la temporada de lluvias.

Material adicional examinado. MEXICO. CHIAPAS: Mpio. Ocosingo, Crucero Corozal, 170 km al SE de Palenque, camino a Boca Lacantum, sobre la carretera fronteriza del sur, 15 Sept. 1985, *E. Martínez S. 13996* (MEXU); 6 Nov. 1985, *Martínez 14982* (MEXU); 29 mayo 1987, *Martínez 21381* (MEXU); 27 Ago. 1987, *Martínez 21822* (MEXU); 10 Dic. 1987, *Martínez 21921* (MEXU).

Lacandoniaceae comparte con Triuridaceae los siguientes caracteres: gineceo apocárpico, óvulos anátropos, polen inaperturado, flores trímeras, tépalos con apéndices, hábito saprofítico, y micorrizas endotróficas. Sin embargo, difiere por: a) La disposición espacial de los órganos reproductores, con los estambres ocupando la parte central de la flor. Tal posición no había sido contemplada antes para angiospermas (A. P. de Candolle, 1813; Hutchinson, 1959; Takhtajan, 1969; Cronquist, 1981). b) La dehiscencia introrsa de las anteras, extrorsa en Triuridaceae (Tomlinson, 1982; Maas & Rübsamen, 1986).

El análisis cromatográfico comparativo entre *Triuris* sp. y *Lacandonia schismatica* indica claras diferencias en el tipo de metabolitos secundarios (G. Delgado, inéd.).

Cronquist (1981) colocó en el orden Triuridales a las familias Petrosaviaceae Hutchinson y Triuridaceae Gardner. Petrosaviaceae comparte con Lacandoniaceae la dehiscencia introrsa de las anteras, el hábito herbáceo, y la micotrofía, pero difiere por presentar estomas, tépalos en dos series, carpelos fusionados basalmente con muchos óvulos, nectarios septales, y granos de polen monosulcados.

Dahlgren et al. (1985) consideraron en Triuridales únicamente a Triuridaceae.

La relación espacial que presentan los órganos reproductores es difícil de explicar a la luz de los conocimientos actuales. En ausencia de información previa, se están llevando a cabo estudios anatómicos (Márquez-Guzmán et al., este tomo) y fitoquímicos que ayuden a esclarecer su posición taxonómica.

El nombre genérico está dedicado a la región Lacandona, asiento del pueblo Lacandón, en el estado de Chiapas, México. El epíteto específico se refiere a los problemas que origina su morfología en la sistemática.

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SYSTEMATICS OF THE AMAZON LILIES, *EUCHARIS* AND *CALIPHRURIA* (AMARYLLIDACEAE)[1]

Alan W. Meerow[2]

ABSTRACT

Eucharis and *Caliphruria* are closely related, neotropical genera of petiolate-leaved, white-flowered Amaryllidaceae found in the understory of primary tropical rain forest. Together with the Peruvian endemic *Urceolina*, *Eucharis* and *Caliphruria* form a monophyletic group within "infrafamily Pancratioidinae" on the basis of leaf and seed morphology and ecological specialization. Seventeen species and two natural hybrids within two subgenera are recognized in *Eucharis*. *Eucharis*, marked by its crateriform or campanulate flowers, curved perianth tube, pigmented androecium usually developed into a staminal cup, and unicellular stigmatic papillae, is distributed from Guatemala to Bolivia, chiefly in the western Amazon basin and adjacent lower slopes of the eastern Andes. Subgenus *Heterocharis* represents three relict species and two natural hybrids with many ancestral characters of the genus. *Caliphruria* (four species, three of which are endemic to Colombia) has funnelform flowers, straight perianth tube, reduced staminal connation, and multicellular stigmatic papillae. Cladistic relationships support the monophyly of *Eucharis*, *Caliphruria*, and *Urceolina* as a unified group. The most parsimonious cladograms suggest that *Eucharis* is paraphyletic if subg. *Heterocharis* is included. An alternative hypothesis of generic relationships is tested, and proves less parsimonious. Recognizing the close phenetic relationship of subg. *Heterocharis* to the rest of *Eucharis*, the high levels of homoplasy within the cladogram, and ambiguity caused by missing character state data, a less parsimonious phylogeny is accepted as the basis for classification. Keys and descriptions are provided for all species of *Eucharis* and *Caliphruria*. *Eucharis caucana*, a novel hexaploid ($2n = 138$) species, is described from Colombia.

The closely related genera *Eucharis* Planchon & Linden and *Caliphruria* Herbert (Amaryllidaceae), the Amazon lilies, comprise respectively 17 and 4 species of bulbous, rain forest geophytes adapted to the low light conditions of the forest understory. Together with the Peruvian endemic *Urceolina* Reichenb., nom. cons., *Eucharis* and *Caliphruria* form a monophyletic group delimited by petiolate leaves with distinctive cuticular striation; a turgid seed with a lustrous, usually black testa; and complete fidelity to the rain forest understory niche. The species are distributed from Guatemala to Bolivia. The major center of distribution for *Eucharis* is in the western Amazon basin (inclusive of major tributary systems, e.g., the Napo, Pastaza, and Huallaga) and the adjoining lower slopes of the eastern Andean cordillera. With the exception of single Peruvian species, *Caliphruria* is restricted to the Cordillera Occidental and Cordillera Central of Colombia. The species of both genera are nowhere abundant, and are found growing only in primary, rarely secondary, forest from

[1] I thank the curators of AAU, B, BM, COL, CUVC, F, FTG, G, GB, GH, GOET, HUNT, K, LE, M, MG, MICH, MO, MPU, NA, NY, OXF, P, QCA, S, SEL, SP, U, UC, US, and VEN for loans of herbarium specimens, and the following individuals or institutions who generously provided living material: James Bauml, Libby Besse, Calaway Dodson, Robert Dressler, Mark Elliot, Thomas Fennell, Fred Fuchs, Harry Luther, Fred Meyer, Timothy Plowman, Phil Silverstone-Sopkin, James Watson, Mark Whitten, Margot Williams, Norris Williams, Marcia Wilson, Bailey Hortorium, Royal Botanic Gardens at Kew and Edinburgh, Longwood Gardens, UC Berkeley Botanical Garden, Honolulu Botanical Gardens, Huntington Botanical Garden, Fairchild Tropical Garden, Marie Selby Botanical Garden, Missouri Botanical Garden, and Strybing Arboretum. Bijan Dehgan provided the supportive environment where much of this work was completed and, along with Walter Judd, Charles Guy, Norris Williams, R. Mitchell Beauchamp, John Kress, and Christiane Anderson, gave helpful criticisms to earlier versions of this monograph. Linda Fisher-Meerow illustrated a number of the species. Portions of this work were supported by NSF Doctoral Dissertation Improvement grant BSR-8401208 and a Garden Club of America/World Wildlife Fund Fellowship in Tropical Botany. This paper represents part of a Ph.D. dissertation submitted to the graduate school of the University of Florida. Florida Agricultural Experiment Station Journal Series No. 7795.

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ca. 50 to 1,800 (rarely to 2,000) m elevation on soils of high fertility. Large-scale deforestation has proven catastrophic to these plants, which are unable to adapt to the higher light intensity of the clearings and soon perish. At least several species are probably extinct, and this number will only increase with time as rain forest destruction continues unabated.

The Amazon lilies are marked by their evergreen, petiolate leaves; white, often pendent, sometimes fragrant flowers with a frequently conspicuous staminal cup or false corona formed by the basal connation of the staminal filaments; obtusely trilobed stigma; and large, turgid, globose or ellipsoid seeds with a black, brown, or metallic blue testa. *Eucharis amazonica* Linden ex Planchon is widely known in horticulture, often erroneously as *E. grandiflora* Planchon & Linden (Meerow & Dehgan, 1984a). Neither genus has ever been critically treated in the taxonomic literature. Baker (1888) provided a key and descriptions for all species known at the time in his *Handbook of the Amaryllideae*, and Macbride (1936) treated the known Peruvian species of *Eucharis* for the *Flora of Peru*. Though species of *Eucharis* have continued to be described well into the present decade, the delimitation of these species from previously described taxa has consistently remained vague. No assessments of variation at either the population or species level have been attempted.

As two of only three genera of neotropical Amaryllidaceae (the other being the related *Urceolina*) exhibiting complete fidelity to a primary rain forest niche, systematic understanding of *Eucharis* and *Caliphruria* offers important information relating to the evolution of the pancratioid Amaryllidaceae ("infrafamily Pancratioidinae" Traub (1957, 1963)),[3] centered in the central Andean region of South America.

No taxonomic scheme can encompass all of the information about the group of organisms under study (Holsinger, 1984, 1985; Ornduff, 1969; Raven, 1976). In genera such as *Eucharis* and *Caliphruria*, rare in the wild and often accessible only with difficulty, and which often exhibit cryptic patterns of variation, this observation becomes much more acute. By accumulating data from as many diverse sources as possible, I have attempted to construct an evolutionary systematic classification of the Amazon lilies that is both practical yet reflects their evolutionary relationships as accurately as these data allow.

Materials and Methods

FIELD STUDIES

Fieldwork was conducted in Peru and Ecuador in July–August 1982, and in Colombia and Ecuador in July–August 1984. Herbarium specimens and living material were collected, and ecological observations of natural populations were made.

ANATOMICAL STUDIES AND SCANNING ELECTRON MICROSCOPY (SEM)

Material was prepared and examined as described in Meerow (1987c).

CLADISTIC ANALYSES

Cladistic analyses were run using PAUP version 2.4.1 by David L. Swofford (Illinois Natural History Survey). All species (and two subspecies) of *Eucharis* and *Caliphruria* (22 evolutionary units, EUs) excluding hybrid taxa were analyzed using forty-one characters (Tables 1–3). For analyses with PAUP, global branch swapping with the MULPARS option was used in all searches for the most parsimonious cladograms. Because of the unavailability of material, all described species of *Urceolina* could not be included in the analysis. *Urceolina* was therefore entered in the analysis at the generic level, with character state data drawn from study of living material of *U. microcrater* Kränzlin and specimens of *U. urceolata* (Ruíz & Pavón) Green and *U. ayacucensis* Ravenna. Character states were determined from examination of living and dried material. Character state polarities were assessed via outgroup comparison (Maddison et al., 1984; Watrous & Wheeler, 1981). Selection of outgroups is discussed later with the results of the analyses.

Of the 41 characters used in the analysis, 23 were simple, two-state characters. The 18 remaining multistate characters (14 three-state, 2 four-state, 1 five-state, and 1 six-state) were treated in preliminary analyses as unordered (Fitch, 1971; Hartigan, 1973) using this option of PAUP, rather than attempting to create any a priori transformation series. This resulted in a preponderance of weak monophyletic groups based on single apomorphies and/or character state reversals, as well as unresolved polytomies among many terminal taxa. In the analyses presented, 11 of these characters were treated as ordered transformation series (the remaining seven as unordered), with one

[3] This unofficial rank is used in this paper as a label of convenience, since there is as yet insufficient evidence to recognize this group of genera as a distinct subfamily.

(number 41, chromosome number) coded in additive binary. Justification for these treatments is discussed with the results of the analyses. Multistate characters were adjusted to equal weight with two-state characters using the "weights scale" option of PAUP. Additionally, an alternative hypothesis of generic relationship was tested by submitting a user-coded tree topology to PAUP for analysis.

HERBARIUM STUDY AND LIVING MATERIAL

Loans or gifts of herbarium specimens were received from the following herbaria: AAU, B, BM, COL, CUVC, F, FTG, G, GB, GH, GOET, HUNT, K, LE, M, MG, MICH, MO, MPU, NA, NY, OXF, P, QCA, S, SEL, SP, U, UC, US, VEN.

Neither *Eucharis* nor *Caliphruria* is well represented in herbarium collections, and critical morphological characters are often obscured by the drying process. Consequently, a living collection of over 100 accessions representing fifteen species and several hybrids was accumulated from botanical gardens, individuals, and field collections by myself and various colleagues. Vouchers for living material are listed with specimens cited for each species.

Taxonomic History

Herbert (1844) described the new genus *Caliphruria* from collections made in New Granada (Colombia) near Guaduas by Hartweg, placing *Caliphruria* in the "section" Pancratiformes of "suborder" Amaryllideae. Genera of this "section" were united by the single character of staminal connation. The small, white, funnelform flowers were marked by the presence of a bristle or slender tooth at either side of the filament. Herbert (1844) made no mention of basal connation of the filaments. The orthography of the name, a single "l" in the Greek stem "calli-," was emended by subsequent workers (e.g., Baker, 1877), but was returned to Herbert's original by Meerow & Dehgan (1984b).

Planchon & Linden (1852) introduced another new pancratioid genus, *Eucharis*. The first species described, *E. candida* Planchon & Linden, collected in New Granada by M. Schlim, was characterized by its crateriform flowers with a conspicuous staminal cup and a widely spreading perianth limb. If these authors were aware of *Caliphruria*, they did not note any relationship between it and *Eucharis*.

Bentham & Hooker (1883) placed *Caliphruria* and *Eucharis* in the tribe *Cyathiferae*. *Caliphruria subedentata* Baker was combined with *Eucharis* in their treatment, while *C. hartwegiana* Herb. was retained. Baker (1888) accepted this treatment, yet described another new species as *C. tenera*. He described *Caliphruria* as "nearly allied to *Eucharis*."

Baillon (1894) described the species *C. castelnaeana* and declared it precisely intermediate between *Caliphruria* and *Eucharis*. He further suggested that *Eucharis* should be treated as a section of *Caliphruria*. Macbride (1931) later transferred *C. castelnaeana* to *Eucharis*.

Nicholson (1884) transferred *C. hartwegiana* (the type species of *Caliphruria*) to *Eucharis*, ignoring the former's nomenclatural priority. Traub (1967) made the formal transfer of the remaining species of *Caliphruria*, *C. tenera* Baker, to *Eucharis* and combined the monotypic genus *Plagiolirion* Baker with *Eucharis*. He had previously listed *Caliphruria*, *Plagiolirion*, and *Mathieua* Klotzsch (another monotypic genus) as synonyms for *Eucharis* in his *Genera of the Amaryllidaceae*, citing Baillon (1894) as a "special reference" (Traub, 1963: 74). The nomenclatural priority of *Caliphruria* Herbert was overlooked. No proposal for the conservation of *Eucharis* Planchon & Linden over *Caliphruria* Herbert has ever been proposed previous to that of Meerow & Dehgan (1984b).

Traub (1971) later combined *Eucharis* with *Urceolina*, a small Andean genus with petiolate leaves and markedly urceolate, brightly colored flowers. He designated five subgenera: *Urceolina*, *Eucharis*, *Caliphruria*, *Mathieua*, and *Plagiolirion*. Traub (1971) offered no explanation for the combination of *Eucharis* and *Urceolina*, but presumably his decision was prompted in part by reports in the literature of two intergeneric hybrids between *Eucharis* and *Urceolina*: ×*Urceocharis clibranii* Masters, an artificial hybrid, and ×*U. edentata* C. H. Wright, putatively discovered in Peru. *Plagiolirion* and *Mathieua* are monotypic genera allied to *Hymenocallis* Salisb. and *Stenomesson* Herbert respectively (Meerow, 1987a).

Vegetative Morphology

BULBS

The globose or subglobose bulbs of *Eucharis* and *Caliphruria*, composed of concentric and modified leaf bases (scales), are characteristic of most members of the Amaryllidaceae. The bulbs are sympodial in growth habit (Arroyo, 1984). The outer scales of *Eucharis* and *Caliphruria* bulbs are modified into an either brown or tan paper tunic. The bulb scales of most species of *Eucharis*

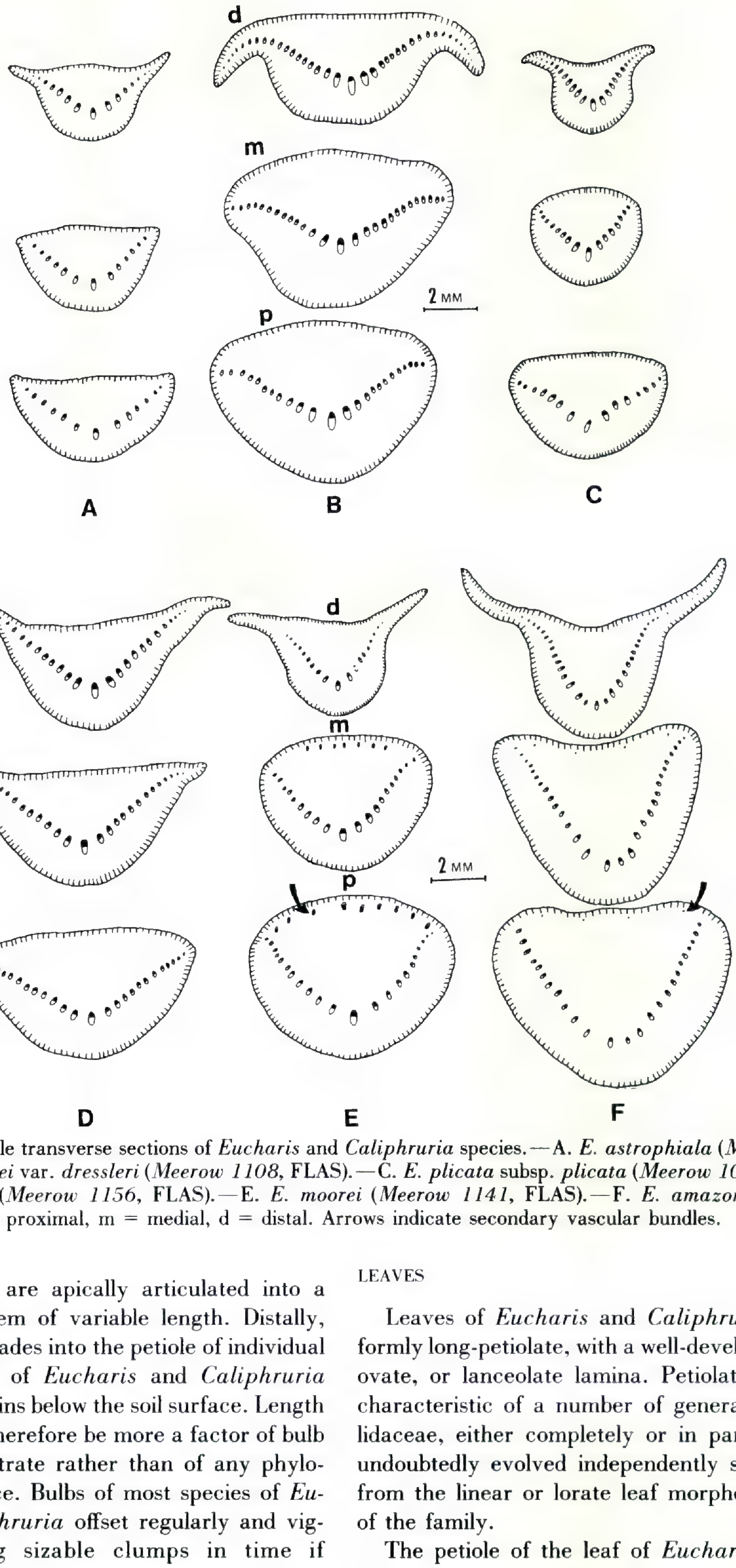


FIGURE 1. Petiole transverse sections of *Eucharis* and *Caliphruria* species.—A. *E. astrophiala* (*Madison 3792*, SEL).—B. *E. bouchei* var. *dressleri* (*Meerow 1108*, FLAS).—C. *E. plicata* subsp. *plicata* (*Meerow 1025*, FLAS).—D. *C. subedentata* (*Meerow 1156*, FLAS).—E. *E. moorei* (*Meerow 1141*, FLAS).—F. *E. amazonica* (*Schunke 14179*, FLAS). p = proximal, m = medial, d = distal. Arrows indicate secondary vascular bundles.

and *Caliphruria* are apically articulated into a neck or pseudostem of variable length. Distally, the pseudostem grades into the petiole of individual leaves. The neck of *Eucharis* and *Caliphruria* bulbs always remains below the soil surface. Length of the neck may therefore be more a factor of bulb depth in the substrate rather than of any phylogenetic significance. Bulbs of most species of *Eucharis* and *Caliphruria* offset regularly and vigorously, forming sizable clumps in time if undisturbed.

LEAVES

Leaves of *Eucharis* and *Caliphruria* are uniformly long-petiolate, with a well-developed elliptic, ovate, or lanceolate lamina. Petiolate leaves are characteristic of a number of genera of Amaryllidaceae, either completely or in part, and have undoubtedly evolved independently several times from the linear or lorate leaf morphology typical of the family.

The petiole of the leaf of *Eucharis* and *Caliphruria* is usually as long or longer than the lamina.

It tends toward subterete cross sections (Fig. 1), rounded abaxially, and flattened adaxially, becoming slightly channeled proximal to the sinus. The petiole is winged proximal to the sinus by attenuation of the lamina. The midrib is pronounced abaxially along the entire length of the lamina, and slightly channeled adaxially, continuous with the petiole.

Leaf shape only rarely provides taxonomically useful information. Length/width ratios are subject to considerable variation even among the leaves of a single bulb. Herbarium specimens will frequently include only a single leaf, with no indication of its developmental age. Taxonomic consistency of leaf shape is exceptional, but useful in the few cases where it occurs. For example, leaves of *E. ulei* Kränzlin are consistently narrowly elliptic. *Eucharis amazonica* (leaf length/width ratio greater than 2) may be delimited from *E. moorei* (Baker) Meerow (l/w less than 2).

The leaves of *Eucharis* and *Caliphruria* are completely glabrous and nonglaucous, with a single exception. *Eucharis bonplandii* (Kunth) Traub, a rare tetraploid species from central Colombia, develops a glaucous bloom that gives the leaf a blue cast in strong light.

The leaf apex of all species is shortly acuminate, the base attenuate. Coarse undulation of the margin will sometimes make the lamina appear cordate at the base. Leaf margins of *Caliphruria* are uniformly nonundulate.

Leaf venation of *Eucharis* and *Caliphruria* is parallelodromous (Hickey, 1973), with a great number of transverse, commissural veins interconnecting the primary vasculature. All species of *Caliphruria* have smooth, nonplicate leaves. *Eucharis* is variable for this character, but the majority of species have plicate leaves.

The adaxial epidermis of most species of both genera is lustrous, dark green; the abaxial surface appears lighter, or silvery green. Only *E. astrophiala* (Ravenna) Ravenna has diverged markedly from the typical morphology and has a uniquely nonlustrous, bullate-pustulate leaf texture.

CUTICLE

Cuticular striation is prominent on the abaxial leaf surfaces of most *Eucharis* and *Caliphruria* species (Figs. 2–6, 8–12). Striae are thickest in *C. subedentata* (Fig. 11). Arroyo & Cutler (1984) recognized eight cuticular sculpturing classes in a survey of 25 genera of Amaryllidaceae. The most common cuticular morphology of *Eucharis* and *Caliphruria* fits their class VII: "thick striae, parallel or not, interlocking, ± transverse."

In a few species of *Eucharis* (*E. amazonica*, *E. moorei* (Fig. 10), *E. bouchei* (Fig. 9)), the striation is much less pronounced. *Caliphruria korsakoffii* (Traub) Meerow (the sole representative of *Caliphruria* outside Colombia) has the most aberrant cuticle morphology (Fig. 12), corresponding more or less to type V of Arroyo & Cutler (1984): "central, thick axial striation with less pronounced striae running from it, directly to anticlinal walls." The adaxial cuticles of *Eucharis* and *Caliphruria* are either smooth or rarely much more finely striate than the abaxial surface, the striations entirely axial in orientation. The adaxial cuticle of *C. korsakoffii* (Fig. 13) has several, thick, transverse striations across each cell, and the epidermis is unusually flat.

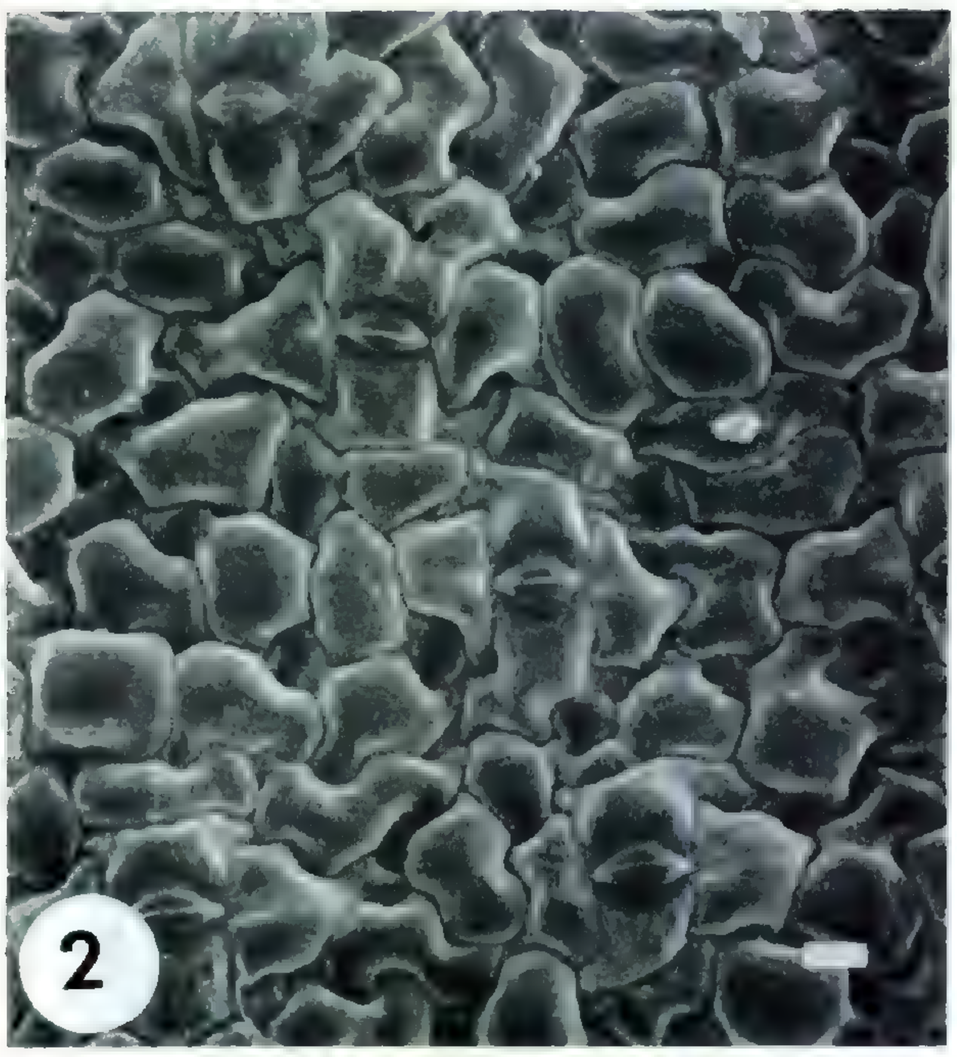
STOMATA

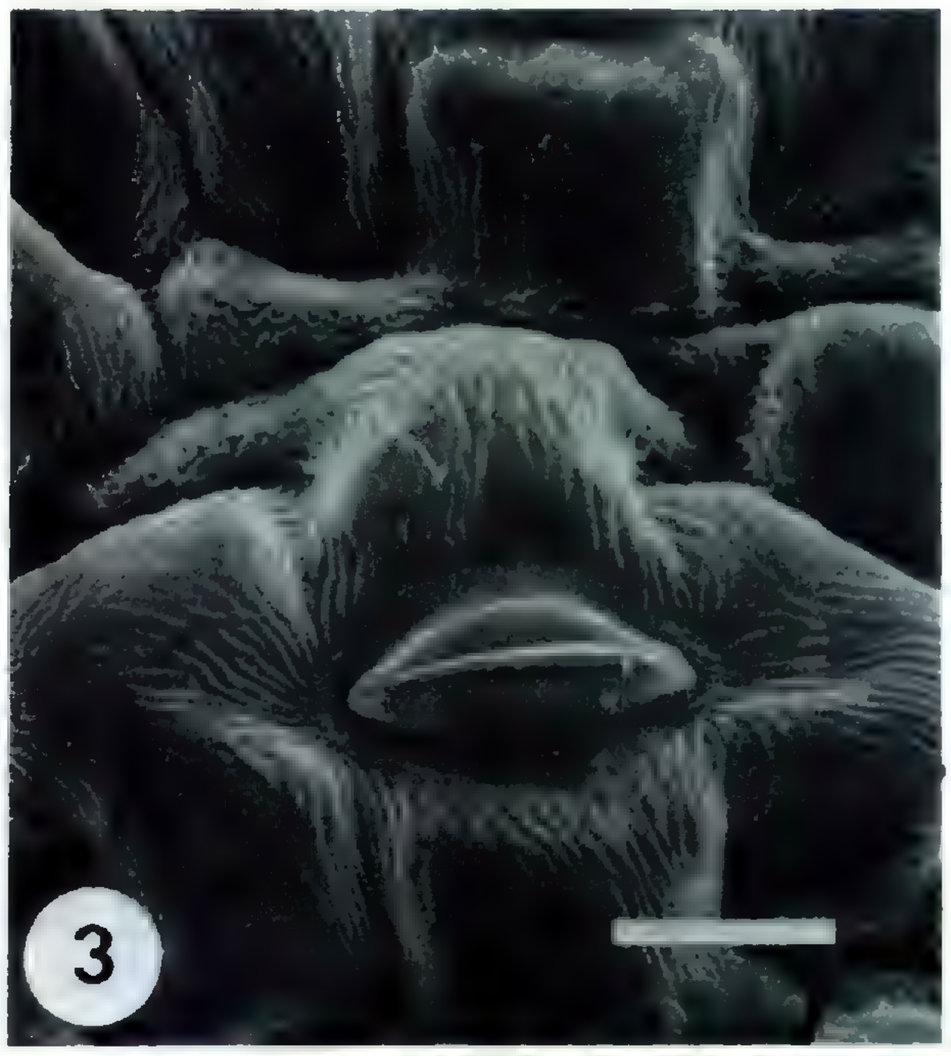
Leaves of *Eucharis* and *Caliphruria* are predominantly hypostomatic. Stomata occur adaxially only along the midrib and vicinity (Fig. 14A), and occasionally in the proximity of primary veins. Stomata are usually absent from the abaxial midrib (Fig. 14B). Intercalary stomata were regularly observed only in *E. cyaneosperma* Meerow (Figs. 7, 15D). The stomata of *Eucharis* and *Caliphruria* are anomocytic, as is typical for Amaryllidaceae (Arroyo & Cutler, 1984; Dahlgren & Clifford, 1982), though *E. astrophiala* exhibits at least slight differentiation of cells neighboring the stomata (Figs. 2, 3) from other epidermal cells. These cells are more densely and regularly striate than other epidermal cells, as well as slightly more raised. The guard cells of *Eucharis* and *Caliphruria* are oriented with their longest axis parallel to that of the leaf.

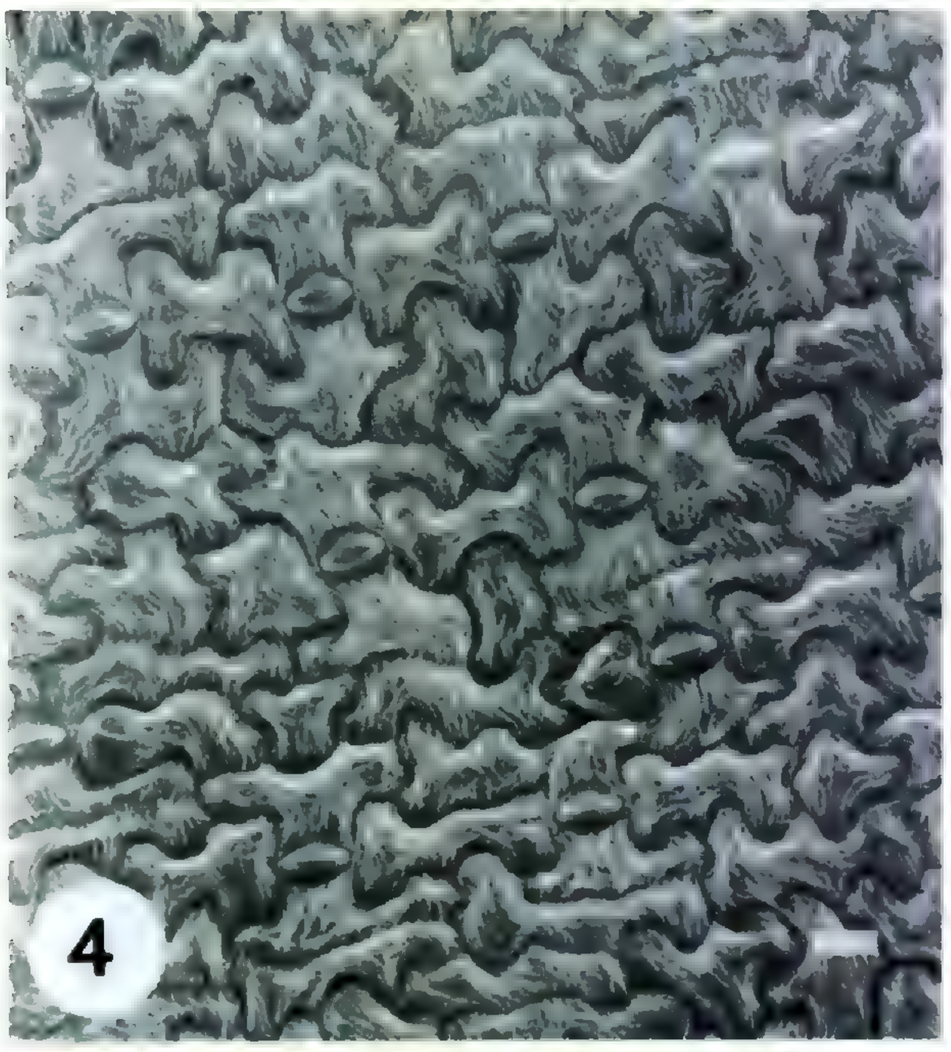
EPIDERMAL CELLS

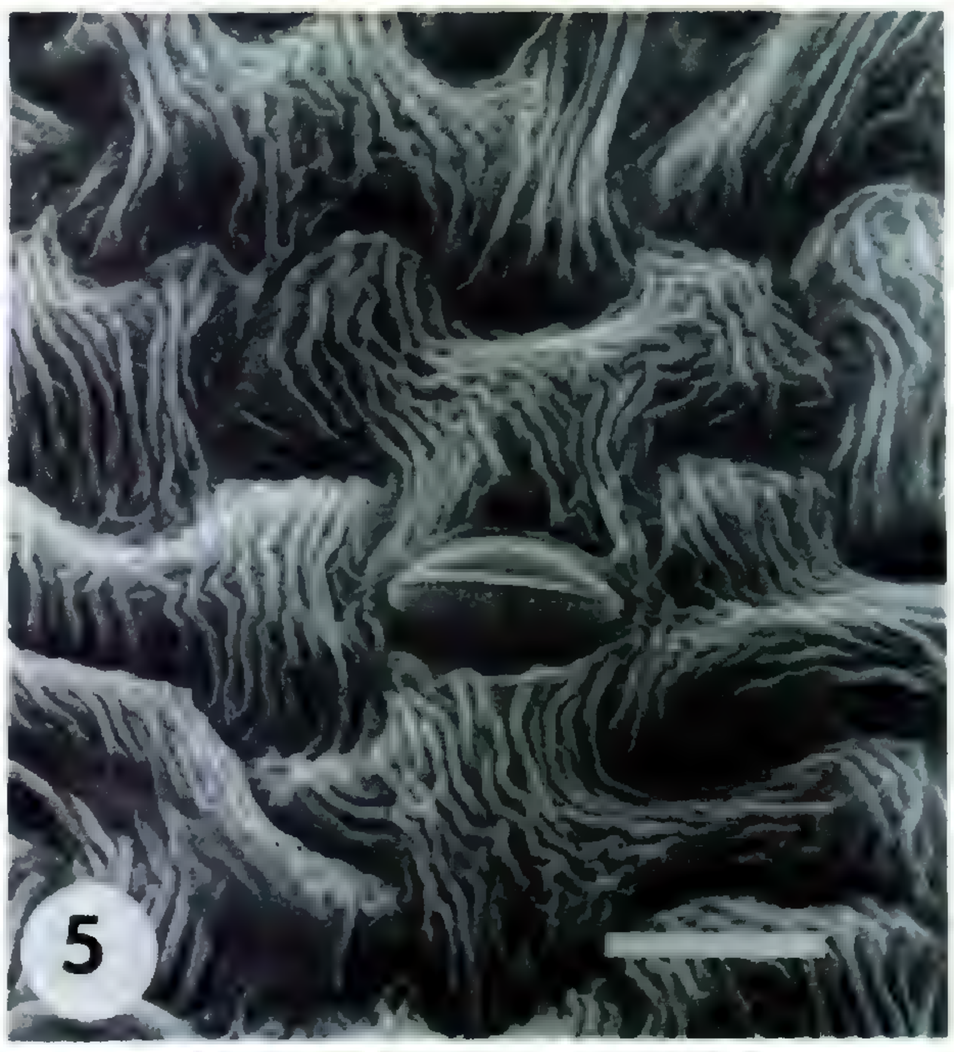
Abaxial epidermal cells range from rectangular to irregular in shape. Adaxial epidermal cells are in almost all cases rectangular. *Eucharis astrophiala* (Fig. 15A) has the most irregularly shaped cells of both the abaxial and adaxial surfaces. In the vicinity of the midrib on both surfaces of the leaf (Fig. 14), epidermal cells become conspicuously elongated, and anticlinal walls are straight. Epidermal cells of the midrib are extremely long and narrow.

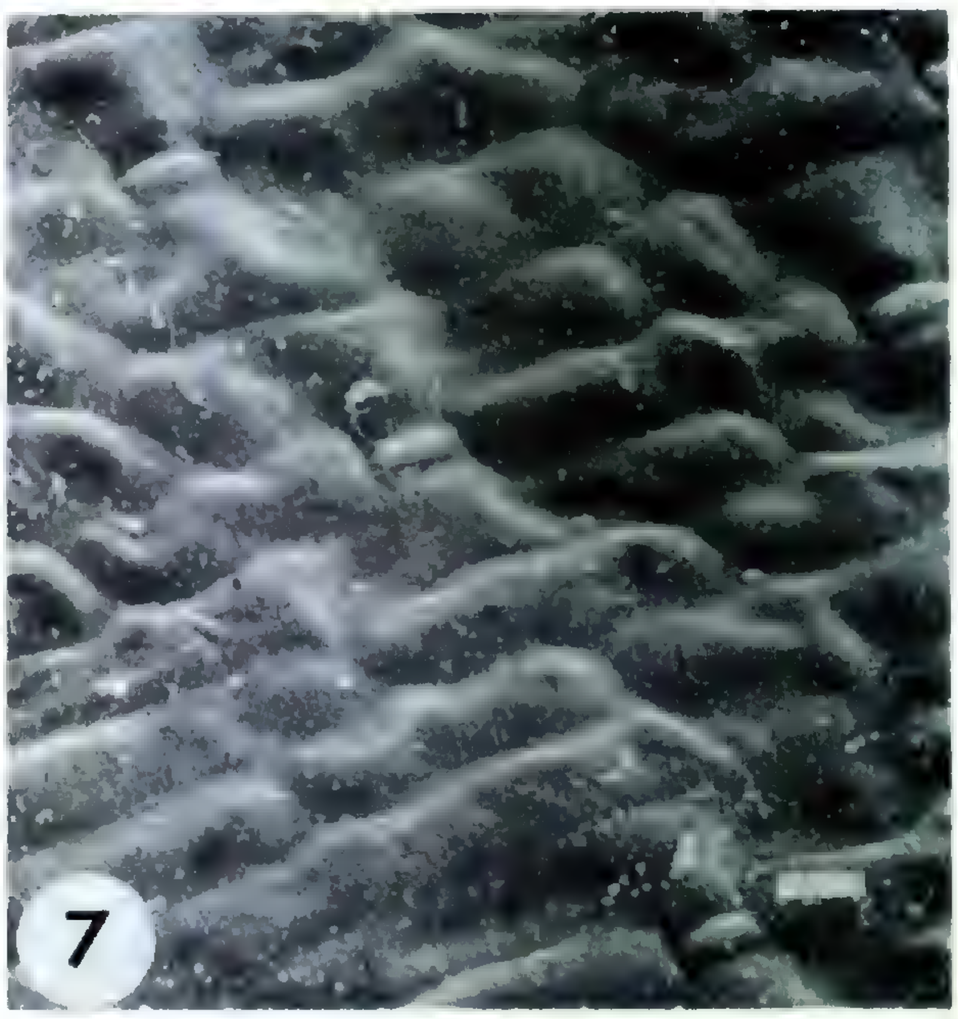
The epidermal cells of all species of *Eucharis* subg. *Eucharis* have strongly undulate anticlinal walls (Fig. 15), as noted by Asatrian (1984) for the few species he surveyed. End walls of both the abaxial and adaxial cells of all species range from oblique to rounded. Abaxial cells are more strongly



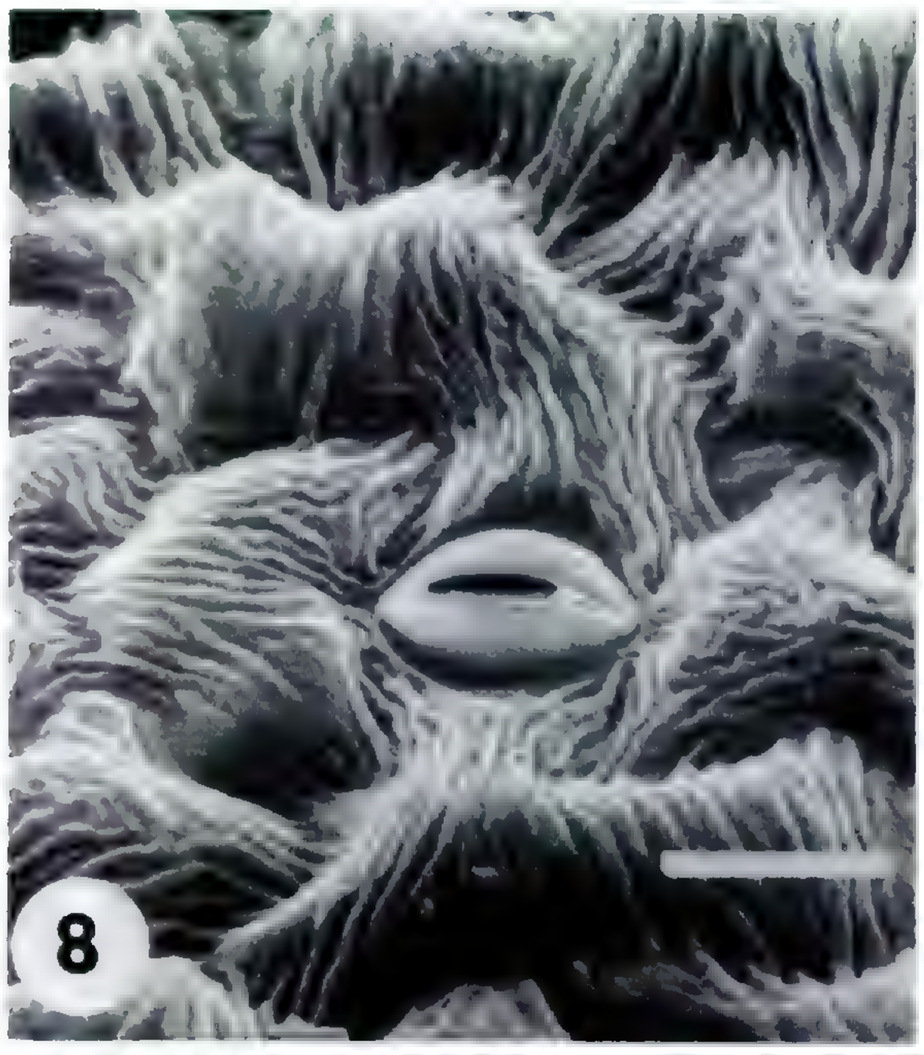


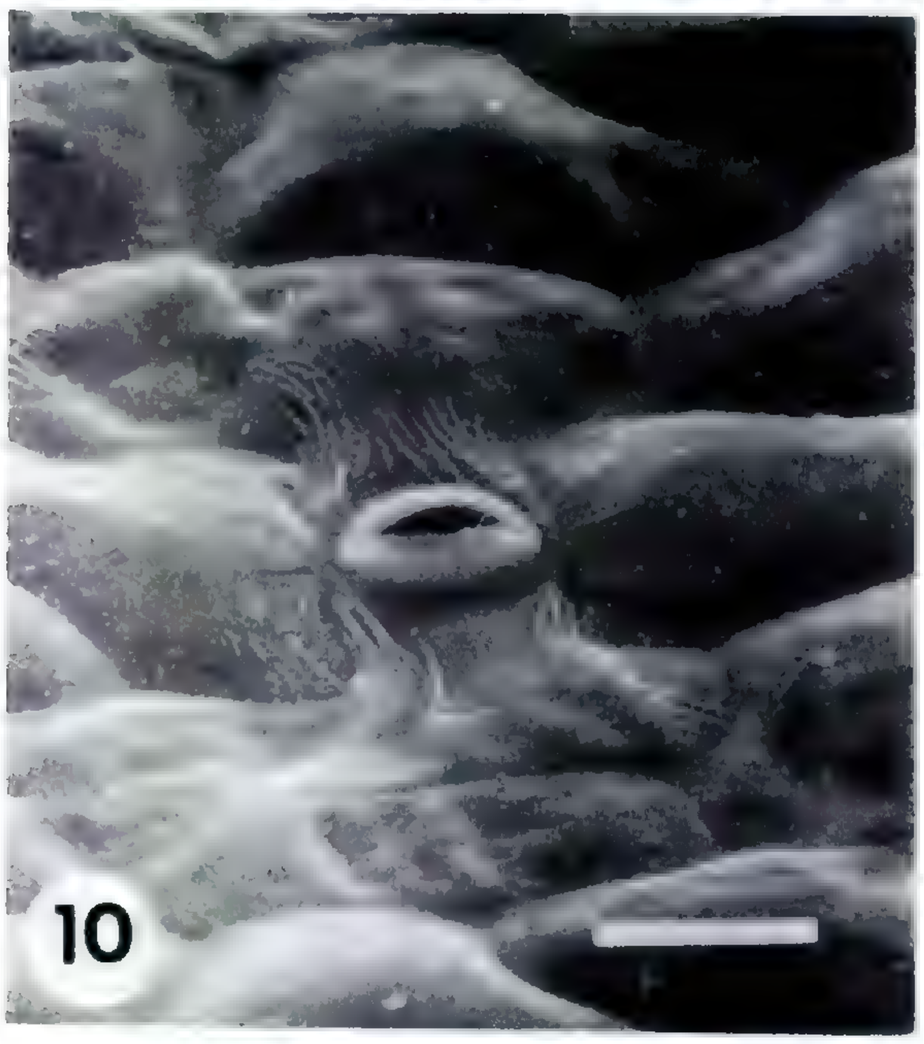


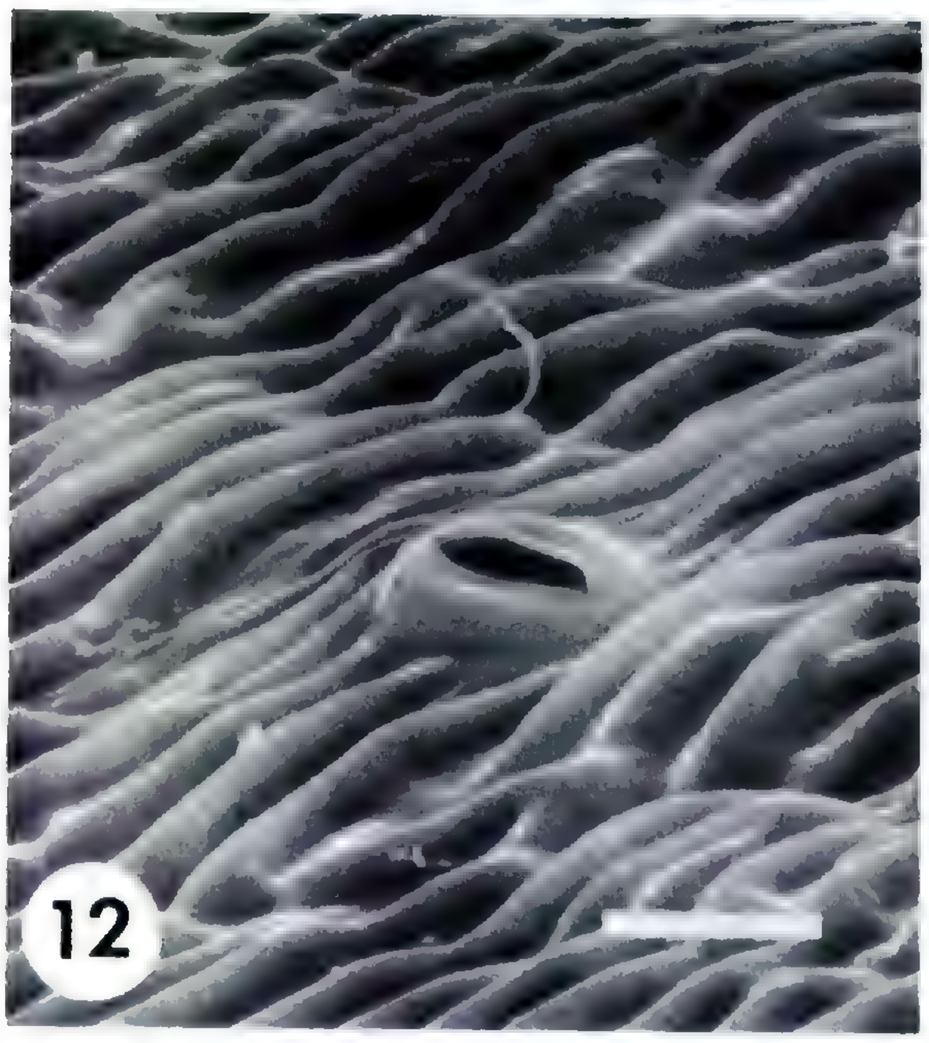


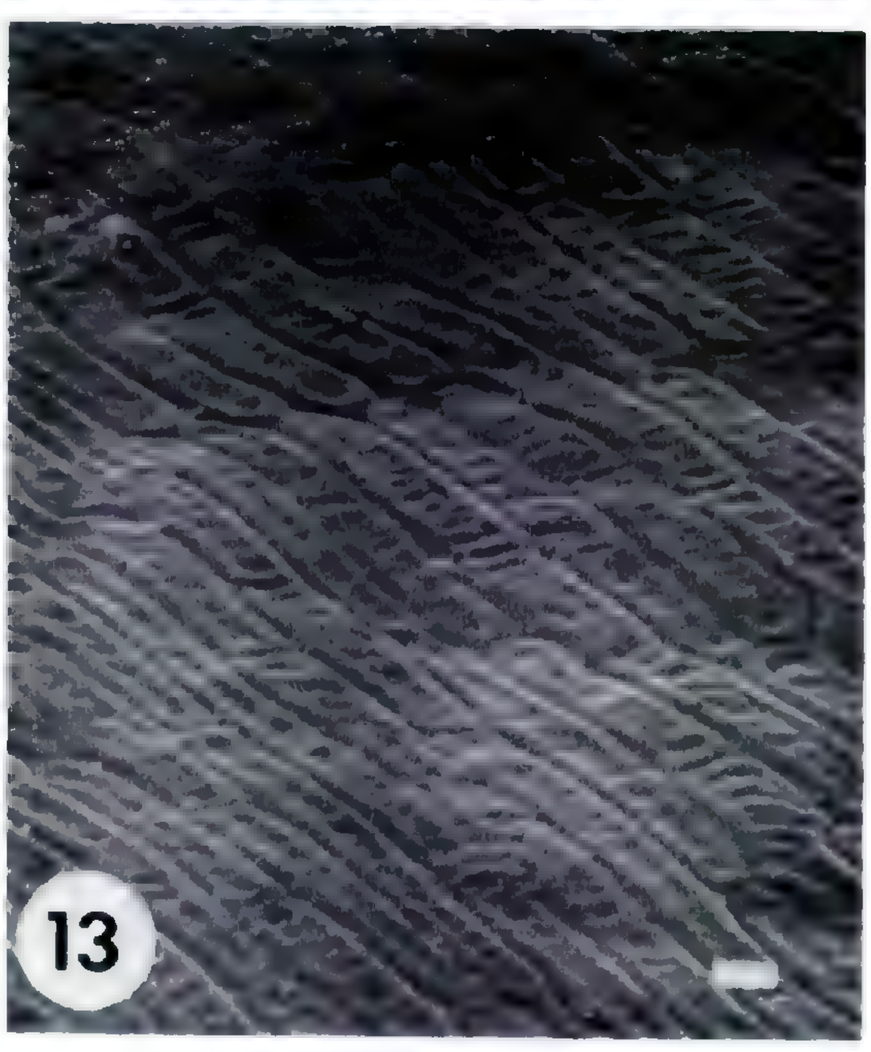


FIGURES 2–7. SEM photomicrographs of *Eucharis* leaf surfaces. 2–6. Abaxial leaf surfaces.—2, 3. *E. astrophiala* (*Meerow 1111*, FLAS).—4, 5. *E. plicata* subsp. *plicata* (*Meerow 1025*, FLAS).—6. *E. cyaneosperma* (*Meerow 1032*, FLAS).—7. Adaxial leaf surface of *E. cyaneosperma* (*Meerow 1032*, FLAS). All scales = 25 μm.









FIGURES 8–13. SEM photomicrographs of *Eucharis* and *Caliphruria* leaf surfaces. 8–12. Abaxial surfaces.—8. *E. bakeriana* (*Meerow 1108*, FLAS).—9. *E. bouchei* var. *dressleri* (*Meerow 1107*, FLAS).—10. *E. moorei* (*Meerow 1141*, FLAS).—11. *C. subedentata* (*Meerow 1109*, FLAS).—12. *C. korsakoffii* (*Meerow 1096*, FLAS).—13. Adaxial surface of *C. korsakoffii* (*Meerow 1096*, FLAS). All scales = 25 μm.

undulate than those of the adaxial surface. Epidermal cells of *Caliphruria* (Fig. 15F) are more weakly undulate than those of *Eucharis*. The anticlinal walls of adaxial cells of *C. korsakoffii* are completely straight. *Eucharis* subg. *Heterocharis* is polymorphic for anticlinal wall morphology. *Eucharis amazonica* and *E. sanderi* have strongly undulate walls, while *E. moorei* (Fig. 15E) has essentially straight walls.

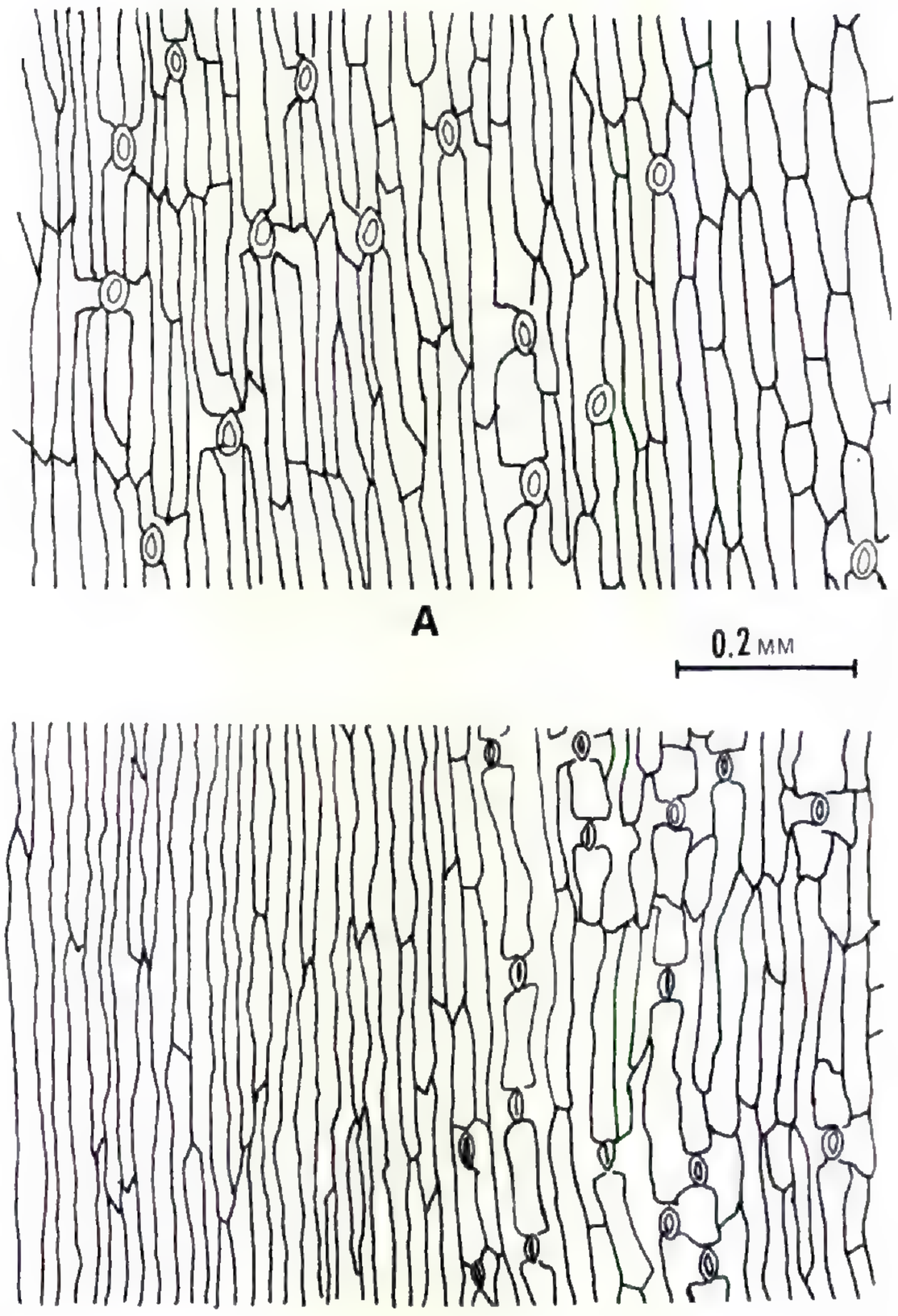


FIGURE 14. Leaf epidermal cell configurations in the vicinity of the midrib of representative *Eucharis* species.—A. *E. formosa* (*Schunke 14174*, FLAS), adaxial surface.—B. *E. plicata* subsp. *plicata* (*Meerow et al. 1025*, FLAS), abaxial surface.

LEAF ANATOMY

In petiolar transverse section, a single arc of vascular bundles is usually observed (Fig. 1). Median bundles are the largest. In petioles of *E. moorei* (Fig. 1E) and the closely related *E. amazonica* (Fig. 1F), both in subg. *Heterocharis*, small secondary bundles were observed near the adaxial surface. These bundles are most conspicuous in *E. moorei*; they are markedly smaller in *E. amazonica*. These secondary vascular traces disappear above the middle of the petiole. Asatrian (1984), who reported on petiole anatomy of three *Eucharis* and *Caliphruria* species, did not observe these bundles in *E. amazonica* (cited as *E. grandiflora*).

The internal morphology of leaves of *Eucharis* and *Caliphruria* (Figs. 16–22) is largely invariant across both genera. No well-defined palisade layer is evident, the absence of which is characteristic of most genera of "infrafamily" Pancratioidinae (Arroyo & Cutler, 1984). Mucilage cells, common throughout the family (Arroyo & Cutler, 1984), are often present near the leaf surface, and raphides are occasionally observed in epidermal cells. The mesophyll consists of several layers of chlorenchyma both ad- and abaxially, and a thicker region of spongy, slightly aerenchymous tissue. Small air cavities occur regularly only directly below stomata. Vascular bundles are surrounded by a sheath of one or two layer(s) of parenchymous cells. The only xylem elements present are tracheids with annular thickenings (Fig. 19).

FLORAL MORPHOLOGY

INFLORESCENCE

The inflorescence of *Eucharis* and *Caliphruria* is a naked scape typical of Amaryllidaceae. The scape is subterete in cross section and has a solid pith. Vascular bundles are distributed in several irregular, concentric rings within the pith. A layer of collenchyma cells occurs just below the epidermis.

The scape is terminated by two valvate-imbricate, ovate-lanceolate bracts that enclose several secondary bracts and the flower buds before anthesis. These bracts vary from green (*E.* subg. *Heterocharis*) to greenish white (most species of subg. *Eucharis*) and are soon marcescent after opening and spreading laterally. Each flower is subtended by a linear-lanceolate bracteole.

The inflorescence of the Amaryllidaceae is traditionally described as "umbellate." Mann (1959) and Stout (1944) demonstrated that the superficially simple umbel of Amaryllidaceae actually represents a complex series of reduced, helicoid cymes. Anthesis occurs in a strict sequence within each cyme from the developmentally oldest flower to the youngest. The peripheral cymes flower first; the central cymes flower last.

Flower number varies in *Eucharis* and *Caliphruria* from 2 to 10, rarely as many as 12 (*C. korsakoffii*, rarely in *E. castelnaeana*). Number of flowers is often a taxonomically useful character, though any species characterized by 8–10 flowers is capable of producing a depauperate inflorescence with fewer florets. An increase in flower number

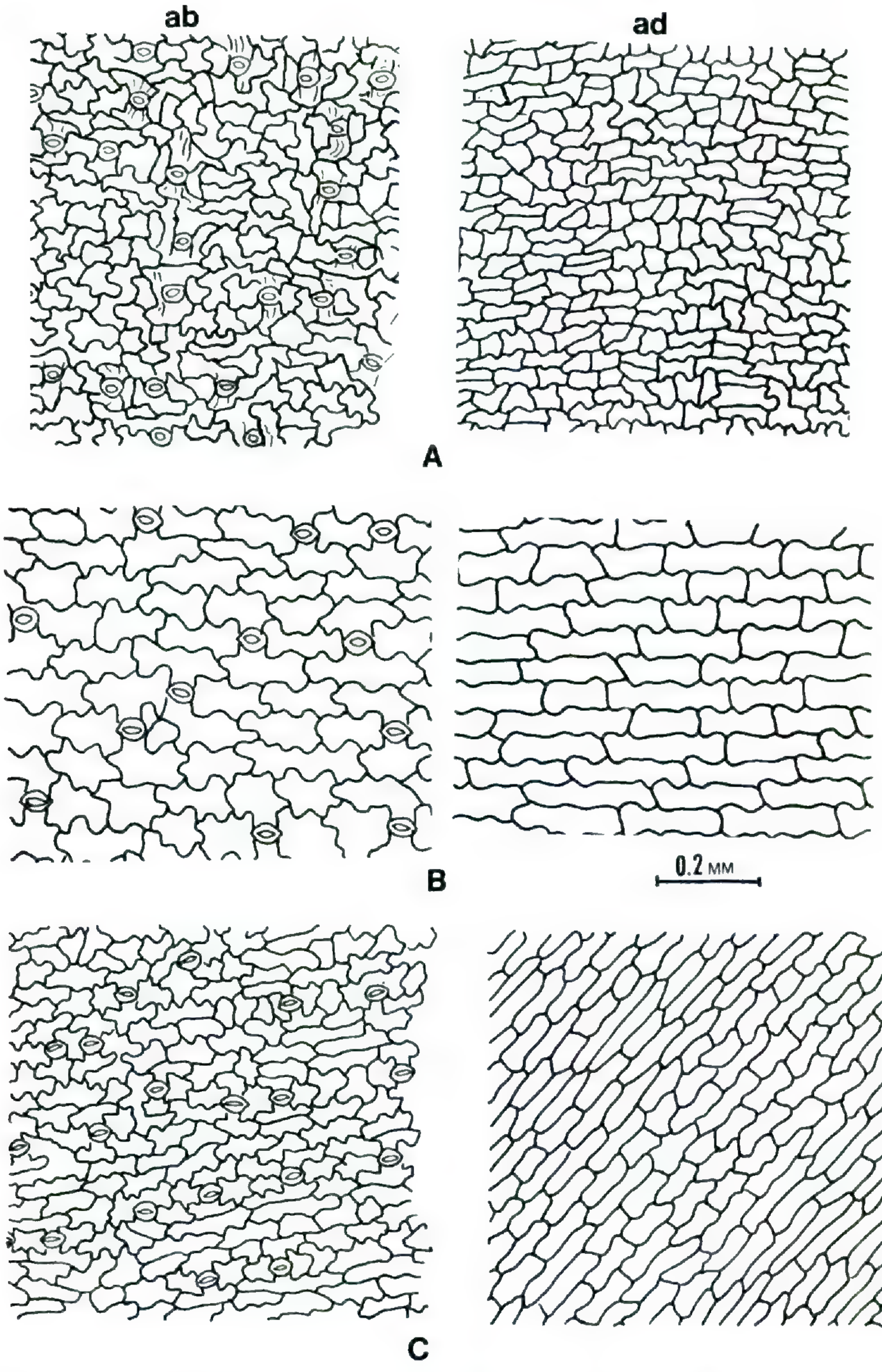


FIGURE 15A–C. Leaf epidermal configurations of representative *Eucharis* and *Caliphruria* species in the intercostal area of the leaf.—A. *E. astrophiala* (*Madison 3792*, SEL).—B. *E. bonplandii* (*Bauml 686*, HUNT).—C. *E. castelnaeana* (*Schunke 14156*, FLAS).

generally does not occur. In some species of subg. *Eucharis* (*E. astrophiala*, *E. bouchei*, *E. ulei*), a flower number of five has become virtually fixed. Reduction in flower number is usually considered the derived state in Amaryllidaceae (Traub, 1962, 1963).

FLOWER SIZE

The largest flowers in *Eucharis* are found in subg. *Heterocharis*, where they average 7–8 cm in length. Flowers of *Caliphruria* are the smallest, never exceeding 4 cm long. Subgenus *Eucharis*, the largest of the two subgenera of *Eucharis*, is variable, with flowers 3–7 cm in length. Within a fairly broad range, flower size can be used to distinguish phenetic species complexes within subg. *Eucharis*; however, most species of this subgenus are quite variable in size (Meerow, 1987d, in press).

FLORAL FRAGRANCE

Subgenus *Heterocharis* is the only subgenus of *Eucharis* with uniformly fragrant flowers. The fragrance of all species of subg. *Heterocharis* is intense and sweet. Flowers of *Caliphruria* do not emit any detectable fragrance. Most species of *Eucharis* subg. *Eucharis* also lack noticeable fra-

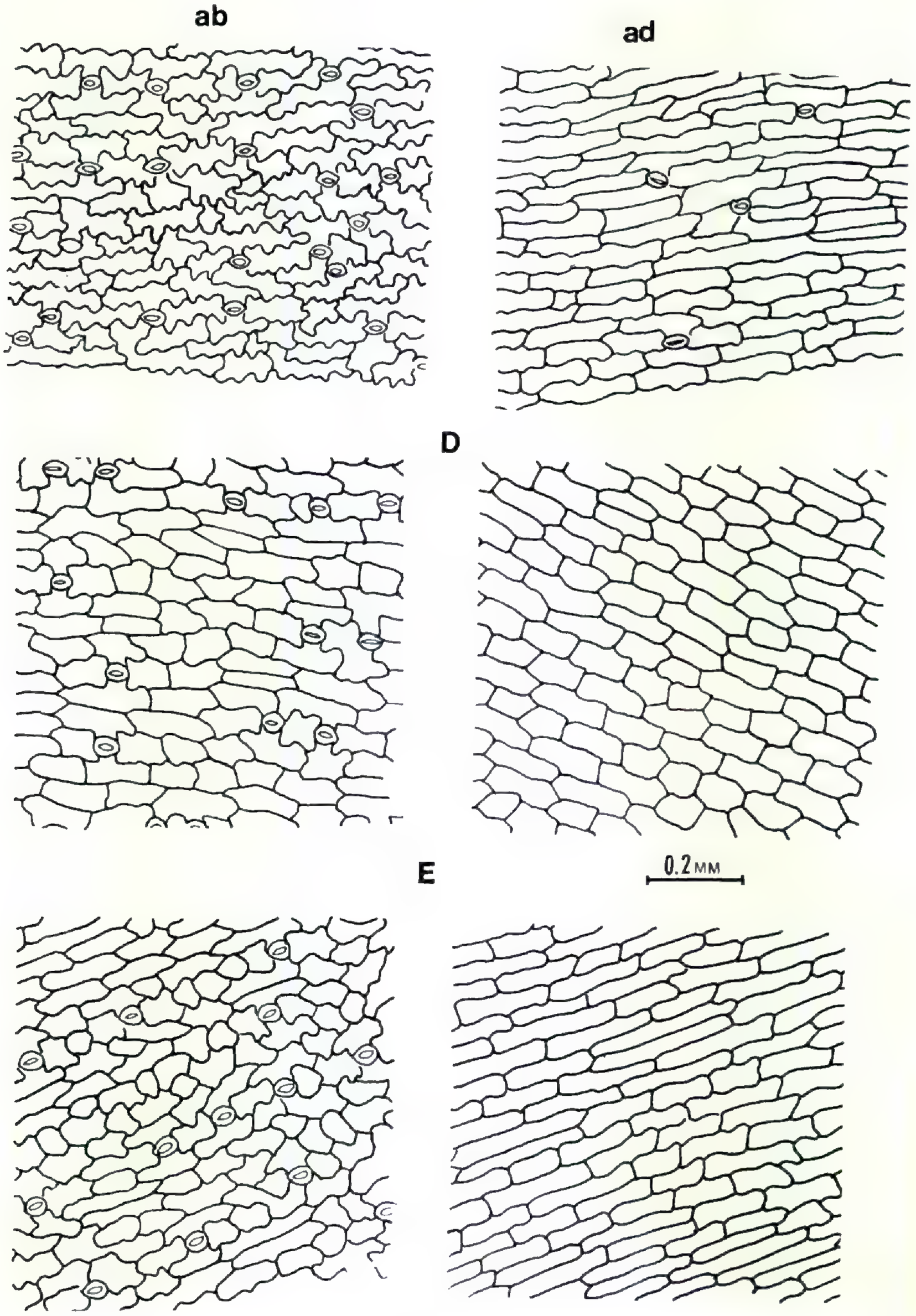


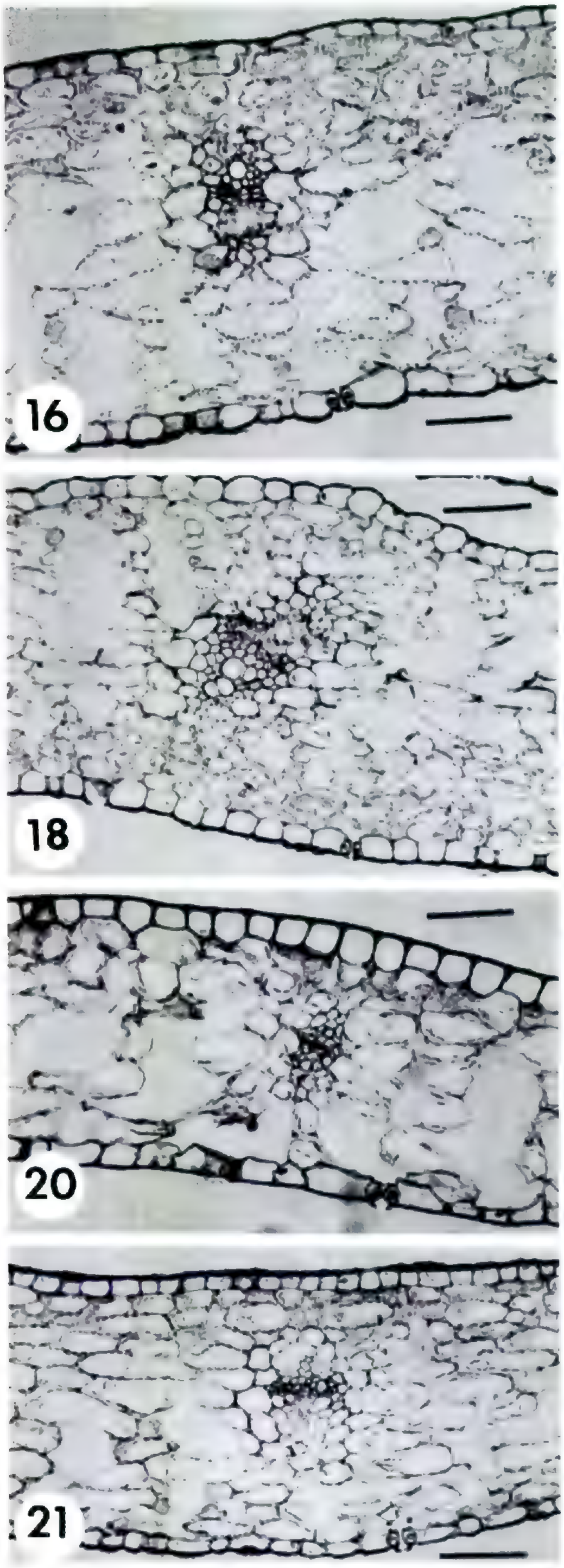
FIGURE 15D–F. Leaf epidermal configurations of representative *Eucharis* and *Caliphruria* species in the intercostal area of the leaf.—D. *E. cyaneosperma* (*Meerow 1032*, FLAS).—E. *E. moorei* (*Meerow 1141*).—F. *C. subedentata* (*Meerow 1123*, FLAS). ab = abaxial, ad = adaxial.

grance. In the few fragrant species of this subgenus (*E. bakeriana* N. E. Brown, *E. castelnaeana* (Baillon) Macbr., *E. formosa* Meerow, and *E. plicata* Meerow subsp. *brevidentata* Meerow), the odor is not intense. In *E. formosa* the odor is slightly fetid.

PERIANTH

The perianth of *Eucharis* and *Caliphruria* consists of six tepals in two whorls, basally connate into a tube of varying length and morphology. The tube of *Eucharis* subg. *Eucharis* (Fig. 23E) is cylindrical for almost its entire length, abruptly dilating near the perianth throat. The tube of subg. *Eucharis* is also strongly curved, either abruptly just above the ovary (*E. bakeriana*, *E. cyaneosperma*) or gradually throughout the proximal half of its length (all other species). The curving of the tube results in the pendent habit of most species of subg. *Eucharis*. The tube is white for its entire length.

The tube of subg. *Heterocharis* (Fig. 23C, D) is tinted green proximally (for as much as half its length). The tube is curved, though not as markedly



FIGURES 16–22. Transverse sections of *Eucharis* and *Caliphruria* leaves.—16. *E. bonplandii* (*Bauml 686*, HUNT).—17. *E. astrophiala* (*Madison 3792*, SEL).—18, 19. *E. formosa* (*Meerow 1103*, FLAS). 19. Tracheid with annular thickenings.—20. *E. bouchei* var. *dressleri* (*Meerow 1107*, FLAS).—21. *C. subedentata* (*Meerow 1123*, FLAS).—22. *C. korsakoffii* (*Meerow 1096*, FLAS). All scales = 100 μm except 25 μm in Figure 19.

as that of subg. *Eucharis*, and the habit of the flowers is either declinate (*E. moorei*, *E. sanderi* Baker) or subpendulous (*E. amazonica*). The tube is cylindrical for ½ to ⅔ of its length; it abruptly dilates in the distal ½ to ⅓. The tube morphology of ×*Calicharis butcheri* (Traub) Meerow (Fig. 23B), putatively an intergeneric hybrid between *E. sanderi* and *C. subedentata*, is intermediate be-

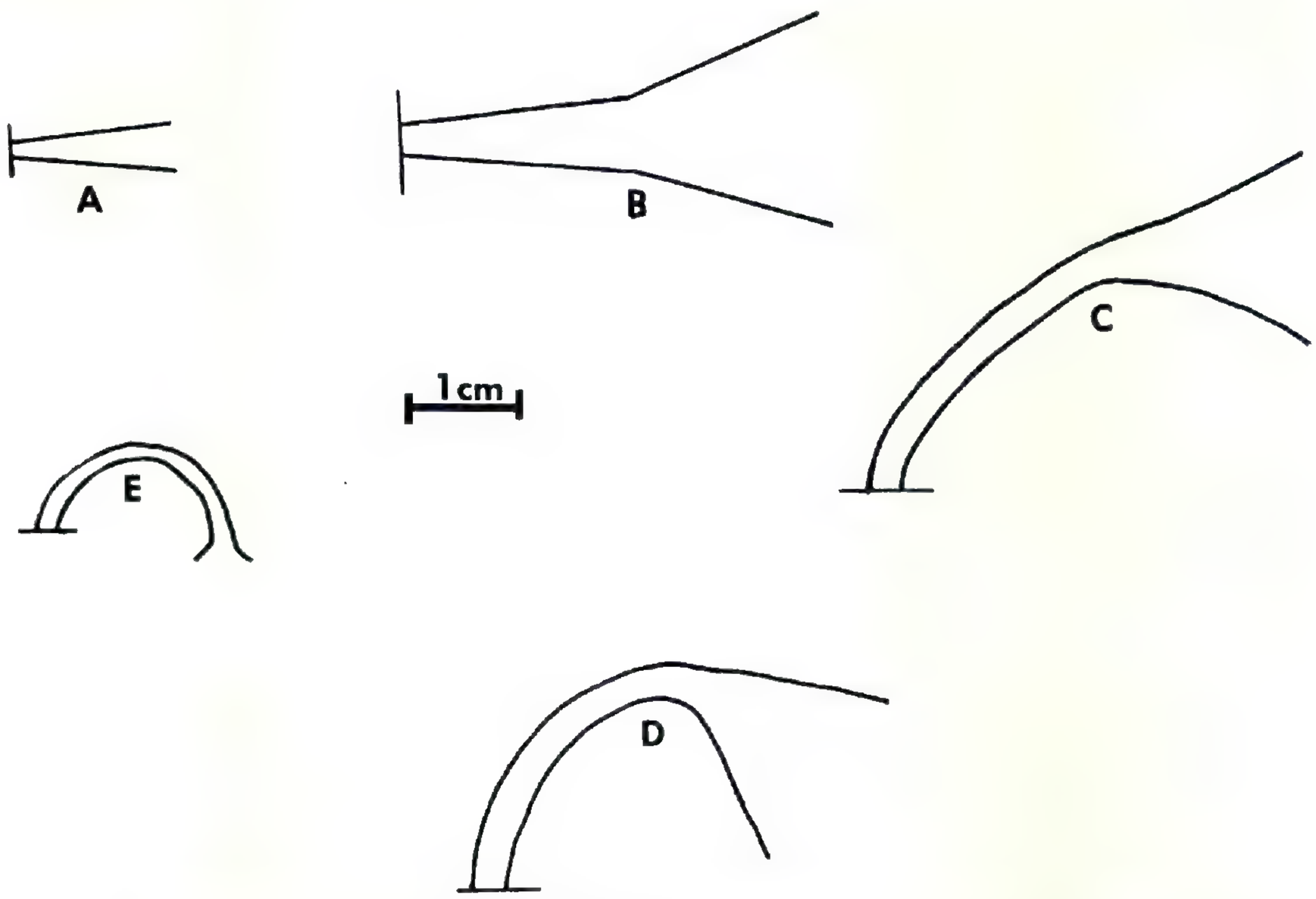


FIGURE 23. Perianth tube morphology of *Eucharis* and *Caliphruria* species or hybrids.—A. *C. subedentata* (*Meerow 1098*, FLAS).—B. ×*Calicharis butcheri* (*Meerow 1110*, FLAS).—C. *E. sanderi* (*Cuatrecasas 16380*, F).—D. *E. amazonica* (*Schunke 14179*, FLAS).—E. *E. astrophiala* (*Madison 3792*, SEL).

tween *Caliphruria* (Fig. 23A) and *Eucharis* subg. *Heterocharis* (Fig. 23C, D).

The tube of *Caliphruria* (Fig. 23A) is straight and dilates gradually from base to throat. It is either subcylindrical (*C. korsakoffii*) or funnelform (all other species). The tube is tinted green proximally (in *C. subedentata*, for ½–⅔ of its length).

The tepals of *Eucharis* and *Caliphruria* flowers are white. Those of the outer series are almost always longer and narrower than the inner tepals. The outer tepals are apiculate. The apiculum frequently has a small, papillate horn on the adaxial surface in *Eucharis* subg. *Eucharis*. The inner tepals vary from acute to obtuse, sometimes minutely apiculate, at the apex.

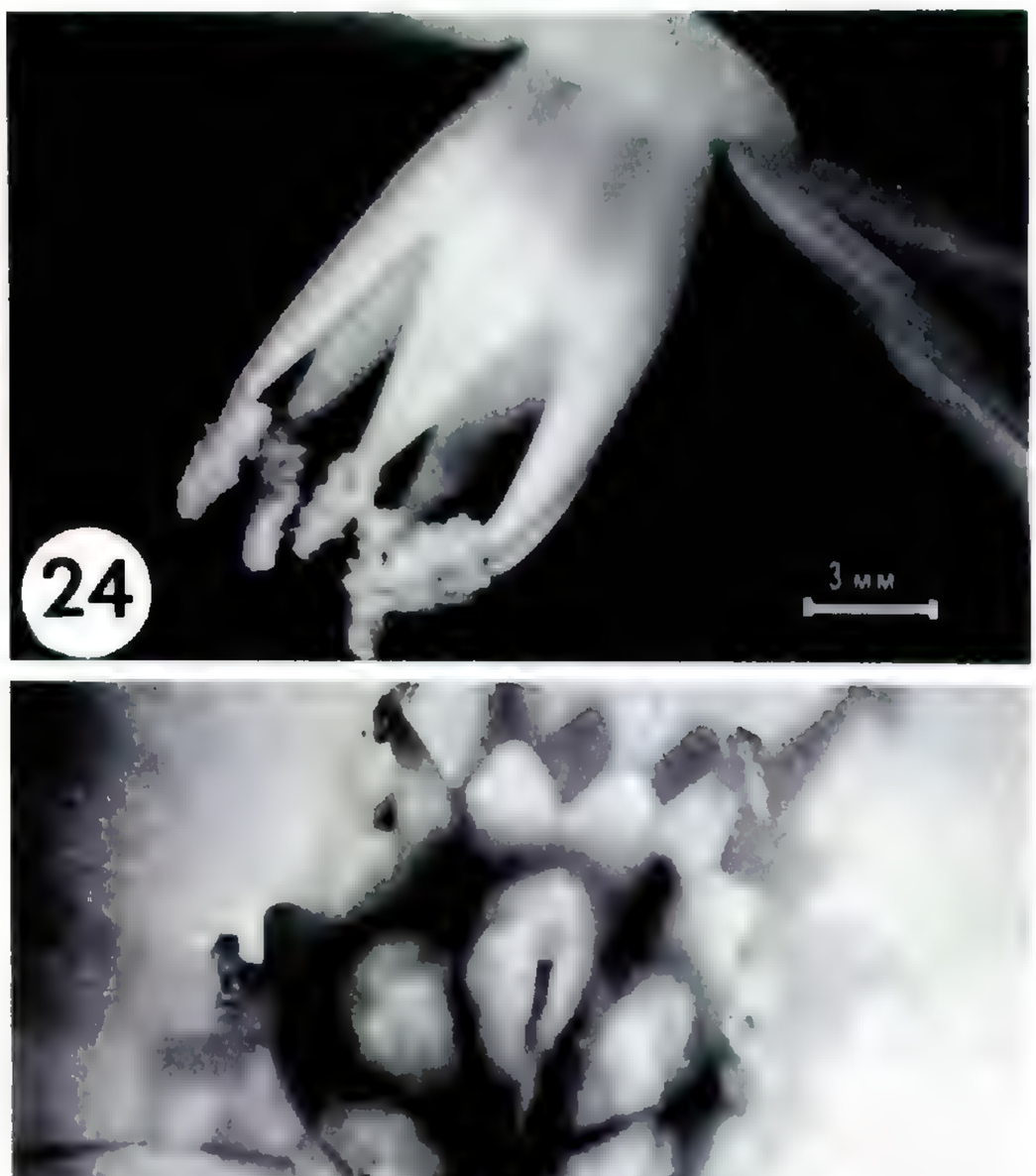
The tepals of most species of subg. *Eucharis* spread at an angle of 90° or more from the throat. Perianth morphology of subg. *Eucharis* is thus predominantly crateriform. At times the tepals may be reflexed strongly above the midpoint of their length, or rarely for their entire length. Tepal habit varies even among flowers of the same inflorescence and shows no taxonomic consistency. If exposed to strong light, the abaxial midrib of the tepals of some species of subg. *Eucharis* may be lightly pigmented yellow.

The perianth of *Caliphruria* is infundibular. The tepals remain imbricate for half their length and spread distally at angles of only 45–60°. The tepals of subg. *Heterocharis* are also for the most part imbricate proximally and spread at 45–60° from the throat. The perianth is more or less campanulate. One species, *E. amazonica*, has the crateriform perianth characteristic of subg. *Eucharis* with a wide-spreading (ca. 90°) limb.

ANDROECIUM

The stamens of *Eucharis* and *Caliphruria* are variously connate proximally. In all but three species of *Eucharis*, a conspicuous staminal cup is present (Figs. 24, 25). In *Caliphruria*, the cup is reduced to a short, membranous, connate portion of the filaments near the perianth throat (Fig. 26). *Eucharis sanderi* (subg. *Heterocharis*) has a reduced staminal cup similar to that of *Caliphruria*. Staminal connation is one of the major characteristics of "infrafamily" Pancratioidinae. Some taxonomic workers considered the staminal cup of pancratioid genera homologous to the corona of *Narcissus* L. (e.g., Pax, 1888). The corona of *Narcissus* is generally considered to be of perianthal origin (Eichler, 1875; Arber, 1937), while the staminal cup of pancratioid taxa has been described as composed entirely of androecial tissue (Arber, 1937; Singh, 1972). Einsiedel (1987) and Müller-Doblies (pers. comm.) consider this distinction artificial and claim that both structures arise from the same meristematic potential, citing putative instances of polymorphy for both types within the same genus.

Stamens of *Eucharis* and *Caliphruria* may be dentate, edentate, or irregularly toothed. Both types of staminal morphology may occur in the same species, and variation may occur even among flow-



FIGURES 24–26. Androecial morphology of *Eucharis* and *Caliphruria* species.—24. *E. astrophiala* (*Madison 3792*, SEL).—25. *E. amazonica* (*Schunke 14179*, FLAS).—26. *C. subedentata* (*Meerow 1109*, FLAS).

ers of a single clone (Meerow, 1986). The presence or absence of staminal dentation has frequently been overweighted in the alpha-taxonomic literature relating to these genera (e.g., Ravenna, 1982) but can still be of taxonomic significance (e.g., *E. astrophiala* (Fig. 24), the only species of subg. *Eucharis* that always has an edentate staminal cup).

A variable pattern of green or yellow pigmentation is present in the androecium of all species of subg. *Eucharis* and *Heterocharis*. Stamens of *Caliphruria* are completely white. In subg. *Heterocharis*, the green (rarely yellowish) pigmentation is largely restricted to the interior of the cup, and extends into the dilated portion of the tube as well (Fig. 25). The coloration is concentrated along the filamental traces, but the tissue between the traces is also suffused with green. In subg. *Eucharis*, pigmentation is present on both the exterior and interior surfaces of the cup, does not extend into the dilated portion of the tube, and takes the form of either broad spots below each free filament or a uniform band of color at the basal ½–⅓ of the cup. In this subgenus, the pattern is of limited taxonomic significance. Whether the pigmentation functions as nectar guides for pollinating animals is unknown.

The stamens of most species of subg. *Eucharis* constrict distally into a broadly subulate portion (greater than 1 mm wide for most of its length) of varying length. Only in *E. astrophiala* (Fig. 24) and *E. bouchei* (in part) do the stamens constrict gradually from the rim of the staminal cup to the apex of the filament. The free filaments of *Caliphruria* are narrowly subulate (less than 1 mm wide for most of their length, Fig. 26). The free filaments of *E. sanderi* (subg. *Heterocharis*) are narrowly subulate and slightly incurved. Those of *E. moorei* and *E. amazonica* are broadly subulate.

Anthers of *Eucharis* are introrse, dehiscing longitudinally, and either dorsifixed or sub-basifixed. They are most frequently oblong but are linear in subg. *Heterocharis*. At anthesis, the anthers of *Caliphruria* and *Eucharis* subg. *Eucharis* are erect but become versatile as they age. In subg. *Heterocharis*, the anthers are versatile at anthesis.

STIGMA AND STYLE

Of the sixteen species of *Eucharis* and *Caliphruria* observed in cultivation, all but *E. castelnaeana* are protandrous. Stigma receptivity does not occur until the second or third day following anther dehiscence. In some cases, the stigma does not fully expand until the perianth has begun to senesce. Successful greenhouse pollinations have been accomplished after the onset of perianth senescence. In the single known autogamous species, *E. castelnaeana*, stigma receptivity and anther dehiscence coincide.

The styles of *Eucharis* and *Caliphruria* are usually exserted beyond the anthers, most fre-

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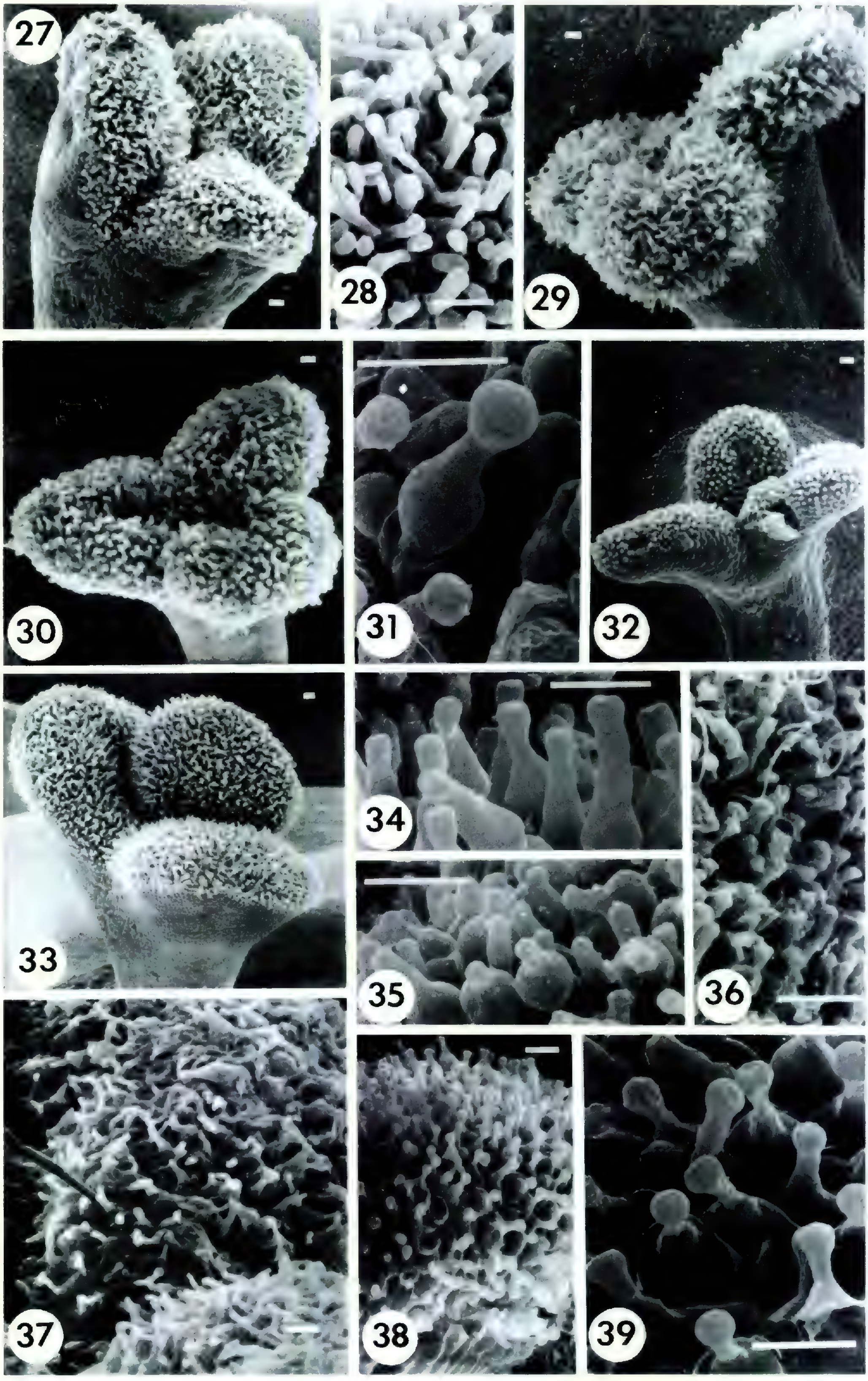
FIGURES 27–39. SEM photomicrographs of *Eucharis* and *Caliphruria* stigmas.—27, 28. *E. astrophiala* (*Meerow 1111*, FLAS).—29. *E. plicata* (*Plowman 13941*, FLAS).—30, 31. *C. subedentata* (*Meerow 1152*).—32. *C. korsakoffii* (*Meerow 1096*, FLAS).—33, 34. *E.* ×*grandiflora* (*Meerow 1127*, FLAS).—35. *E. moorei* (*Meerow*



1141, FLAS).—36. *E. sanderi* (*Cuatrecasas 16350*, F).—37. *E. amazonica* (*Schunke 14179*, FLAS).—38, 39. ×*Calicharis butcheri* (*Meerow 1110*, FLAS). All scales = 50 μm.

FIGURES 40–43. Fruits and seeds of *Eucharis* subg. *Eucharis*. 40, 41. Mature capsules.—40. *E. formosa* (*Schunke 14174*, FLAS).—41. *E. castelnaeana* (*Schunke 14156*, FLAS). 42, 43. Seeds.—42. *E. bouchei* var. *bouchei* (*Meerow 1125*, FLAS).—43. *E. castelnaeana* (*Schunke 14156*, FLAS).

quently 0.5–1 cm. In subg. *Heterocharis*, the styles are somewhat assurgent away from the stamens and are exserted well over 1 cm past the anthers. In two species of subg. *Eucharis*, *E. castelnaeana* and *E. plicata*, the style is included within the cup. In the former species, self-pollination occurs regularly, and stigma receptivity coincides with anthesis.

Stigmas of *Eucharis* and *Caliphruria* (Figs. 27, 29, 30, 32, 33) are obtusely trilobed. Trilobed stigmas are relatively rare in the Pancratioidinae, and *Urceolina*—sister group to *Eucharis* and *Caliphruria*—has a capitate, entire stigma. Traub (1963) and Traub & Moldenke (1949) considered a trilobed or trifid stigma the ancestral state in the Amaryllidaceae.

The stigmatic papillae of *Eucharis* are unicellular (Figs. 28, 34–37), while those of *Caliphruria* (Fig. 31) are multicellular, consisting of both a stalk cell and globose head cell. ×*Calicharis butcheri*, putatively a natural hybrid of *E. sanderi* and *C. subedentata*, has the multicellular stigmatic papillae (Figs. 38, 39) characteristic of *Caliphruria*. Heslop-Harrison & Shivanna (1977) characterized the stigmas of *Eucharis* and *Caliphruria* as dry-type.

OVARY AND OVULES

The ovary of *Eucharis* and *Caliphruria* is inferior and contains septal nectaries. It is green, with the exception of two species, *E. astrophiala* and *E. castelnaeana* (subg. *Eucharis*), in which the ovary is white at anthesis. Ovaries of *Eucharis* and *Caliphruria* range from oblong-ellipsoid (subg. *Heterocharis*) to globose or subglobose (*Caliphruria* and *Eucharis* subg. *Eucharis*). The ovary of subg. *Heterocharis* appears rostellate after senescence of the perianth.

The ovules of *Eucharis* and *Caliphruria* are globose, anatropous, and borne on axile placentae. Ovule number is quite variable throughout both genera. Within limits, however, this number is characteristic of species or species complexes. Subgenus *Heterocharis* has the largest ovule number in *Eucharis*, generally 16–20 per locule, but occasionally as low as 7 in *E. sanderi* (which otherwise has 16–20 throughout most of its range) and 9–12 in *E. amazonica*. In both *Caliphruria* and *Eucharis* subg. *Eucharis*, ovules do not number more than ten per locule. *Eucharis astrophiala*, *E. bouchei*, *E. bonplandii*, *E. cyaneosperma*, and *E. ulei* characteristically have two ovules per locule, but rarely as many as five.

FRUIT

The mature fruit of *Eucharis* and *Caliphruria* is a triloculicidal capsule typical of the nonbaccate-fruited Amaryllidaceae. In fruit, the pedicel elongates to two or more times its length at anthesis. In *Caliphruria* and *Eucharis* subg. *Heterocharis* (*E. moorei*), the capsule is thin-walled and green, sometimes turning yellow or brown at dehiscence. In subg. *Eucharis*, however, the capsule is leathery and bright orange (Fig. 40), contrasting vividly with the shiny black or blue seeds at dehiscence. It is probable, though unsubstantiated, that the combination of fruit and seed color functions mimetically to attract avian dispersal agents (sensu van der Pijl, 1982). In the single known exception to this characteristic fruit morphology in subg. *Eucharis*, the fruit of *E. castelnaeana* (Fig. 41) remains green until shortly before dehiscence, at which time it yellows and finally turns brown. It is often tardily dehiscent and sometimes abscises before opening, though the seeds within are ripe.

SEED

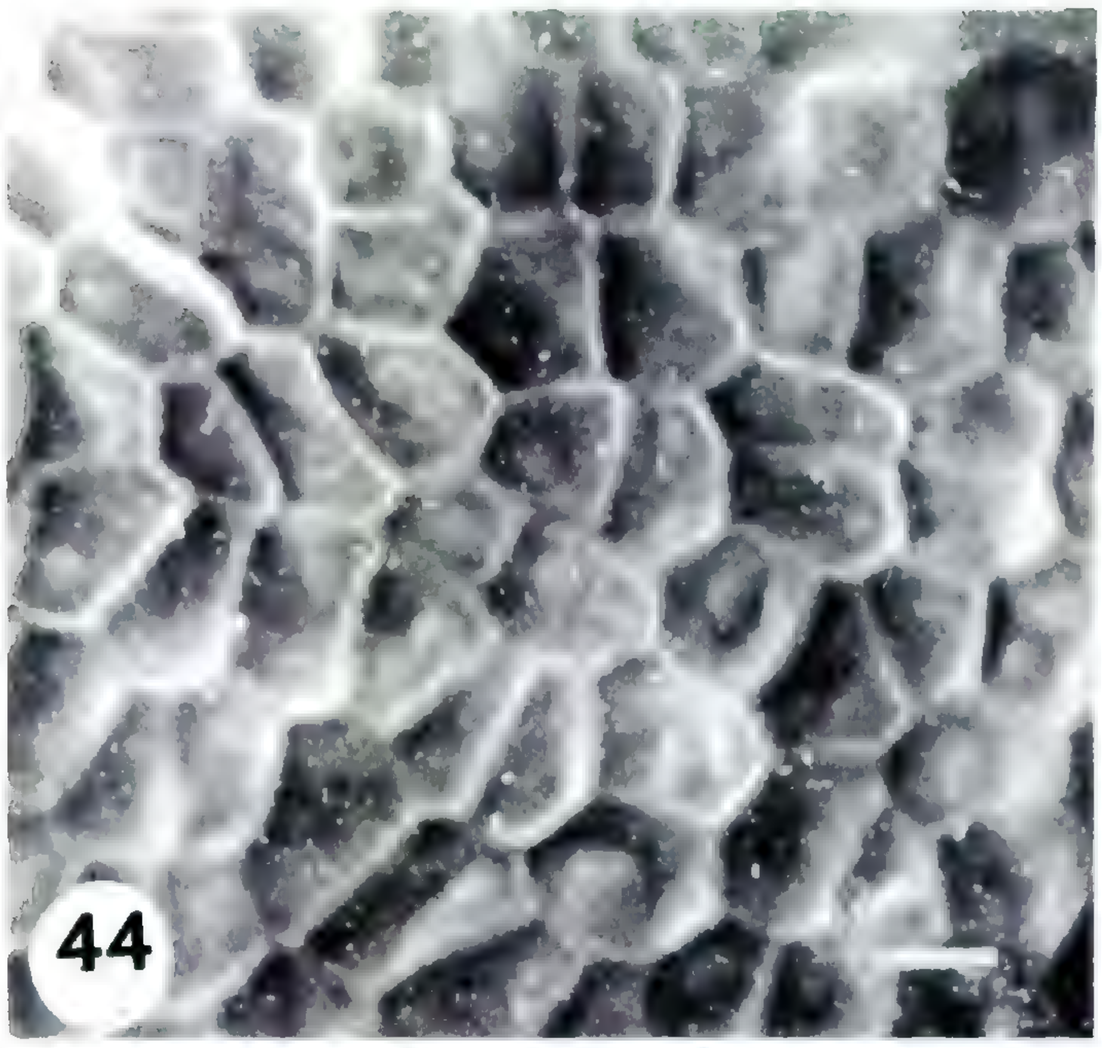
Regardless of the number of ovules per locule in any species of *Eucharis* and *Caliphruria*, all but a few abort as the fruit matures. Generally one to three seeds are present per locule in mature capsules, but as many as four have been observed (Fig. 40).

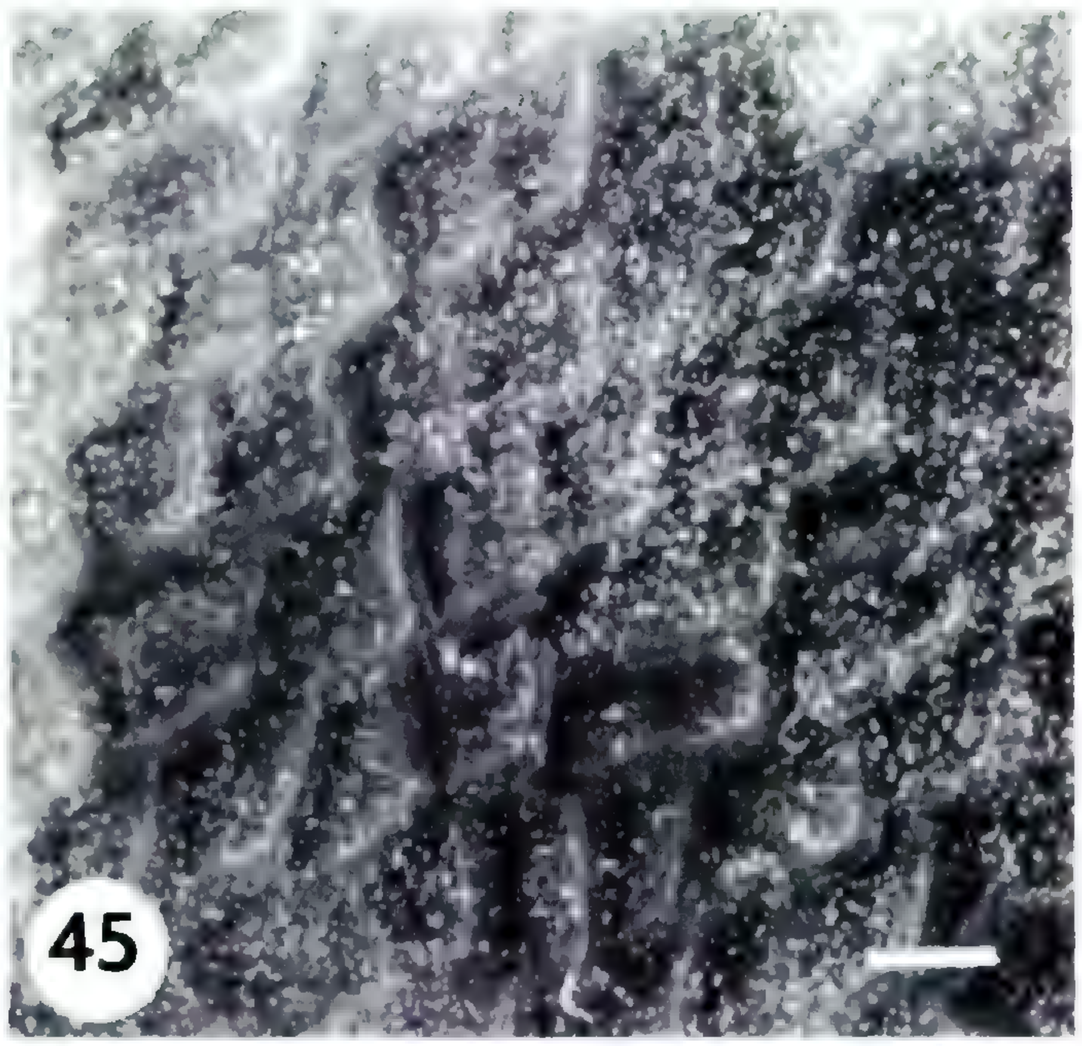
The seeds of both *Eucharis* and *Caliphruria* are globose or ellipsoid and turgid, the consequence of copious, oily endosperm and a high moisture content. Left at room temperature, the seeds will shrink away from the testa somewhat as moisture is lost but remain capable of germination. Long-term viability has not been tested.

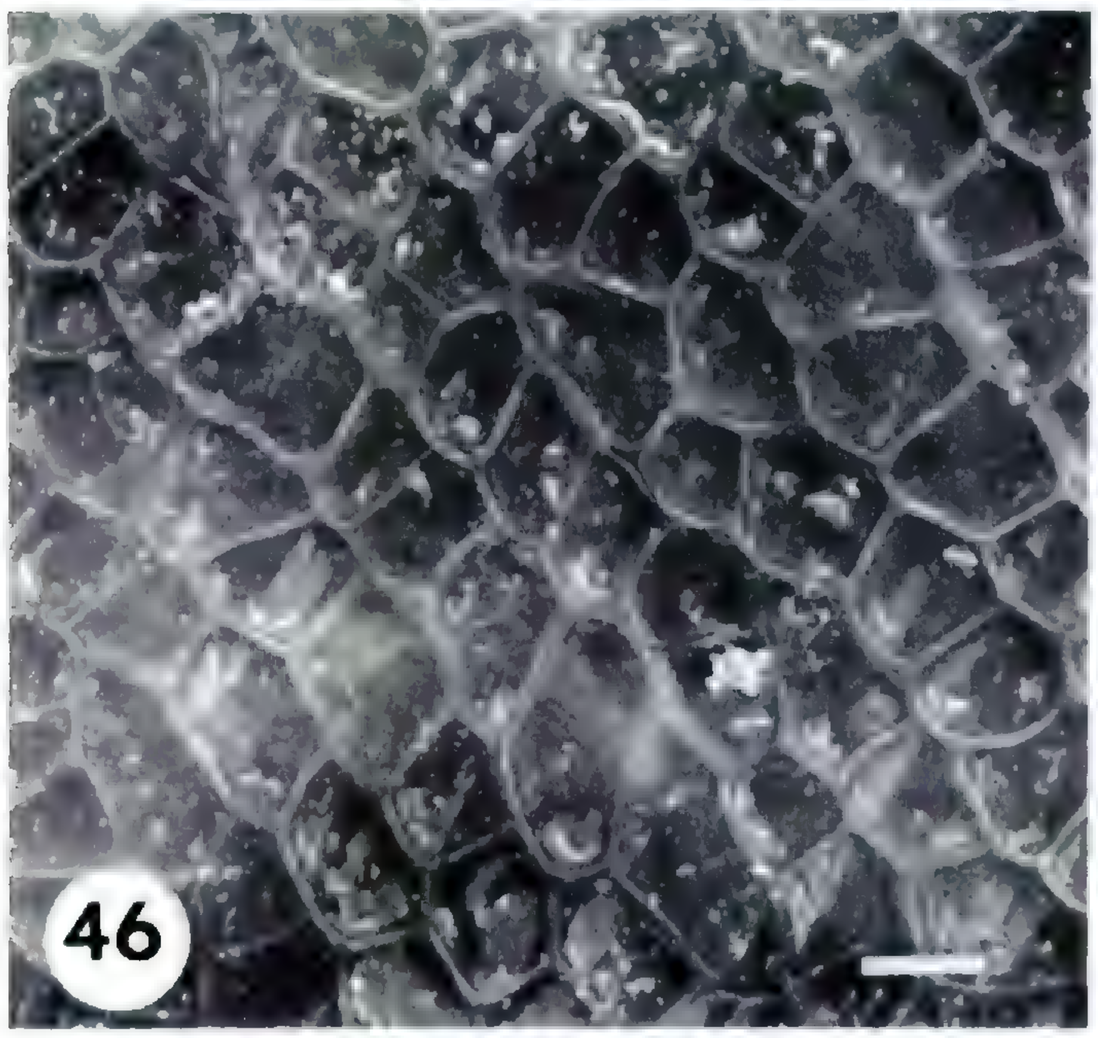
The seed of subg. *Eucharis* (Fig. 42) is characteristically ellipsoid and has a shiny, smooth black (blue in *E. cyaneosperma*) testa. The single exception so far known is again *E. castelnaeana* (Fig. 43). The seed of this species is wedge-shaped by compression in the capsule, is less turgid than seeds of consubgeneric species, and has a dull, rugose testa. The seed of *E. moorei* (subg. *Heterocharis*) is globose to very slightly compressed and has a brown, slightly rugose testa.

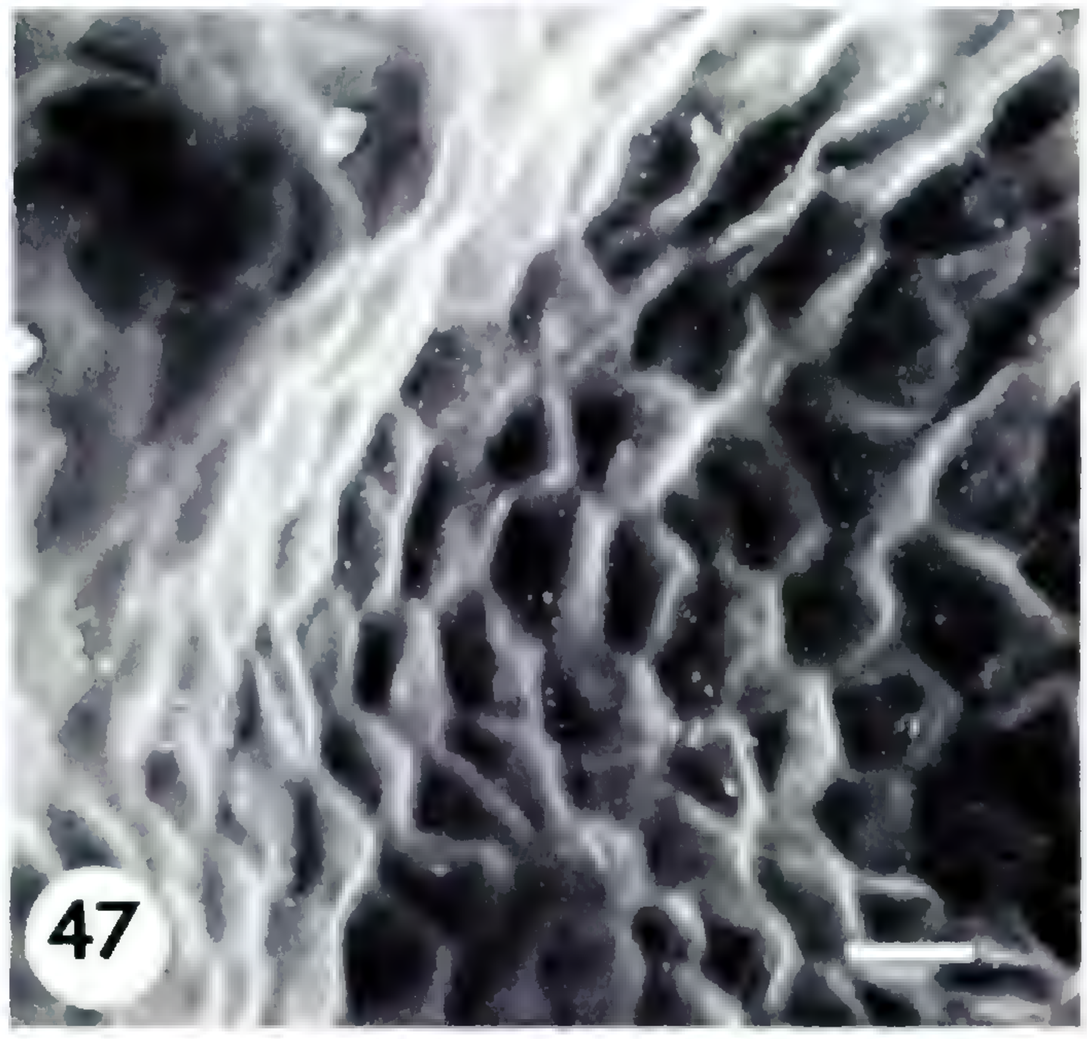
In *Caliphruria*, the seeds of only *C. korsakoffii* and *C. subedentata* are known. Seeds of *C. korsakoffii* are globose, turgid, and have a smooth, lustrous brown testa. Seed of *C. subedentata* is slightly compressed, with a lustrous black but rugose testa.

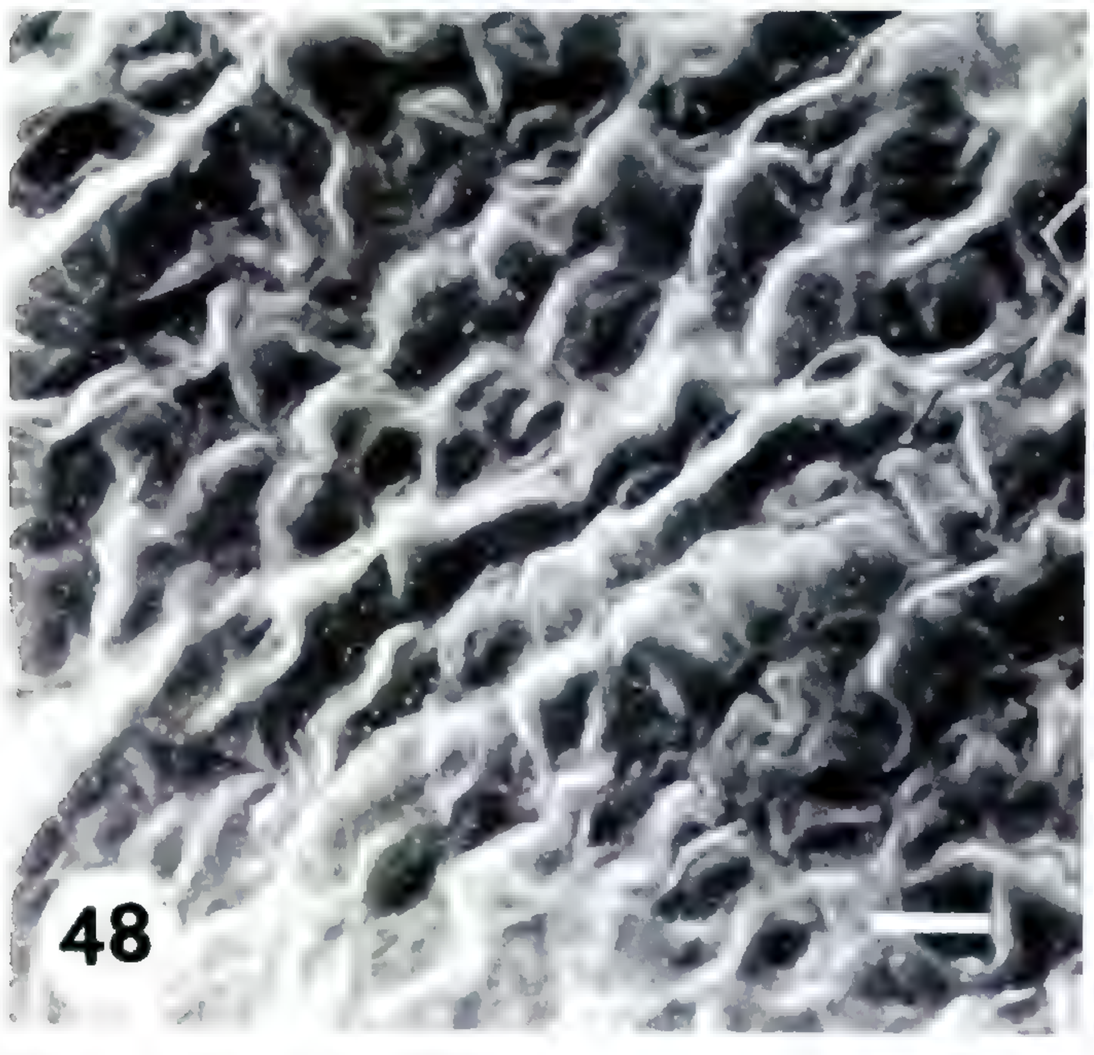
The testa is alveolate in all species examined (Figs. 44–49). In *E. bouchei* var. *dressleri* Meerow (Fig. 45), abundant wax extrusions are found across the surface. The testa of *Eucharis* and *Caliphruria* seeds is composed of phytomelan (Huber, 1969), a simple, largely inert, carbonaceous compound characteristically present in the seed coat of nonbaccate-fruited Amaryllidaceae (Dahlgren & Clifford, 1982; Huber, 1969). Werker & Fahn (1975) reported the occurrence of phenolic quinones in the phytomelan layer of *Pancratium* seeds. In most species of *Eucharis* and *Caliphruria*, the phytomelan layer is all that remains of the integuments (Figs. 51, 57). In *E. bouchei*, however, there is an additional layer of integument tissue about five cells thick, interposed between the phytomelan and the endosperm (Fig. 55). Whether this may be a consequence of the

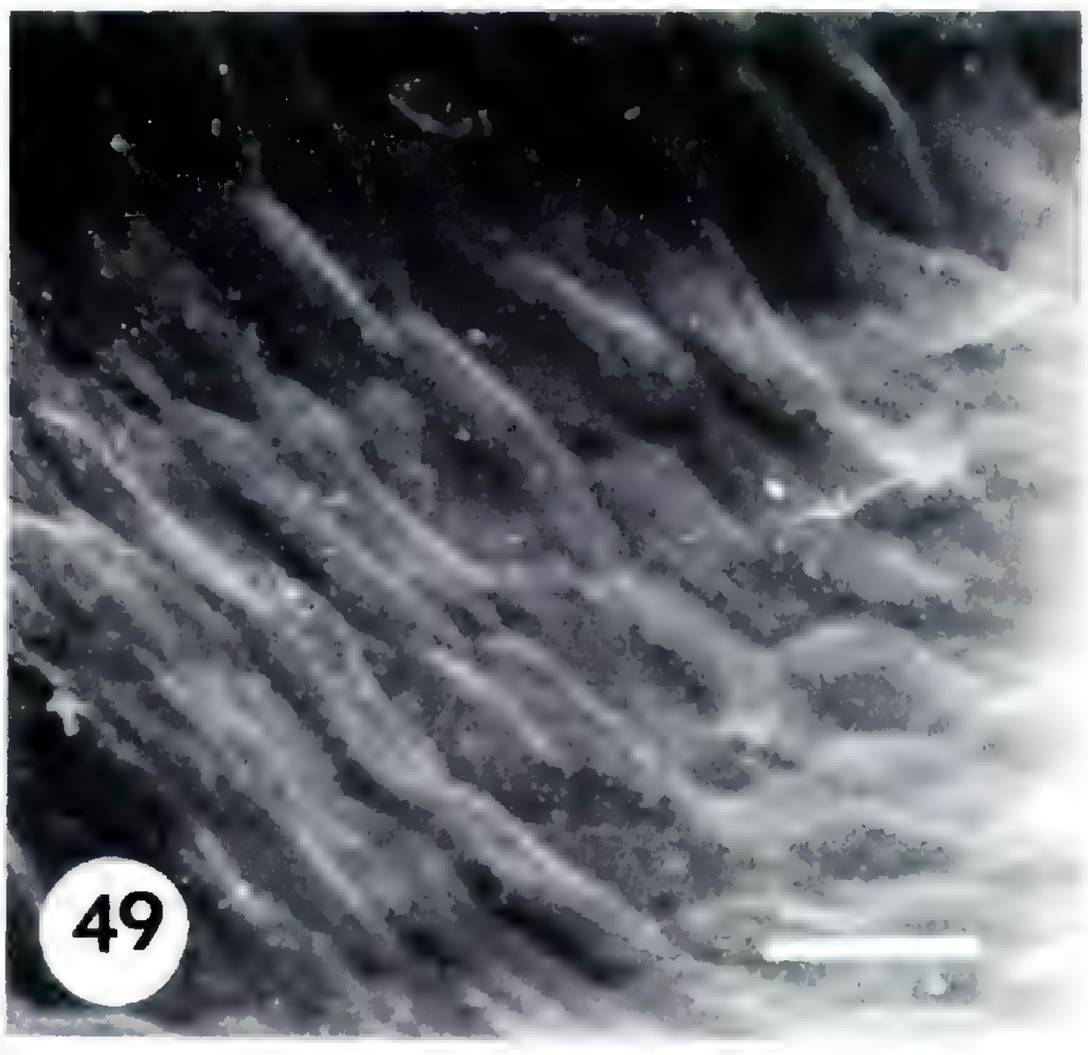




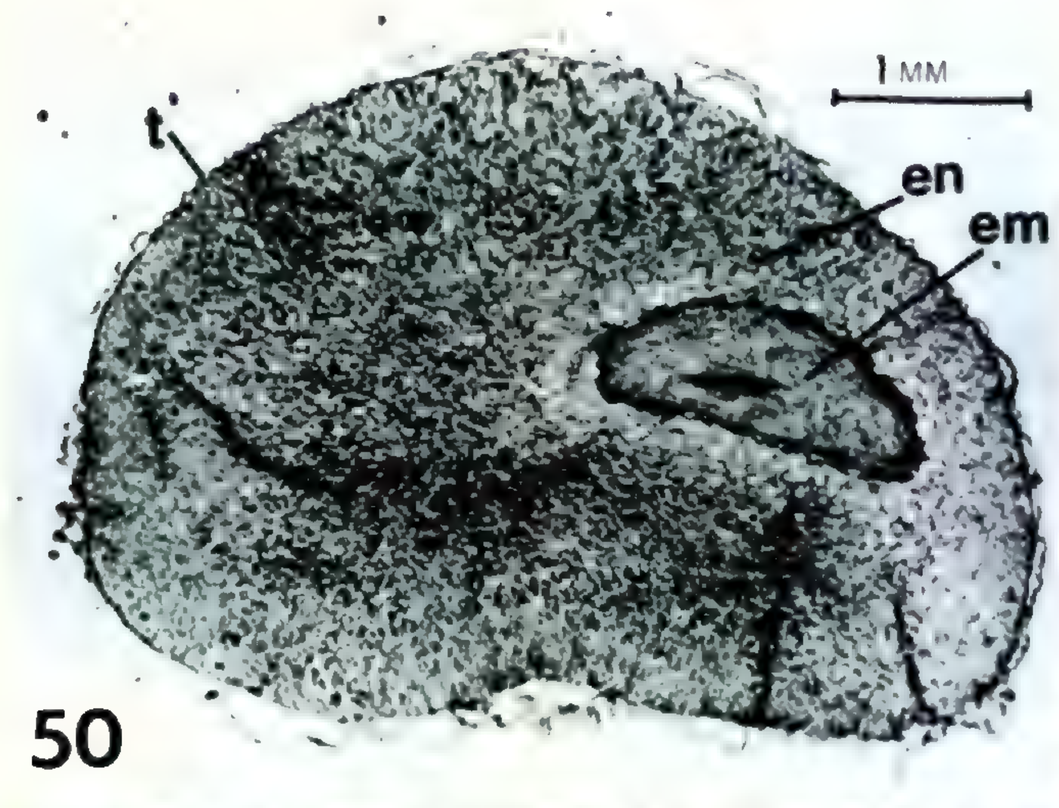








FIGURES 44–49. SEM photomicrographs of *Eucharis* and *Caliphruria* seed surfaces.—44. *E. astrophiala* (*Meerow 1111*, FLAS).—45. *E. bouchei* var. *dressleri* (*Meerow 1107*, FLAS).—46. *E. formosa* (*Meerow 1103*).—47. *E. castelnaeana* (*Schunke 14156*, FLAS).—48. *C. korsakoffii* (*Meerow 1096*, FLAS).—49. *C. subedentata* (*Meerow 1152*, FLAS). All scales = 50 μm.



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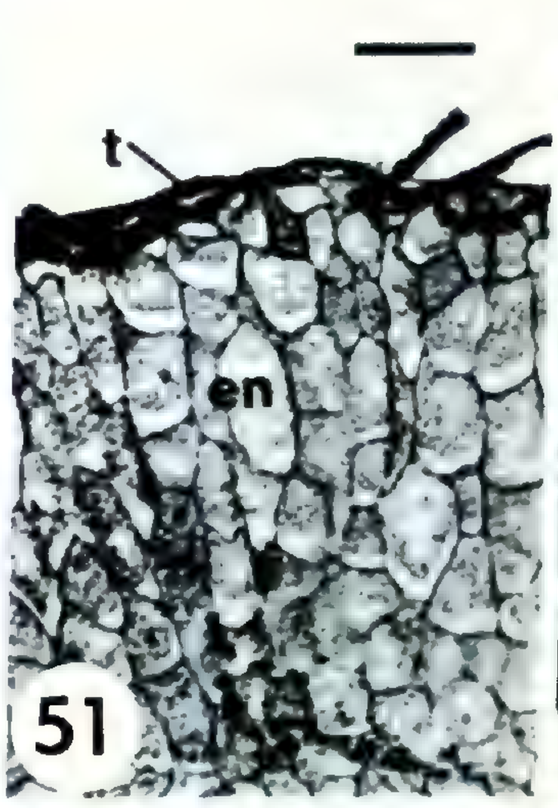

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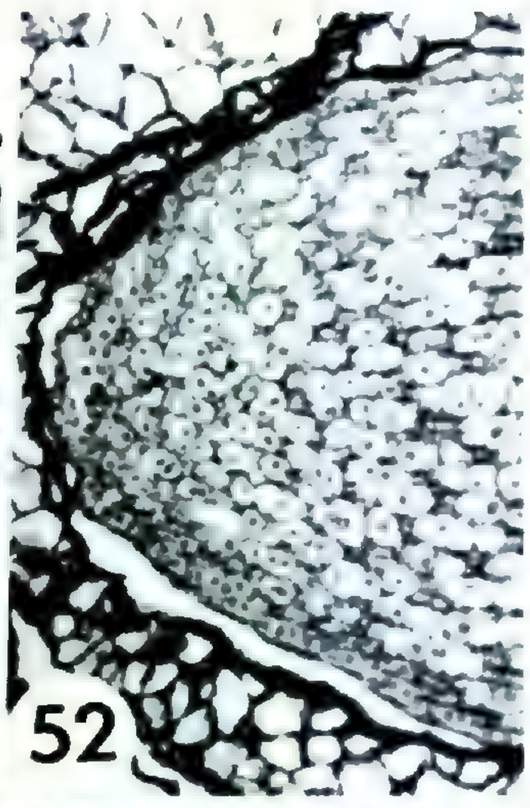

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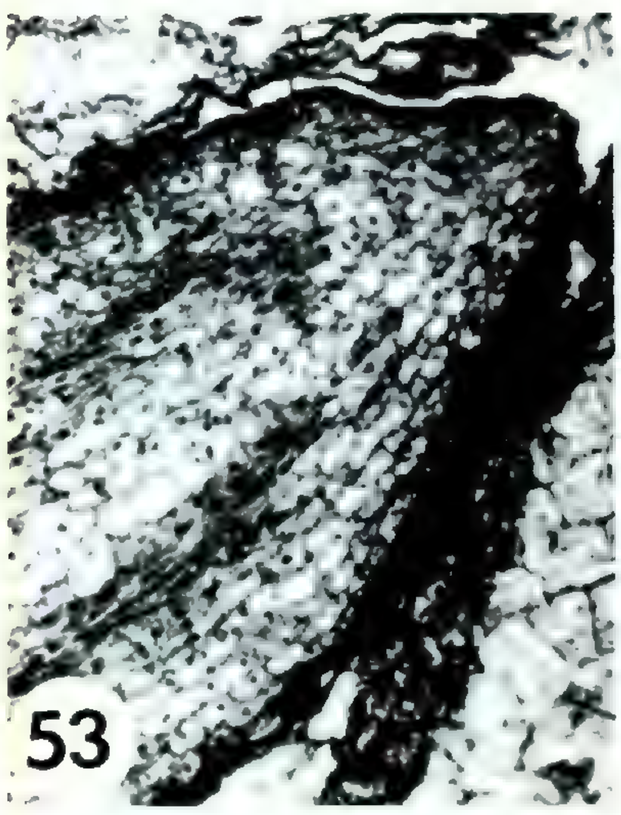

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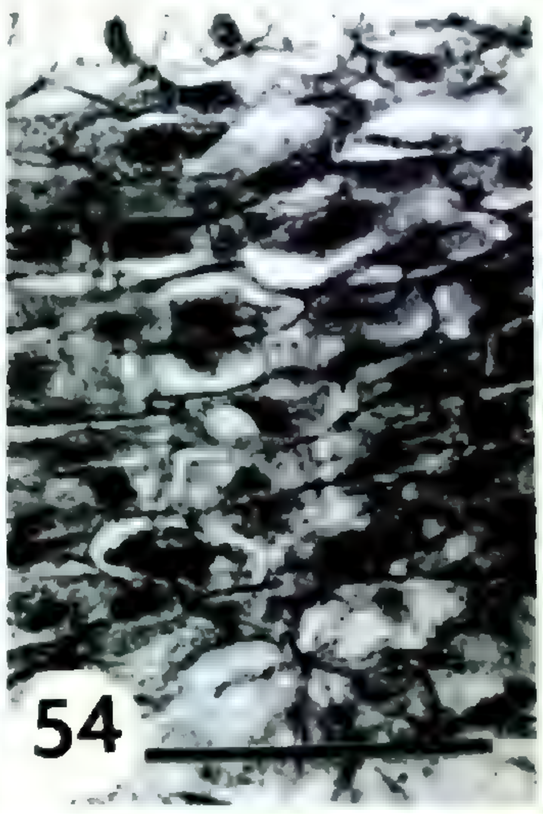

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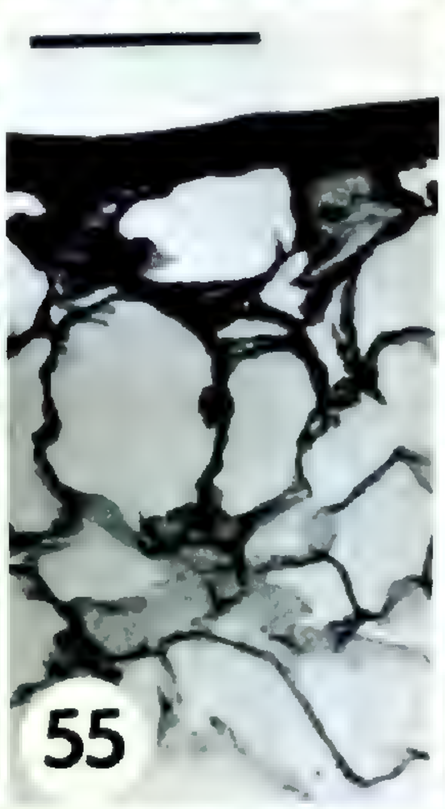

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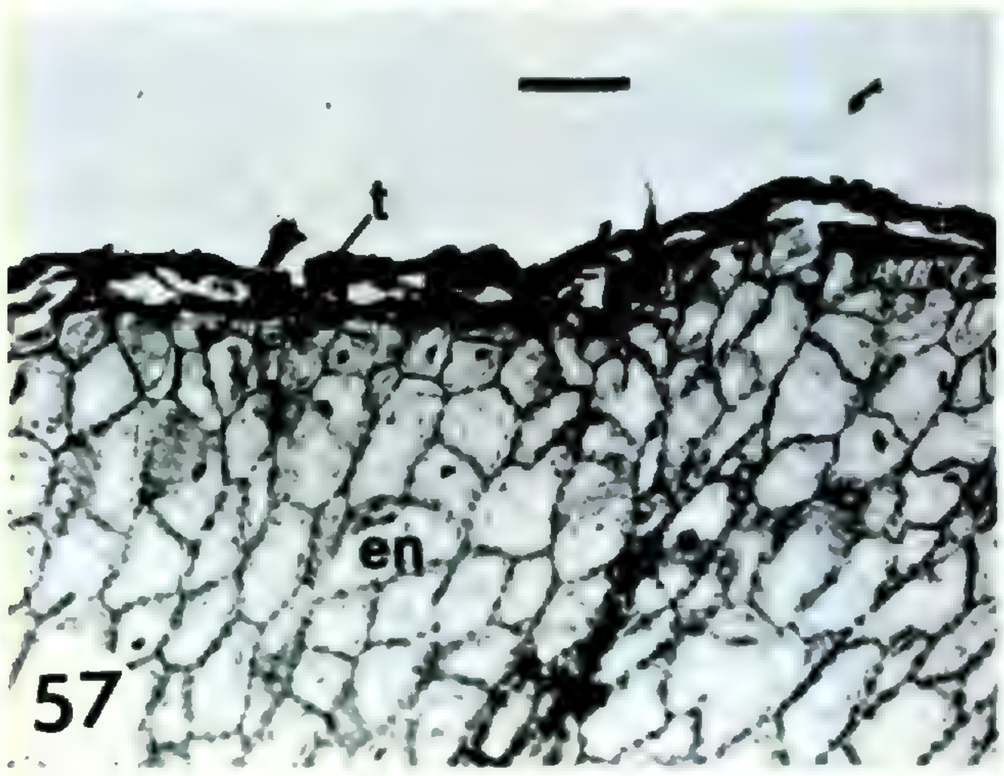

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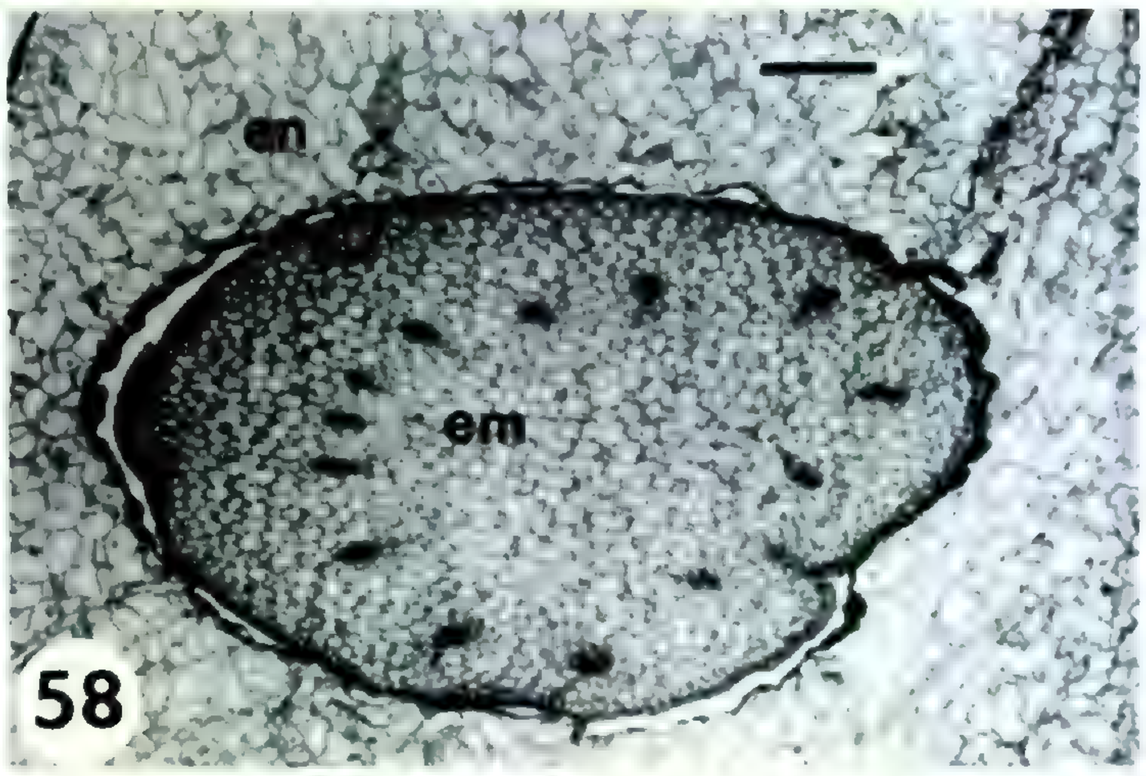

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FIGURES 50–58. Photomicrographs of *Eucharis* and *Caliphruria* seed anatomy. 50–54. *C. korsakoffii* (*Meerow 1096*, FLAS).—50. Longitudinal section through whole seed.—51. Transverse section through testa and part of endosperm.—52. Longitudinal section through radicle of embryo.—53. Longitudinal section through apex of embryo.—54. Longitudinal section through vascular initial of embryo. 55, 56. *E. bouchei* var. *bouchei* (*Meerow 1125*, FLAS).—55. Transverse section through testa. Note several layers of additional integument cells below outer phytomelan layer.—56. Endosperm. Note transfer tissue with pitted walls and plasmodesmata. 57, 58. *E. castelnaeana* (*Schunke 14156*, FLAS).—57. Transverse section through testa and part of endosperm.—58. Transverse section through embryo. All scales = 100 μm except 40 μm in Figure 54. em = embryo, en = endosperm, t = testa.

tetraploid condition of this species is unknown. Most of the seed body of *Eucharis* and *Caliphruria* is taken up by a copious quantity of endosperm characterized by abundant transfer cells (Fig. 56). At maturity, no remnants of the nucellus were observed.

Most workers (e.g., Baker, 1888; Traub, 1963; Hutchinson, 1959; Dahlgren et al., 1985) have allied *Eucharis* and *Caliphruria* with *Hymenocallis*, *Eurycles*, and *Calostemma* (e.g., tribe Eucharieae, or Eucharideae) on the basis of "fleshy seeds." The last-mentioned three genera do indeed have fleshy, bulbiform, sometimes viviparous seeds, but they are not homologous structures. The "pseudoseed" of *Eurycles* and *Calostemma* is actually an adventitious bulbil (Rendle, 1901). The bulbi-

form propagules of *Hymenocallis*, while true seeds, have thick, fleshy chlorenchymous integuments with a well-developed vascular system and a starch-storing embryo (Rendle, 1901; Whitehead & Brown, 1940). These important seed differences have been overlooked by most phylogenists of the Amaryllidaceae.

The turgid seed of *Eucharis* and *Caliphruria*, despite a high moisture content when first ripe, cannot be accurately described as fleshy. This becomes evident if the seed is allowed to dehydrate slightly at room temperature, and is most apparent in the hard seeds of *E. castelnaeana*, which, at capsule dehiscence, are less turgid than seeds of other species of subg. *Eucharis*. Seeds of *Eucharis* and *Caliphruria* have a reduced integument, represented in most cases only by the compressed phytomelan layer, and have never been observed to germinate viviparously. Phytomelan is absent from the testa of the pseudoseeds of *Eurycles* and *Calostemma*. It is present in only a single species of *Hymenocallis*, *H. quitoensis* Herbert (and probably its close relative *H. heliantha* Ravenna), which has been segregated into the separate genus *Lepidochiton* Sealy (1937) on this basis.

Seeds of *Pancratium* are structurally most similar to those of *Eucharis* and *Caliphruria*. Although variable in shape and surface features (Werker & Fahn, 1975), all species of *Pancratium* have a hard, turgid, ovoid or compressed seed body with copious endosperm (Meerow, unpubl. data; Werker & Fahn, 1975). All examined species of *Pancratium* have a phytomelanous and alveolate testa. Seeds of *Eucharis* and *Caliphruria* have a higher moisture content than those of *Pancratium*, all species of which occur in xeric to seasonally dry habitats.

Pollen Morphology

Pollen morphology of *Eucharis* and *Caliphruria* is reviewed in detail elsewhere (Meerow & Deghan, 1988) and will only be summarized here. Pollen grains of all species of *Eucharis* and *Caliphruria* (Figs. 59–62) are boat-shaped elliptic, monosulcate, heteropolar, and bilaterally symmetrical. The sulcus runs the length of the distal face of the grain. Exine sculpturing is semitectate/reticulate in all species examined.

Pollen of most *Eucharis* falls into Walker & Doyle's (1975) large size class (longest equatorial diameter 50–100 μm). A single species, *E. caucana*, has very large pollen (longest equatorial diameter as much as 110 μm). Pollen of *Eucharis* has average longest equatorial diameters greater than 60 μm, with two exceptions: *E. castelnaeana* and *E. plicata* subsp. *brevidentata*, the two smallest-flowered species. Most species of *Eucharis* have pollen grains with longest equatorial diameters beteen 65 and 75 μm. Pollen of *Caliphruria* falls into the medium size class of Walker & Doyle (1975), with average longest equatorial diameters near 50 μm. Polar diameter of pollen of most *Eucharis* species ranges from 45 to 60.6 μm—diameters less than 40 μm are rare. Polar diameter of pollen of *Caliphruria* is always less than 40 μm. Exine reticulation of *Eucharis* is characteristically coarse (Figs. 59–61), while that of *Caliphruria* is fine (Fig. 62).

Chromosome Cytology

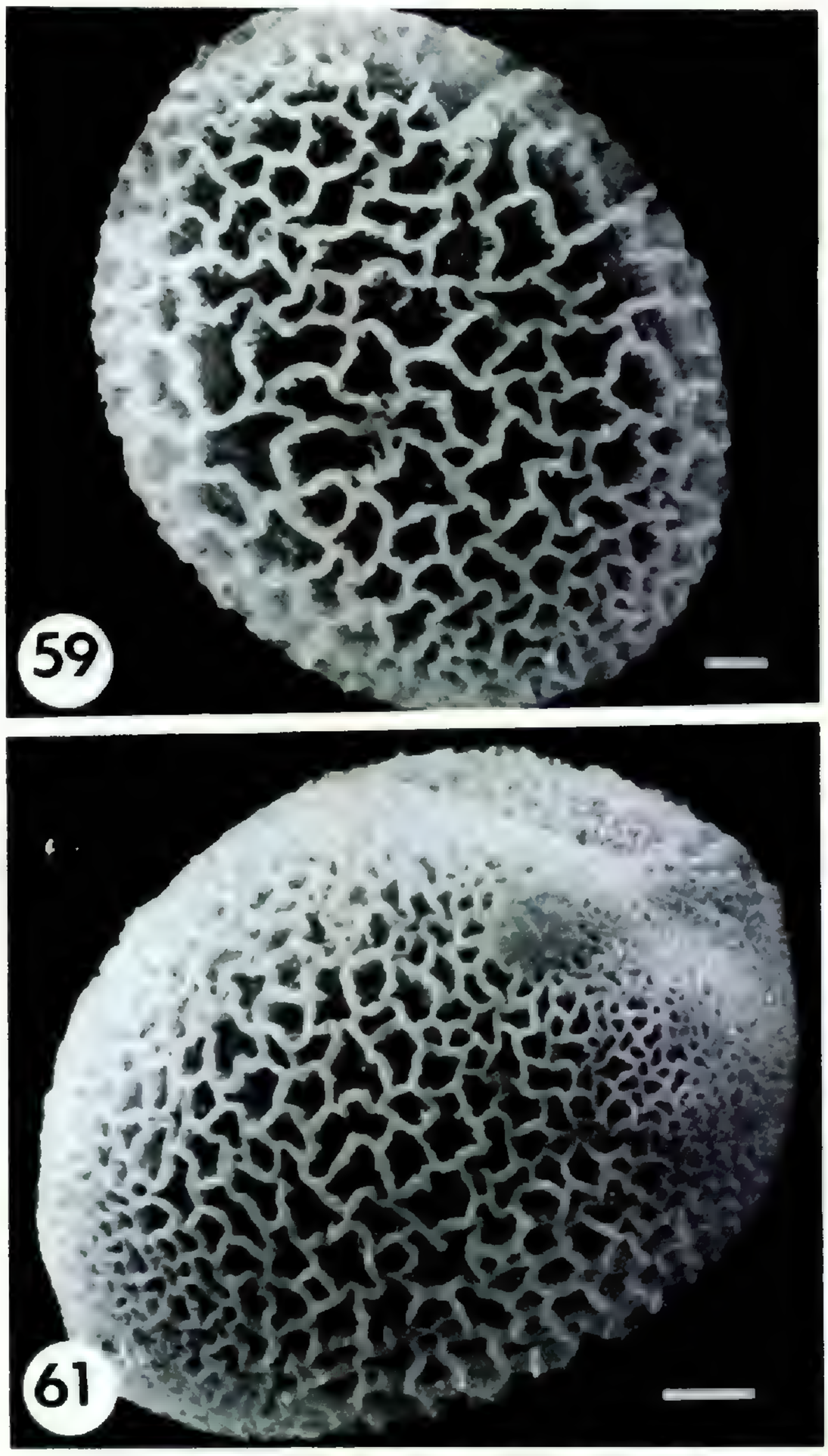
A somatic chromosome number of $2n = 46$ largely characterizes both genera (Meerow, 1987b). Two tetraploid species ($2n = 92$), *E. bonplandii* from Colombia and *E. bouchei* from Central America, are known. *Eucharis caucana*, described in this paper from Colombia, is a hexaploid with the largest chromosome number in the genus ($2n = 138$). *Eucharis amazonica*, $2n = 68$, is the only known departure from these $2x$, $4x$, or $6x$ karyotypes. A somatic chromosome number of $2n = 46$ (or derivations thereof) is characteristic of most genera of neotropical Pancratioidinae (Di Fulvio, 1973; Flory, 1977; Meerow, 1987b, c; Williams, 1981).

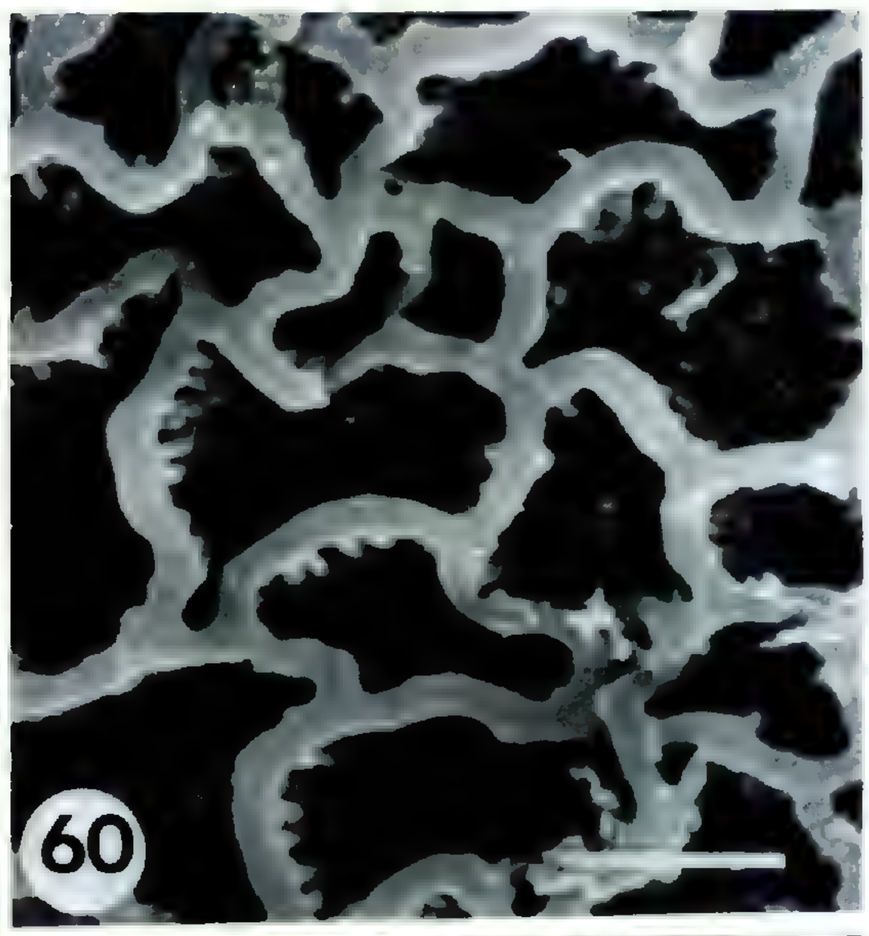
Ecology and Phytogeography

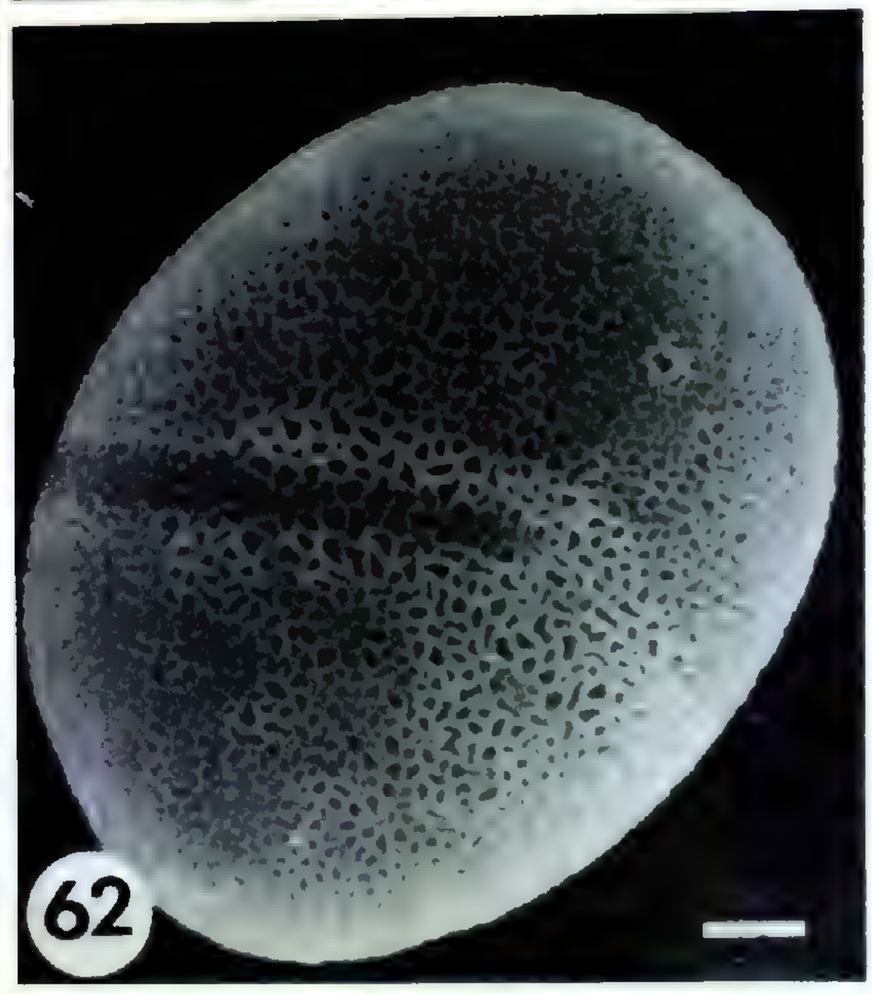
Ecology

All species of *Eucharis* and *Caliphruria* exhibit high fidelity to a primary forest habitat, and severe disturbance of the forest canopy is catastrophic to the plants. In recently cleared forest sites, the bulbs persist for a few seasons, but the leaves developed in sunlight show chlorosis and necrosis. Wilkins (pers. comm.) reported that leaves of *E. amazonica* are damaged at light levels above 5,000 foot candles, an observation confirmed by Rees (1985). Fidelity of these genera to mesic, low-light habitats suggests a strongly evolved adaptive complex. Only two other genera of pancratioid Amaryllidaceae are completely adapted to forest understory: *Eurycles*, a small Australasian genus, and *Urceolina*, sister group to *Eucharis* and *Caliphruria*.

Eucharis populations are often largest on floodplains of small rivers and creeks where frequent short-term inundation is likely. *Eucharis* is also found in more upland sites, but usually in less abundance. No fully deciduous species of subg.







FIGURES 59–62. Representative pollen grains of *Eucharis* and *Caliphruria*. 59, 60. *E. formosa* (*Meerow 1103*, FLAS).—59. Whole grain, proximal polar view.—60. Detail of the exine surface.—61. *E. sanderi* (*Killip 35401*, US), oblique lateral longitudinal view.—62. *C. subedentata* (ex hort. *s.n.*, K), proximal polar view. All scales = ca. 5 μm.

Eucharis have been observed, though *E. astrophiala*, endemic to the western slopes of north-central Ecuador, enters a season of dormancy when growth ceases. Yet several leaves may persist for the duration.

The rarity of *Eucharis* and *Caliphruria* species throughout their range is a striking characteristic of their distribution. Single, widely dispersed clumps of bulbs are more the rule than the exception. Herbarium collections are usually unicates and often indicate the relative infrequency with which the plants were encountered in the forest. The largest population of *Eucharis* that I have observed consisted of about 30 individuals of *E. moorei* in an approximate half-hectare area. Throughout eastern Ecuador, populations of only two or three clonal clumps or single bulbs (and frequently as low as one) of *E. candida*, *E. formosa*, and *E. moorei* are common. In eastern Peru, a careful search through a five-hectare area turned up only two plants of *E. cyaneosperma*. Edaphic conditions are probably important in limiting colonization and establishment of *Eucharis* species. Restriction to sites of high fertility is evident for all species of *Eucharis* and has been noted by floristic workers in the Amazon basin and Chocó region of Colombia (A. Gentry, pers. comm.).

No species of *Eucharis* are found natively above 1,800 m. The overwhelming majority of collections are from elevations below 1,000 m and, of these, more than half are below 500 m. *Caliphruria* is primarily collected at sites above 1,000 m ("selva-subandina" of Cuatrecasas, 1958). Most collections of *Caliphruria* (*C. subedentata*) were from the Río Cauca River valley of western Colombia, an area now largely deforested. In July 1984, I was not able to find members of this genus in any of its historical localities.

PHYTOGEOGRAPHY

More than half of the known species of *Eucharis* subg. *Eucharis* are found on the eastern slopes of the Andes. The majority of these species are concentrated along the Amazon and its main tributaries, e.g., the Napo and Pastaza system in Ecuador and the Huallaga of Peru. Seven of the fourteen extant species of subg. *Eucharis* are endemic to the premontane Andean–Amazonas interface, but no species has been reported east of 68°W longitude. Thus the genus appears to be absent from the great, largely Brazilian expanse of lowland Amazonas. Five peripheral isolate species from the premontane Andean–Amazonian center of distribution show some degree of morphological novelty (see Taxonomic Treatment). *Eucharis corynandra*, very closely related to *E. castelnaeana* and *E. plicata*, and *E. oxyandra*, of uncertain phylogenetic relationship, are both known only from the "ceja de la selva" forest formations of north-central eastern Peru. *Eucharis astrophiala* is endemic to a relatively small area of western Ecuador. *Eucharis lehmannii* and *E. caucana* are restricted to western Columbia. Of the five species, only *E. astrophiala* is known from other than the type locality.

Three of the four species of subg. *Eucharis* that occur above 2°N latitude are polyploids (chromosome number is unknown for *E. lehmannii*). *Eucharis bonplandii* ($2n = 92$), endemic to the Cordillera Oriental and Cordillera Central of Colombia is rare and infrequently collected. The *E. bouchei* complex ($2n = 92$), a series of geographically isolated and morphologically distinct population clusters (Meerow, 1987d), is endemic to Central America, chiefly Panama. *Eucharis caucana* is a hexaploid ($2n = 138$).

Subgenus *Heterocharis* is widely dispersed from Colombia to Peru, but each of its three species are narrowly distributed. With the exception of a single collection from northern Peru, *E. moorei* is not found outside of Ecuador. It is the only species of *Eucharis* found on both sides of the Andes. *Eucharis amazonica* occurs natively within a narrow area of the Río Huallaga valley in Peru. *Eucharis sanderi* is endemic to the Chocó region of Colombia.

Caliphruria is almost completely western Colombian, most prominently in the Río Cauca valley, with a secondary distribution in the Río Magdalena valley. *Caliphruria korsakoffii* is Peruvian.

ETHNOBOTANY

Labels of a number of herbarium specimens of *Eucharis* species indicate that lowland native people collect the bulbs for use as poultices. The bulbs are mashed, heated, and applied to sores and tumors. Lewis (1986) described the use of mucilage from *Eucharis* bulbs (the plant illustrated is *E. formosa*) by the Jivaro Indians of Peru for treating facial blemishes and acne. Indian women of the Pastaza valley in Ecuador reportedly quite actively collect the plants in flower for reasons they would not disclose (N. Whitten, pers. comm.). Most local inhabitants whom I met while collecting *Eucharis* in the Oriente were readily familiar with the plants when shown photographs.

That various neotropical Amaryllidaceae have been cultivated in their native countries for many years cannot be discounted. Motifs recognizable as species of *Zephryanthes* Herbert and *Stenomesson* Herbert appear on ceremonial Incan vases (Vargas, 1981). The seasonal mass-blooming of *Hymenocallis amancaes* (Ruíz & Pavón) Nichols. on the dry hills near Lima, Peru, has long been the nucleus of an annual festival named for that species (Herbert, 1839). I have suggested that frequent sympatric occurrence of *E. candida* and *E. formosa* in eastern Ecuador may have been influenced by cultivation by transient agriculturists (Meerow, 1987e). Further circumstantial evidence for this hypothesis is the persistence in nature of sterile hybrid taxa such as *E.* ×*grandiflora* and ×*Calicharis butcheri*. Almost all collections of the former are remnants of cultivation. *Eucharis oxyandra* is known only from bulbs found uprooted by an abandoned dwelling in Peruvian rain forest (see Taxonomic Treatment).

REPRODUCTIVE BIOLOGY

PHENOLOGY

Eucharis and *Caliphruria* species are largely seasonal flowering. Very well-collected species, such as *E. candida* or *E. formosa*, show flowering patterns skewed toward certain months (January to March), but at least several flowering collections have been made throughout the year. Species in Amazonian Peru have been collected in flower most frequently from June to September. Each inflorescence is moderately long-lived, two to three weeks, but usually no more than one to three flowers are open at any one time.

In the greenhouse, observations over a five-year period confirm an annual flowering for most *Eucharis* and *Caliphruria* species. *Eucharis amazonica*, however, flowers two or three times during the year. Van Bragt & Sprenkels (1983) have regularly induced flowering in this species at any time of the year after treatment at 27°C for at least two weeks. Collection data for this species

throughout its narrow range indicate that twice-annual phenology may occur in habitat as well. *Eucharis castelnaeana* mass-flowers in the greenhouse several times per year. Other well-collected species (e.g., *E. candida* and *E. formosa*) that show a peak period of flowering in certain months in nature are strictly annual-flowering in cultivation.

POLLINATION BIOLOGY

Data on pollination ecology of Amaryllidaceae in general are scant and represent an area sorely in need of investigation. No information on pollination of *Caliphruria* is available. The large, white, heavily and sweetly fragrant flower of *E. amazonica* (subg. *Heterocharis*) was considered a model moth-pollinated flower by Percival (1965). She noted that the nectar level in the tube rises to a maximum height of 23% tube length, thus effectively preventing access to all but long-tongued insects. The large, heavily fragrant flowers of subg. *Heterocharis* fit the syndrome of sphingid moth pollination (sensu Faegri & van der Pijl, 1979). Other related genera of "infrafamily" Pancratioidinae with similar flower morphology are specialized for hawkmoth pollination (*Hymenocallis*: Bauml, 1979; Grant, 1983; *Pancratium*: Morton, 1965).

Floral fragrance is rare in subg. *Eucharis*, occurring in only *E. bakeriana*, *E. castelnaeana*, *E. formosa*, and *E. plicata* subsp. *brevidentata*. However, floral fragrance is only weakly developed in these species, and in *E. formosa* the odor is slightly fetid. Vogel (1963) reported euglossine bees visiting *Eucharis bakeriana*. Visitation by an unidentified euglossine has been reported for other, unidentified species of subg. *Eucharis* in Peru (J. Schunke, pers. comm.). Unfortunately, neither report indicated the sex of the visitor. The phenology of *Eucharis* (rarely more than one or two flowers open per inflorescence at any one time over a period of two or three weeks, and the often successive appearance of inflorescences from a clonal clump of bulbs) and the dispersed distribution of plants in the wild suggests pollination by a trap-lining organism (see Janzen, 1971).

DISPERSAL

The leathery, bright orange fruit of *Eucharis* subg. *Eucharis* is a major apomorphy that defines the subgenus. At dehiscence, the contrast between the capsule and the lustrous black or blue seeds creates a striking visual display in the forest understory, but there are no recorded observations of visitation to the ripe capsules.

BREEDING SYSTEM

On the basis of greenhouse pollination attempts, virtually all species of *Eucharis* and *Caliphruria* demonstrate some degree of self-incompatibility. This observation suggests that most species are predominantly outcrossing. Capsules have been set readily with sibling pollen on all species in cultivation with the exception of *E. amazonica* and functionally sterile hybrid taxa (*E.* ×*grandiflora*, ×*Calicharis butcheri*). Further evidence of outcrossing is the marked protandry of most *Eucharis* species (with the exception of *E. castelnaeana*, in which stigma receptivity coincides with anthesis) and the presence of putative interspecific hybrids in nature (*E. candida* × *E. formosa* (Meerow, 1988), *E. plicata* subsp. *plicata* × *E. ulei* (Meerow, in prep.)). Of all species in cultivation, only *E. castelnaeana* sets capsules with self-pollen. Autogamy in *E. castelnaeana* is associated with a number of other divergent character states for subg. *Eucharis*. This species has a mass-flowering phenology; the smallest flowers in the genus; a green, often tardily dehiscent capsule; a less turgid seed with a dull, rugose testa; and telocentric chromosomes.

Reproductive biology of *Eucharis* and *Caliphruria* is thus still largely conjectural. Annual flowering patterns, short-term pollen viability, and susceptibility to systemic diseases in cultivation impede greenhouse exploration of these questions, and the rarity of the plants is an obstacle to field studies. The disappearance of populations of these genera and their pollinating agents, concurrent with rain forest destruction, may be the final impediment to investigation of this aspect of their biology.

Phylogenetic Relationships

Eucharis and *Caliphruria* have been variously treated as separate genera (Baker, 1888; Bentham & Hooker, 1883; Pax, 1888; Hutchinson, 1959), a single genus (Traub, 1963), and as subgenera of *Urceolina* (Traub, 1971). As a group, *Eucharis*, *Caliphruria*, and *Urceolina* appear to represent a distinct tribal assemblage within "infrafamily" Pancratioidinae Traub (1957, 1963), a group delimited by various patterns of staminal connation, somatic chromosome number frequently of $2n = 46$, and an Andean center of diversity (Meerow, 1985, 1986, 1987a, c).

PHYLOGENETIC ANALYSIS

Despite a lack of consensus on generic and specific limits in Amaryllidaceae, cladistic analysis has only twice before been applied to such problems

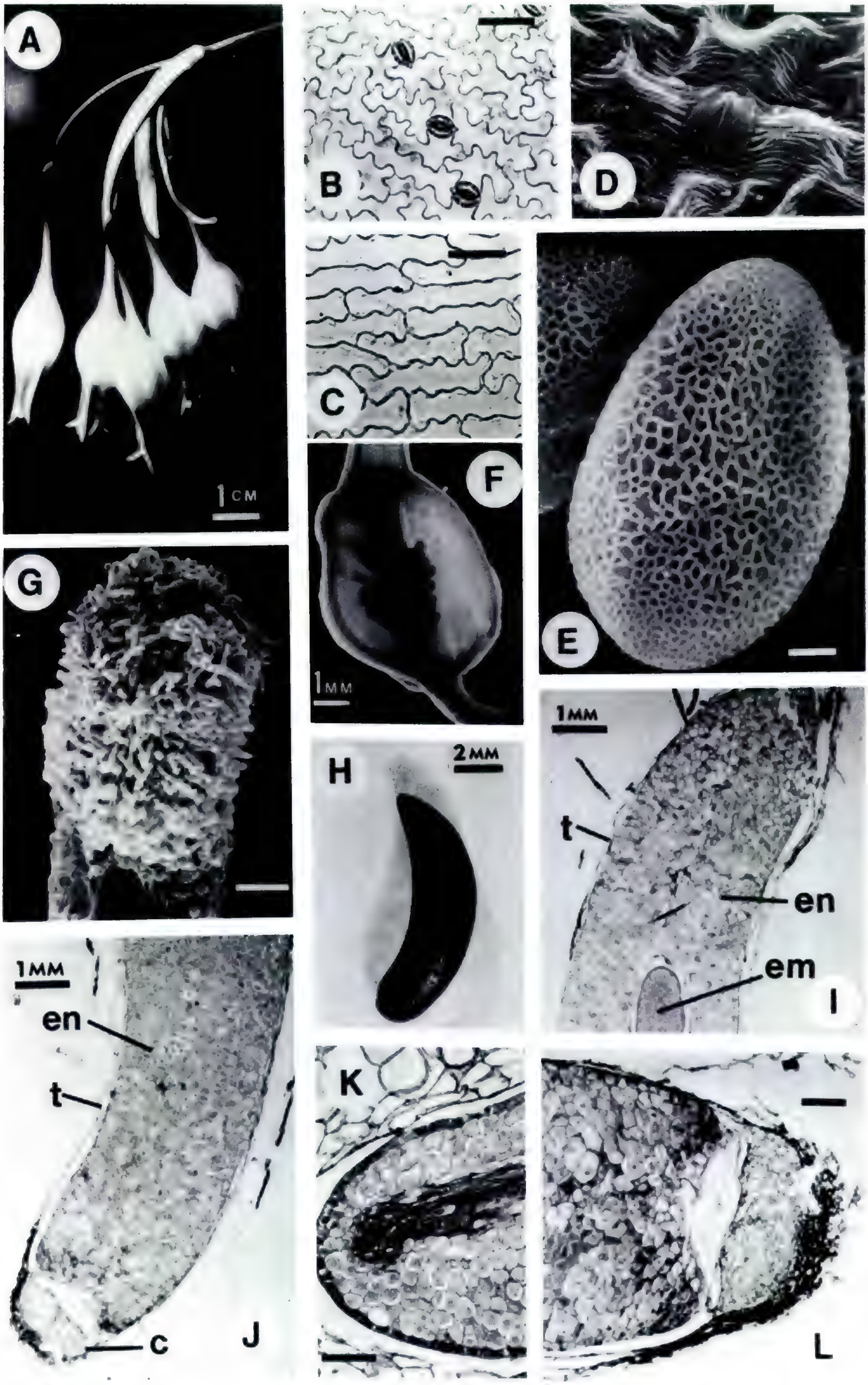


FIGURE 63. Character states of *Urceolina*. All photos are *U. microcrater* Kränzl. (*Schunke 13633*, FLAS) unless otherwise stated.—A. Flowers (*Plowman & Kennedy 5721*, GH). Photo courtesy T. Plowman. B, C. Leaf epidermal cell configurations.—B. Abaxial surface.—C. Adaxial surface.—D. SEM photomicrograph of abaxial leaf surface.—

in the family, by Nordal & Duncan (1984) for *Haemanthus* L. and *Scadoxus* Raf., two closely related, baccate-fruited African genera; and Meerow (1987c) for *Eucrosia* Ker Gawler. The generic limits of *Eucharis* and *Caliphruria* in relation to *Urceolina*, as well as interspecific relationships in the former genera, seemed two areas that would benefit from the application of cladistic analysis. Before assessing these relationships cladistically, a brief review of character states in *Urceolina* is necessary.

Urceolina (ca. 6–8 species; Fig. 63) is so far known only from central and southern Peru on the eastern Andean slopes (Fig. 64) at elevations of 700–2,000 m. The relationships of *Urceolina* have long been misunderstood, most workers (Baker, 1888; Pax, 1888; Hutchinson, 1959) placing *Urceolina* near *Stenomesson* Herbert. Traub (1957) was the first to recognize its affinities with *Eucharis*. The problem no doubt stemmed from the inclusion of a species of *Stenomesson* (*S. miniatum* (Herbert) Ravenna) in *Urceolina* as *U. miniata* (Herbert) Benth. & Hook. Despite the ventricose aspect of the corolla morphology of *S. miniatum*, which is similar to that of *Urceolina*, the species clearly belongs to *Stenomesson* as evidenced by its narrow, subpetiolate leaves, the morphology of its staminal cup, and its numerous flat, black seeds (Ravenna, 1978).

Urceolina is easily distinguished by its brightly colored, urceolate corolla formed by the coherence of the tepals throughout most of their length (Fig. 63A). Vargas (1960) described the genus *Pseudourceolina* to accommodate a species of *Urceolina* in which the tepals are supposedly more laxly coherent. The morphology of the flower in *Urceolina* strongly suggests ornithophily (sensu Faegri & van der Pijl, 1979), i.e., vivid, "parrot" colors, ventricose corolla, pendulous habit, and absence of odor. As in *Caliphruria*, the staminal cup of *Urceolina* is reduced to a minute, membranous, basal connation of the filaments, which are otherwise linear throughout their length. The leaves of *Urceolina*, in thickness and lack of both surface plication and marginal undulation, resemble *Caliphruria* more closely than *Eucharis*. At least one species is hysteranthous (*U. microcrater* Kränzlin), but all species enter a leafless dormant period in the wild. In size the pollen grains of *Urceolina* (Fig. 63E) are similar to those of *Caliphruria*. The coarseness of the reticulum is intermediate between that of *Eucharis* and *Caliphruria*. In all species of *Urceolina* the small stigma is capitate and entire (Fig. 63G) versus the trilobed stigma found in *Eucharis* and *Caliphruria*. *Urceolina* species have 10–20 ovules. The ripe fruit of *Urceolina* is a thin-walled, yellow-green, turbinate capsule. The seeds of *U. microcrater* (Fig. 63H) are narrowly oblong, ca. 8 mm long, and 2.5 mm wide, and curved. The seeds have a unique anatomical feature: at the chalazal end, a dam of poorly differentiated tissue separates a "cap" composed of many small cells from the endosperm (Fig. 63J, L). The cells of the "cap" do not have pitted walls with plasmodesmata as is characteristic of the endosperm cells. There is no obvious surface feature on the seed corresponding to the area of this "cap," and its function is unknown.

Outgroup selection. Preliminary cladistic analyses of the pancratioid Amaryllidaceae (Meerow, 1985) indicate that within the Pancratioidinae, a large, white, fragrant, crateriform flower with a conspicuous staminal cup ("pancratioid," cf. *Pancratium* L.), involved with sphingid moth pollination (Bauml, 1979; Grant, 1983; Morton, 1965), may be symplesiomorphous. In other words, while the pancratioid flower was a major apomorphy defining the Pancratioidinae as a distinct group within the Amaryllidaceae, it is the ancestral floral morphology from which all other pancratioid taxa have diverged. I have used the term "the pancratioid base" to define the five genera of Pancratioidinae with this type of flower morphology (Meerow, 1985). These five genera are *Eucharis*, *Hymenocallis*, *Pancratium*, *Pamianthe* Stapf, and *Paramongaia* Velarde. All but *Pancratium* are entirely neotropical in distribution. The pancratioid flower correlates repeatedly with the largest pollen grain size within the Pancratioidinae (Meerow, 1985; Meerow & Dehgan, 1985). Putatively basal complexes within each pancratioid lineage also have numerous ovules per locule (ca. 20 or more), a character state considered primitive in the Amaryllidaceae (Traub, 1963).

Pollen morphology provides the best evidence for the monophyly of the Pancratioidinae. The large pollen grains of most species of the pancratioid base are uniformly coarsely reticulate, with some in each genus exhibiting a striking exine

←

E. SEM photomicrograph of *U. urceolata* pollen grain (*Weberbauer 7822*, US), proximal polar view.—F. Ovary.—G. SEM photomicrograph of stigma.—H. Seed. I–L. Longitudinal transverse sections of seed. em = embryo, en = endosperm, t = testa, c = cap.—I. Micropylar end of seed.—J. Chalazal end of seed.—K. Apex of embryo.—L. Internal chalazal "cap." Scale bars B, C, G, K = 100 μm; D = 25 μm; E = 5 μm; L = 200 μm.

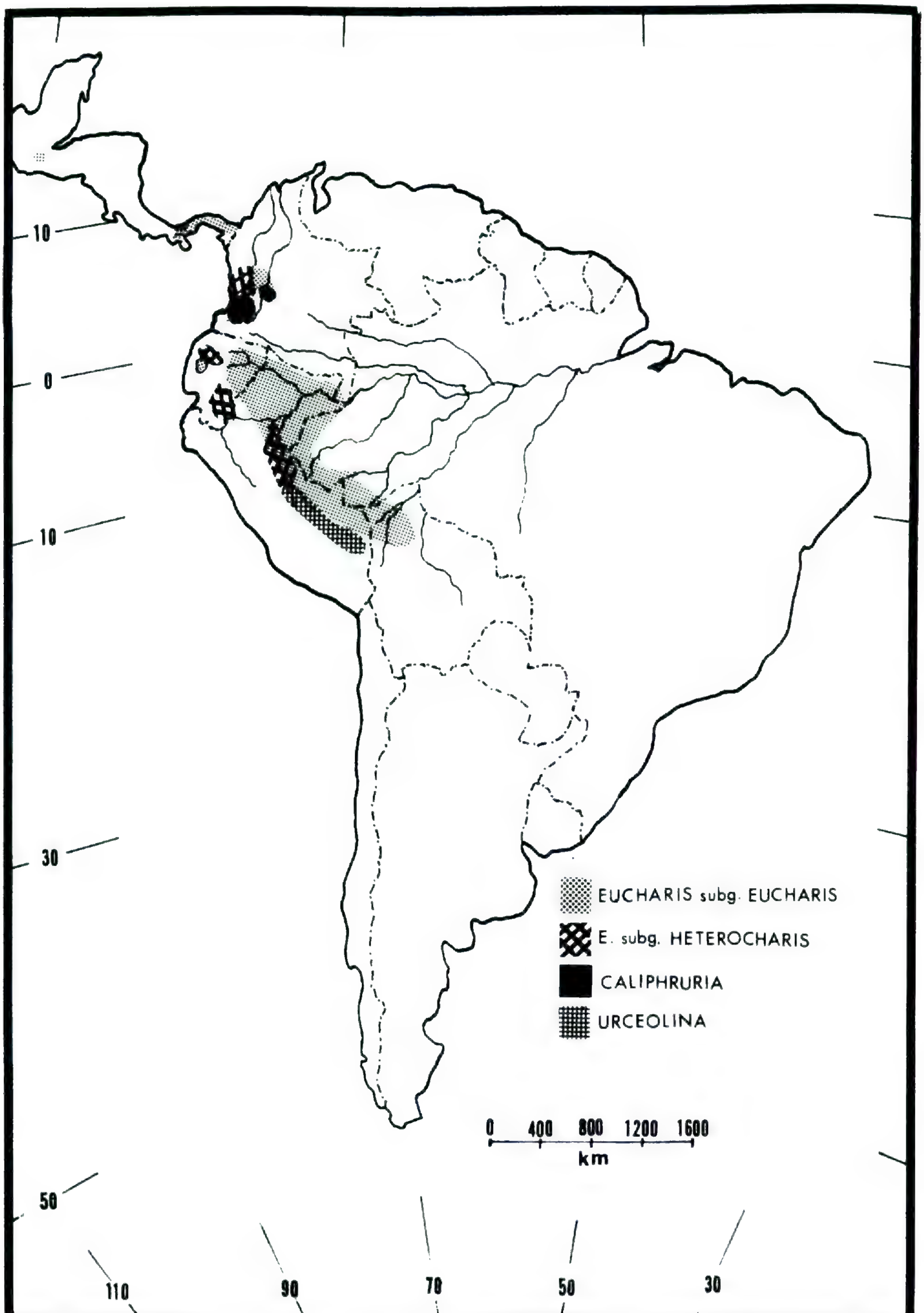


FIGURE 64. Generalized distributions of *Eucharis*, *Caliphruria*, and *Urceolina* in Central and South America.

dimorphism at the equatorial ends of the grain (Meerow, 1985; Meerow & Dehgan, 1985). Nonetheless, separate origins of the pancratioid flower in the Neo- and Paleotropics cannot be ruled out.

That the neotropical tribes of the Pancratioidinae represent a monophyletic group is a much more robust hypothesis. All neotropical pancratioid genera have $2n = 46$ as the most common somatic chromosome number (Di Fulvio, 1973; Flory, 1977; Meerow, 1985, 1987a, c; Williams, 1981). This number may be derived from $2n = 22$, the most common somatic chromosome number in the family

TABLE 1. List of EUs and label designations for cladistic analysis of *Eucharis* and *Caliphruria*. * = outgroup.

Taxon	Designation
Eucharis amazonica Linden ex Planchon	AMA
E. astrophiala (Ravenna) Ravenna	AST
E. bakeriana N. E. Brown	BAK
E. bonplandii (Kunth) Traub	BON
E. bouchei Woodson & Allen	BOU
E. candida Planchon & Linden	CAN
E. castelnaeana (Baillon) Macbride	CAS
E. caucana Meerow	CAU
E. corynandra (Ravenna) Ravenna	COR
E. cyaneosperma Meerow	CYA
E. formosa Meerow	FOR
E. lehmannii Regel	LEH
E. moorei (Baker) Meerow	MOO
E. oxyandra (Ravenna) Ravenna	OXY
E. plicata subsp. *brevidentata* Meerow	PLI-B
E. plicata Meerow subsp. *plicata*	PLI-P
E. sanderi Baker	SAN
E. ulei Kränzlin	ULE
Caliphruria hartwegiana Herbert	HAR
C. korsakoffii (Traub) Meerow	KOR
C. subedentata Baker	SUB
C. tenera Baker	TEN
**Pancratium* L.	PAN
Urceolina Reichb.	URC
Lepidochiton Sealy (*Hymenocallis quitoensis* & *H. heliantha*)	LEP

(Flory, 1977; Goldblatt, 1976; Meerow, 1984) via duplication or fragmentation of a chromosome, followed by doubling of the genome (Lakshmi, 1978; Sato, 1938). All paleotropical pancratioid genera have 22 or 20 chromosomes (Ponnamma, 1978; Zaman & Chakraborty, 1974).

Pancratium (ca. 17 species) and two species of *Hymenocallis* (*H. quitoensis* Herbert and *H. heliantha* Ravenna) were used as the primary outgroups in the analyses presented. Character state data on these taxa were accumulated from study of living material, herbarium specimens and literature (Björnstad, 1973; Meerow & Dehgan, 1985; Morton, 1965; Ponnamma, 1978; Ravenna, 1980; Traub, 1962; Werker & Fahn, 1975). *Pancratium* is putatively the least derived genus of the pancratioid base (Meerow, 1985). It is the only paleotropical genus of the group, and the only member with $2n = 22$ (Ponnamma, 1978), considered by most workers as the ancestral somatic chromosome number in the family (Flory, 1977; Goldblatt, 1976; Meerow, 1984).

The two species of *Hymenocallis* are undoubtedly a monophyletic group. They are the only two

TABLE 2. Characters, character states, and transformation series for cladistic analysis of *Eucharis* and *Caliphruria*. * = unordered multistate character. A linear transformation series is implied for all ordered multistate characters except 41.

1. Leaves: 0, linear or lorate, sessile; 1, petiolate. **2*.** Leaves: 0, deciduous; 1, deciduous and hysteranthous; 2, persistent. **3.** Leaves: 0, plicate; 1, smooth. **4.** Leaf margins: 0, nonundulate; 1, undulate. **5.** Petiolar secondary bundles: 0, absent; 1, present. **6.** Abaxial cuticular striations: 0, absent or nearly so; 1, dense, well developed. **7.** Epidermal cell anticlinal walls: 0, more or less straight; 1, undulate. **8.** Flowers: 0, more than 7 cm long; 1, 5–7 cm long; 2, less than 5 cm long. **9.** Floral fragrance: 0, heavy; 1, mild; 2, absent. **10.** Flower number: 0, more than 5; 1, ca. 5; 2, less than 5. **11*.** Flower color: 0, white; 1, white or yellow; 2, yellow or orange. **12*.** Flower habit: 0, erect or suberect; 1, declinate or pendent by curving of tube; 2, declinate or pendent by laxness of pedicel. **13.** Pedicel length: 0, flower (sub)sessile; 1, less than 0.5 cm; 2, greater than 0.5 cm long. **14.** Tube habit: 0, straight; 1, curved. **15.** Tube length: 0, longer than tepals; 1, equal to or shorter than tepals. **16.** Tube color: 0, green; 1, concolorous with tepals. **17*.** Tube morphology: 0, cylindrical proximally, dilating at ½–⅓ of its length; 1, funnelform, dilating gradually from the base; 2, cylindrical for most of its length, dilating abruptly near the throat. **18*.** Perianth morphology: 0, crateriform; 1, campanulate; 2, funnelform; 3, urecolate. **19.** Staminal cup: 0, well developed; 1, reduced. **20.** Androecial pigmentation: 0, present; 1, absent. **21.** Staminal cup: 0, nonplicate; 1, plicate. **22.** Staminal cup: 0, shallowly cleft between stamens (< 2 mm); 1, deeply cleft (> 2 mm). **23.** Free filament: 0, linear (< 1 mm wide); 1, subulate (> 1 mm wide). **24.** Staminal dentation: 0, present; 1, polymorphic; 2, absent. **25.** Staminal teeth: 0, shorter than free filament; 1, more or less equal to free filament; 2, longer than free filament. **26.** Anthers: 0, versatile at anthesis; 1, erect at anthesis. **27.** Pollen longest equatorial diameter: 0, greater than 80 μm; 1, 76–80 μm; 2, 66–75 μm; 3, 60–65 μm; 4, 50–59 μm. **28.** Pollen exine reticulation: 0, coarse; 1, moderately coarse; 2, fine. **29.** Exine dimorphism: 0, present; 1, absent. **30.** Style exserted: 0, greater than 1 cm beyond anthers; 1, 1 cm or less beyond anthers, but above the rim of the staminal cup; 2, to or below the rim of the staminal cup. **31.** Stigma: 0, trilobed; 1, capitate, entire. **32.** Stigmatic papillae: 0, unicellular; 1, multicellular. **33.** Ovary color: 0, green; 1, white. **34.** Ovary: 0, rostellate; 1, not rostellate. **35.** Ovule number (per locule): 0, 10–20; 1, 7–10; 2, 3–6; 3, 2–3. **36.** Ripe capsule: 0, green, relatively thin-walled; 1, leathery, thick-walled, orange. **37*.** Seeds: 0, compressed; 1, globose or ellipsoid; 2, narrowly oblong, curved. **38*.** Testa: 0, black; 1, blue; 2, brown. **39.** Testa: 0, dull; 1, lustrous. **40.** Testa: 0, smooth; 1, rugose. **41.** Somatic chromosome number: A (00000), 22; B (10000), 34; C (01000), 46; D (01010), 68; E (01100), 92; F (01101), 138. A → B, A → C → D, C → E, E → F.

TABLE 3. Character state matrix for cladistic analysis of *Eucharis* and *Caliphruria*. Refer to Table 1 for key to EU abbreviations, to Table 2 for characters. 9 = missing or inapplicable character state data. * = outgroup.

	Character																				
EU	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
AMA	1	2	0	1	1	0	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0
MOO	1	2	0	1	1	0	0	0	0	1	0	1	1	1	0	0	0	2	0	0	0
SAN	1	2	1	1	0	1	1	0	0	2	0	1	1	1	0	0	0	2	1	0	9
AST	1	2	1	1	0	1	1	2	2	1	0	1	2	1	0	1	2	0	0	0	0
BAK	1	2	0	0	0	1	1	1	1	0	0	1	2	1	0	1	2	0	0	0	1
BON	1	2	0	0	0	1	1	1	2	1	0	1	2	1	0	1	2	0	0	0	0
BOU	1	2	0	0	0	0	1	1	2	1	0	1	1	1	0	1	2	0	0	0	0
CAN	1	2	1	1	0	1	1	1	2	0	0	1	2	1	0	1	2	0	0	0	0
CAS	1	2	1	1	0	1	1	2	1	0	0	1	2	1	0	1	2	0	0	0	1
CAU	1	2	1	1	0	1	1	1	2	2	0	1	1	1	0	1	0	1	1	0	9
COR	1	2	9	9	0	9	9	2	9	0	0	1	2	1	0	1	2	0	0	9	1
CYA	1	2	1	1	0	1	1	1	2	1	0	1	2	1	0	1	2	0	0	0	0
FOR	1	2	1	1	0	1	1	1	1	0	0	1	2	1	0	1	2	0	0	0	0
LEH	1	2	9	9	0	9	9	1	0	1	0	1	2	1	0	9	2	0	0	9	9
OXY	1	2	9	9	0	9	9	2	9	0	0	1	2	1	0	9	2	9	1	9	9
PLI-P	1	2	0	1	0	1	1	2	2	0	0	1	2	1	0	1	2	0	0	0	1
PLI-B	1	2	0	1	0	1	1	2	1	0	0	1	2	1	0	1	2	0	0	0	1
ULE	1	2	1	1	0	1	1	1	2	1	0	1	2	1	0	1	2	0	0	0	0
HAR	1	2	0	0	0	9	9	2	2	0	0	2	2	0	0	0	1	1	1	1	9
KOR	1	2	0	0	0	1	0	2	2	0	0	2	2	0	1	0	1	1	1	1	9
SUB	1	2	0	0	0	1	1	2	2	0	0	2	2	0	0	0	1	1	1	1	9
TEN	1	1	9	9	0	9	9	2	2	0	0	2	2	0	1	9	1	1	1	1	9
URC	1	1	0	0	0	1	1	1	2	0	2	2	2	0	0	1	2	3	1	1	9
LEP	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0
PAN*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

species of *Hymenocallis* with phytomelanous seed coats. All evidence suggests that possession of phytomelan is the ancestral condition in the Amaryllidaceae, and despite several independent losses, no reversal to the ancestral state has been proposed (Dahlgren & Clifford, 1982; Dahlgren & Rasmussen, 1983; Dahlgren et al., 1985; Huber, 1969). *Hymenocallis quitoensis* was segregated into a separate genus, *Lepidochiton* Sealy (1937) on the basis of phytomelanous seed. Both *H. quitoensis* and *H. heliantha* are ephemeral components of the xeric flora of southwestern Ecuador and northwestern Peru, and differ only in flower color. Traub (1962) considered *H. quitoensis* a relict and the most primitive species of *Hymenocallis* on the basis of ovule number (ca. 20 per locule; 2–10 occurs in all other species) and chromosome number ($2n = 24$, based on Snoad, 1952); however, collections from Peru and Ecuador that I have examined have $2n = 34$. These are the lowest reported chromosome numbers in the genus (Flory, 1976). These species will be called *Lepidochiton* in the following discussion. Additional analyses were run using other members of the pancratioid base as outgroups (*Hymenocallis* subg. *Hymenocallis*, *H.* subg. *Ismene* (Salisb.) Baker ex Traub, *Pamianthe*, and *Paramongaia*). The resulting cladograms were either equal in length or slightly less parsimonious than those presented here; they did not show changes in the resolution of terminal taxa from the cladograms presented.

Ordered characters. Ten of the 18 multistate characters (Table 2) used in these analyses (8, 9, 10, 13, 24, 25, 27, 28, 30, and 35) were ordered into linear transformation series. Study of character state correlations among all genera of the pancratioid Amaryllidaceae (Meerow, 1985, 1987a, c) strongly suggests that flower size reduction (8), loss of floral fragrance (9), flower number (10), pedicel length (13), staminal tooth length (25), style length (30), and reduction in ovule number (35) have evolved in this stepwise manner with no evidence of reversal. Numerous ovules per locule (20 or more) characterizes all basal genera of the pancratioid Amaryllidaceae and is generally considered the ancestral condition for the family (Traub, 1962, 1963; Traub & Moldenke, 1949). Though the

TABLE 3. Continued.

Character																			
22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	9	0	9	9	01010
0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	1	2	0	1	01000
9	0	2	9	0	3	0	0	0	0	0	0	0	0	9	9	9	9	9	99999
1	1	2	9	1	0	0	1	1	0	0	1	1	3	1	1	0	1	0	01000
0	1	0	0	1	1	0	1	1	0	0	0	1	1	1	1	0	1	0	01000
1	1	0	0	1	3	0	1	1	0	0	0	1	3	1	1	0	1	0	01100
1	1	1	1	1	2	0	1	0	0	0	0	1	3	1	1	0	1	0	01100
1	1	1	0	1	2	0	1	1	0	0	0	1	2	1	1	0	1	0	01000
0	1	0	0	1	4	0	1	2	0	0	1	1	2	0	0	0	0	1	01000
9	1	2	9	1	0	0	1	1	0	0	0	1	2	1	1	0	1	0	01011
0	1	0	0	1	9	0	1	1	0	0	9	1	2	9	9	9	9	9	99999
1	1	1	0	1	2	0	1	1	0	0	0	1	3	1	1	1	1	0	01000
1	1	1	0	1	2	0	1	1	0	0	0	1	1	1	1	0	1	0	01000
1	0	0	1	1	9	9	9	1	0	0	9	9	1	9	9	9	9	9	99999
9	0	1	0	1	2	1	0	1	0	0	9	1	1	9	9	9	9	9	99999
0	1	0	2	1	2	0	1	2	0	0	0	1	1	1	1	0	1	0	01000
0	1	0	1	1	3	0	1	2	0	0	0	1	2	1	1	0	1	0	01000
1	1	1	0	1	2	0	1	1	0	0	0	1	3	1	1	0	1	0	01000
9	0	0	1	1	4	2	1	1	0	1	0	1	3	0	9	9	9	9	99999
9	0	2	9	1	4	1	0	1	0	1	0	1	2	0	1	2	0	0	01000
9	0	2	9	1	4	2	1	1	0	1	0	1	2	0	0	0	0	1	01000
9	0	0	2	1	4	2	1	1	0	1	0	1	3	0	9	9	9	9	99999
9	0	0	0	0	4	1	0	0	1	0	0	1	0	0	2	0	1	0	01000
0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	0	0	10000
0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	00000

evidence from phenetic studies of *Eucharis* (Meerow, 1987d, in press) and from study of other genera of the pancratioid Amaryllidaceae (e.g., Meerow, 1987c) indicates that androecial characters are among the most plastic morphological characters in this group, examination of the evolutionary patterns of staminal dentation (24) within various genera (Meerow, 1987c, in press) suggests that a reversal to the dentate state is unlikely once dentation is lost completely. Complete loss of staminal dentation often accompanies overall phenetic divergence among the pancratioid genera (Meerow, 1985, 1987c; see *E. astrophiala* in this paper). Polymorphism for the character is not uncommon, however, and is conceived in the transformation series as the intermediate between the two fixed states of toothed or edentate stamens. Ordering of pollen size (27) and exine morphology (28) is based on data presented in Meerow (1985, 1987c) and Meerow & Dehgan (1985), as well as unpublished palynological data accumulated for many genera in the family. A single character, chromosome number (41), was coded in additive binary on the basis of much literature on amaryllid cytology (Flory, 1976, 1977; Goldblatt, 1976; Lakshmi, 1978; Meerow, 1984, 1987b; Ponnamma, 1978; Sato, 1938; Snoad, 1952), which strongly supports this concept of chromosome number evolution.

Results and discussion. Twelve most parsimonious trees without any differences in topology resulted when either *Pancratium* or *Lepidochiton* was used as the outgroup. The twelve trees differed only in the branch lengths of a few internal nodes, and resolution of terminal taxa did not change among them. One of the twelve with *Pancratium* used as outgroup is illustrated and discussed in detail (Fig. 65). The cladogram has a length of 92.4 steps (fractional lengths are a result of weight scaling), and a consistency index (CI; Kluge & Farris, 1969) of 0.487. *Lepidochiton* is the first terminal EU to resolve in the cladogram after the outgroup, *Pancratium*. Character state changes from the outgroup to the ancestral node of *Lepidochiton* (flower number reduction, globose seeds) could not be polarized. Uniflory, perianth color polymorphism, brown seed testa, and $2n = 34$ are the four apomorphies of *Lepidochiton*. The next internal node of the cladogram is the hypothetical ancestor to *Eucharis*, *Caliphruria*, and *Urceolina*,

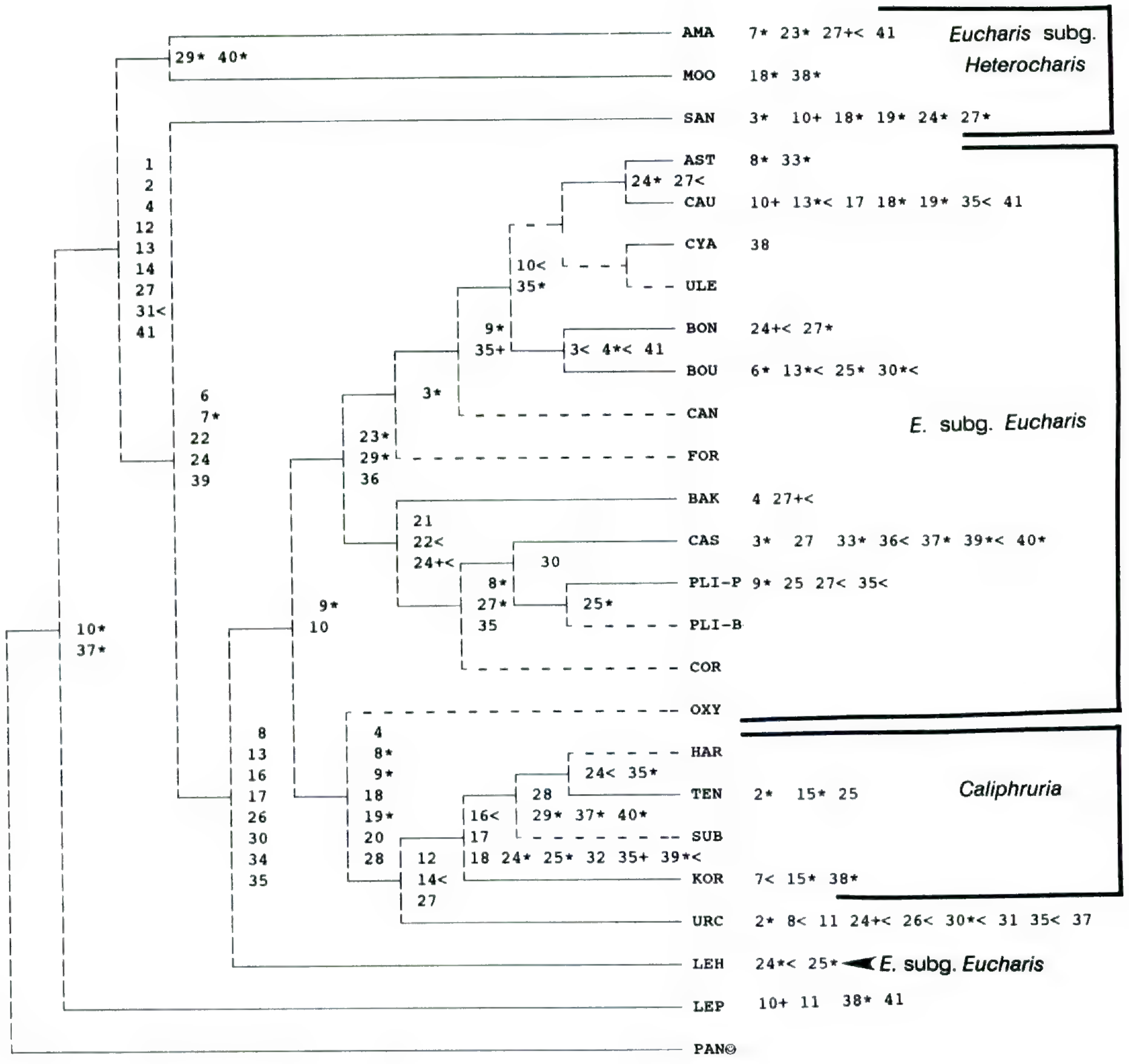


FIGURE 65. Cladogram of *Eucharis* and *Caliphruria*, based on data matrix in Table 3. Broken horizontal line indicates zero-length branch. Numbers inside refer to apomorphies of adjacent EU or internal node. Refer to Table 1 for EU designations.

all of which thus form a monophyletic group. Nine apomorphies occur at this node. The most important are the evolution and fixation of the evergreen, petiolate leaf; the changes in flower habit, pedicel length, tube morphology, and pollen size; trilobed stigmas; and increased chromosome number.

The rest of the cladogram forms two monophyletic groups. The smaller group represents part of my concept of subg. *Heterocharis*, *E. amazonica* and *E. moorei*, linked by three apomorphies: secondary petiolar bundles, loss of pollen exine dimorphism, and rugose testa (the state for the last-mentioned character is unknown for *E. amazonica*). The larger monophyletic group represents *E. sanderi*, *Eucharis* subg. *Eucharis*, *Caliphruria*, and *Urceolina*. Five apomorphies define the ancestral node: densely striate abaxial cuticle, undulate anticlinal walls (homoplasious with *E. amazonica*), deeply cleft staminal cup, polymorphism in staminal dentation, and lustrous testa. It is thus obvious that subg. *Heterocharis* is paraphyletic according to this cladogram. *Eucharis moorei* and *E. amazonica* also resolve cladistically as the most basal species of *Eucharis*.

Eucharis sanderi is cladistically basal to the remaining EUs with which it forms a monophyletic

group. The six apomorphies of *E. sanderi* are plicate leaves, reduction in flower number, campanulate perianth (homoplasious with *E. moorei*), reduced staminal cup, loss of staminal dentation, and yet further reduced pollen grain size.

The next monophyletic group is supported by eight apomorphies and comprises *Eucharis* subg. *Eucharis*, *Caliphruria*, and *Urceolina*. Apomorphies at the ancestral node are reduced flower size, increased pedicel length, loss of green tube pigmentation, change in tube dilation, erect anthers, decreased style exsertion, nonrostellate ovary, and decreased ovule number. *Eucharis lehmannii* is cladistically basal to the remaining EUs in the cladogram and is defined by two apomorphies: a reversal to dentate stamens and an increase in the length of the teeth. The remainder of the cladogram forms two monophyletic groups. All but two species of *Eucharis* subg. *Eucharis* comprise one, and *Caliphruria*, *Urceolina*, and *E. oxyandra* constitute the second. Only two apomorphies define this clade: reduction in floral fragrance and an increase in flower number.

The three apomorphies at the ancestral node of the *Eucharis* subg. *Eucharis* clade are subulate free filaments (homoplasious with *E. amazonica*), loss of exine dimorphism (homoplasious with the ancestor of *E. amazonica* and *E. moorei*), and an orange capsule. Within this clade, two monophyletic groups are evident. The larger of the two is defined by a single apomorphy, plicate leaves. *Eucharis formosa* is the first terminal EU to resolve but terminates a zero-length branch. *Eucharis candida* also terminates a zero-length branch, the ancestral node of which is defined by two apomorphies: loss of floral fragrance and reduction in ovule number. The next monophyletic group encompasses all species of subg. *Eucharis* with about five flowers and about two ovules per locule. The hypothetical ancestor of *Eucharis astrophiala* and *E. caucana* forms an unresolved polytomy at the ancestral node with *E. cyaneosperma*, *E. ulei*, and the hypothetical ancestor of tetraploid species *E. bonplandii* and *E. bouchei*.

Three apomorphies define the ancestral node of the second clade within subg. *Eucharis*: a plicate staminal cup, a reversal to shallowly cleft staminal cups, and a reversal from polymorphism in staminal dentation to fixed dentation. *Eucharis bakeriana* is the first terminal EU to resolve, on the basis of two apomorphies: loss of leaf margin undulation and increase in pollen size. The remaining species are the smallest-flowered species in the subgenus. The remaining apomorphies at the ancestral node are a decrease in pollen size and ovule number. The first terminal EU to resolve is *E. corynandra*, from a zero-length branch. It should be noted, however, that two autapomorphies of this species, a short staminal cup and club-shaped free filaments, were not included in the data matrix. The ancestor of the two subspecies of *E. plicata* form a monophyletic group with *E. castelnaeana* on the basis of style length. Subspecies *brevidentata* terminates a zero-length branch. *Eucharis castelnaeana* has the greatest patristic distance of the three EUs (seven apomorphies).

The final large clade constitutes *Caliphruria*, *Urceolina*, and the cladistically basal *E. oxyandra*. Apomorphies are nonundulate leaf margins, small flowers, loss of floral fragrance, urceolate corolla (which does not apply to *E. oxyandra*, the corolla shape of which is either crateriform or campanulate but could not be coded as one or the other with certainty), reduction of the staminal cup, loss of androecial pigmentation, and moderately coarse exine. The character state of *E. oxyandra* is unknown for four of these seven. Within this monophyletic group, *Urceolina* and the hypothetical ancestor of *Caliphruria* resolve as sister groups on the basis of three apomorphies: declinate or pendent flowers via pedicel habit, straight tubes, and small pollen grains. Nine and eight apomorphies define *Urceolina* and the hypothetical ancestor of *Caliphruria*, respectively. Within *Caliphruria*, the sole representative of the genus outside Colombia, *C. korsakoffii* is the first terminal EU to resolve, on the basis of three apomorphies: straight anticlinal epidermal walls, short tubes (homoplasious with *C. tenera*), and brown testa. *Caliphruria subedentata* terminates a zero-length branch from the hypothetical ancestor of the Colombian species of the genus. Apomorphies at the ancestral node are finely reticulate exines, loss of exine dimorphism, compressed seeds, and rugose testa (the states for the last two characters are known only for *C. subedentata*). *Caliphruria hartwegiana* and *C. tenera* form a monophyletic group on the basis of toothed stamens and reduced ovule number, but *C. hartwegiana* terminates a zero-length branch.

The cladogram presented in Figure 65 contains 70 parallel origins of character states and 29 reversals (unordered characters not included). This may raise questions concerning the homology of characters that manifest low consistency. If the data matrix is analyzed with all characters removed that exhibit three or more independent origins for the same state (characters 3, 4, 8, 9, 10, 18, 19, 24, 25, 27, 29, 35, 37, 38, 40), the three trees that result have a fourfold increase in zero-length

branches and unresolved polytomies. Invariably, it is androecial characters (including pollen size) in which a great deal of homoplasy has occurred. Three of all the androecial characters, 24 (staminal dentation), 25 (length of teeth), and 27 (pollen size), are particularly homoplasious. When the data matrix was run with only these characters deleted, no change occurred in the resolution of terminal taxa from the cladogram in Figure 65. Finally, the data matrix was analyzed with all staminal cup characters (19, 20, 21, 22, 23, 24, 25), and pollen size (27) deleted. The resulting three cladograms (differing only by one internal branch length) placed *Caliphruria* and *Urceolina* within a monophyletic group including *E. bakeriana*, *E. bonplandii*, and *E. bouchei*, on the basis of a single apomorphy, nonundulate leaf margins.

Regardless of how the character-state data are manipulated, a number of monophyletic groups appear particularly robust. That *Eucharis*, *Caliphruria*, and *Urceolina* represent a monophyletic group is uncontested. The monophyly of *Eucharis moorei* and *E. amazonica* is also strongly supported, and these two species are the most cladistically basal of the eucharoid lineage. These species have the greatest number of putatively primitive characters and seem to represent the more ancestral species in the genus. Nonetheless, according to the cladogram in Figure 65, retaining subg. *Heterocharis* in *Eucharis* renders the genus paraphyletic. Subgenus *Heterocharis* is a fairly heterogeneous group from the perspective of apomorphic characters alone. Each of the three species may be characterized by autapomorphies, but only plesiomorphies join them. By including subg. *Heterocharis* in *Eucharis*, *Eucharis* becomes paraphyletic according to this cladogram. However, it should be noted that it is unknown whether secondary petiolar bundles (which require fresh material to observe), an important apomorphy which links *E. amazonica* and *E. moorei*, are present in *E. sanderi*. In the generalized sense, the distribution of subg. *Heterocharis* is quite broad, from Colombia to Peru (Fig. 64). However, each of the three species of subg. *Heterocharis* itself are only narrowly distributed. *Eucharis sanderi* is known only from the Chocó region of Colombia. *Eucharis amazonica* is found natively only in the middle Río Huallaga valley of Peru. *Eucharis moorei* has been collected outside of Ecuador only once. More significantly, *E. moorei* is the only species of *Eucharis* found on both sides of the Andes. I believe that all three species of subg. *Heterocharis* represent the relictual remnants of the ancestral eucharoid complex, each of which has remained isolated long enough to evolve its respective cohort of autapomorphies.

The sister group relationship between *Urceolina* and *Caliphruria* also seems to be a robust cladistic hypothesis, with *E. oxyandra* potentially ancestral to both. *Eucharis oxyandra* is a taxonomically perplexing species in its characters of morphological intermediacy (androecium and pollen morphology) between *Eucharis* and *Urceolina*. it is known only from bulbs found in local, transient cultivation in Peru, near the single recorded point of geographic sympatry between *Eucharis* (*E. amazonica*) and *Urceolina* (*U. microcrater*). The absence of much character state data, but particularly those on fruit and seed morphology, further occludes resolution of its phylogeny, and any of several hypotheses concerning its origins are possible (see Taxonomic Treatment). *Eucharis lehmannii*, which usually resolves within a cladistic "no man's land" between paraphyletic subg. *Heterocharis* and all other clades, presents a similar problem, though Regel's (1889) figure strongly suggests affinity to subg. *Eucharis*. In the initial analyses, in which all multistate characters were treated as unordered, this poorly known species resolved as sister group to *E. bouchei*. I believe that *E. lehmannii* is a sister species to *E. caucana*, to which it bears much phenetic resemblance, and that its unusual resolution in the cladogram is a result of the great deal of missing character state data. Fruit and seed morphology clearly place *E. caucana* in subg. *Eucharis*, even though it shows as much novelty as *E. oxyandra* or *E. lehmannii* in other characters.

Excluding *E. lehmannii* and *E. oxyandra*, *Eucharis* subg. *Eucharis* forms another clearly monophyletic group. Species with five flowers and two ovules per locule (*E. astrophiala*, *E. cyaneosperma*, *E. ulei*, along with the tetraploids, *E. bonplandii* and *E. bouchei*) form a very natural group with karyotypic similarity as well (Meerow, 1987b). The sister species relationship of *Eucharis caucana* to *E. astrophiala* within this group may be as equivocal as the basal resolution of *E. lehmannii*, since it is based on two apomorphies (pollen size and lack of staminal dentation), the latter of which is highly homoplasious. I believe the reversal in ovule number necessary for *E. caucana* to share common ancestry with *E. astrophiala* is very unlikely.

Eucharis candida and *E. formosa*, two often sympatric (and possibly sibling) species, are cladistically close and basal to the five-flowered clade. The small-flowered species (*E. castelnaeana*, *E. corynandra*, and *E. plicata*) form another very

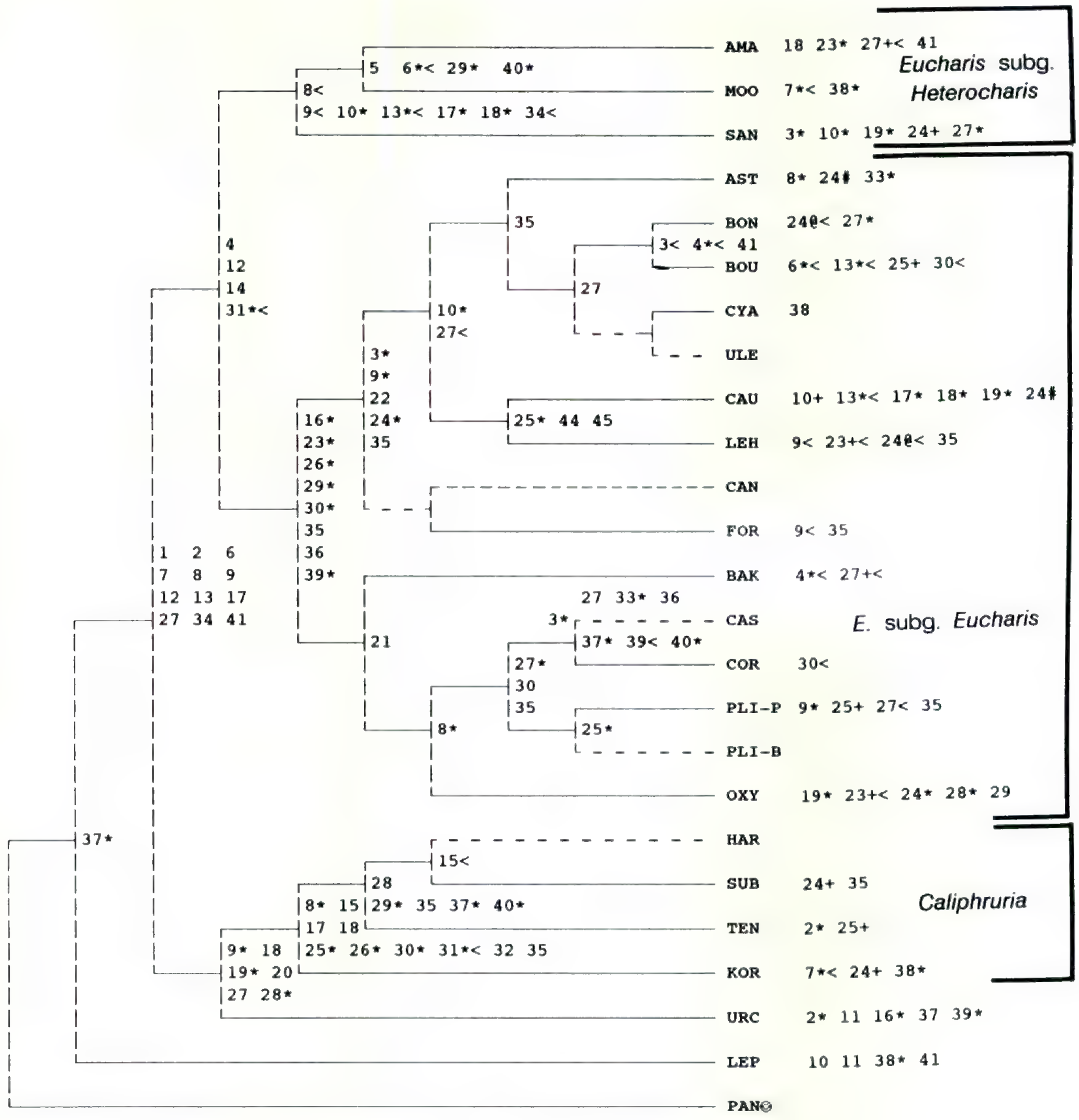


FIGURE 66. User-generated cladogram of *Eucharis* and *Caliphruria*. Broken horizontal line indicates zero-length branch. Numbers inside refer to apomorphies of adjacent EU or internal node. Refer to Table 1 for EU designations.

natural group. The position of *E. bakeriana* as basal to this clade, largely on the basis of a plicate staminal cup, may be equivocal. Karyotype analysis (Meerow, 1987b) suggests putative relationship of *E. bakeriana* to *E. formosa*.

An alternative hypothesis of phylogenetic relationship is presented in Figure 66. The cladogram is a user-generated tree in which *Caliphruria* and *Urceolina* are placed as sister groups to a monophyletic *Eucharis*. The topology of subg. *Eucharis* in this cladogram represents my concepts of their evolutionary relationships based on phenetic resemblance, phytogeography, and chromosome data. The major differences from the cladogram in Figure 65 are the sister species relationship of *E. caucana* and *E. lehmannii*, the ancestral node of which forms a monophyletic group with the five-flowered, two-ovuled species complex; and the positioning of *E. oxyandra* as part of the small-flowered species group of subg. *Eucharis*. This user-generated cladogram had a length of 100.6 steps, with a CI of 0.443. There are 82 parallelisms represented among the character state changes, and 29 reversals. The user-generated tree (Fig. 66) is thus somewhat less parsimonious than the cladogram in Figure 65. Of particular interest in the user-gen-

erated cladogram is the resolution of the larger monophyletic groups constituting genera or subgenera, and the accompanying character state changes within these clades.

In Figure 66, a monophyletic subg. *Heterocharis* is supported by seven apomorphies, four of which are reversals (unordered characters not counted). Some of these reversals are very unlikely (e.g., reversal to larger, heavily fragrant flowers; see previous discussion of ordered characters) and would thus represent retention of ancestral states.

In the user-generated tree, a monophyletic subg. *Eucharis* is supported by a greater number of apomorphies (eight in Fig. 66) than in the parsimony cladogram (three). *Caliphruria* as a monophyletic group is best supported by Figure 66 (ten apomorphies) versus eight in Figure 65.

The results of these various cladistic treatments illuminate the problems inherent in phylogenetic reconstruction of large, "messy" character state data sets, and particularly with taxa whose evolution has involved large-scale homoplasy. The user-generated cladogram in Figure 66 represents my preferred hypothesis of phylogeny within the *Eucharideae*; nonetheless I cannot deny the compelling evidence that *Eucharis*, by the inclusion of subg. *Heterocharis*, may be paraphyletic.

From an orthodox cladistic perspective (Wiley, 1981), Traub's (1971) concept of a single polymorphic genus, *Urceolina*, is supported by the criterion of parsimony. From a phenetic (and pragmatic) standpoint, I find this unsatisfactory due to the close phenetic relationship between subg. *Heterocharis* and *Eucharis*. This relationship is most conspicuous if one compares *Eucharis bakeriana* and *E. formosa* (the most basal species of subg. *Eucharis*) with *E. amazonica* and *E. moorei* (subg. *Heterocharis*). I prefer to recognize *Urceolina* and *Caliphruria* as distinct genera, despite the attendant risk of a paraphyletic *Eucharis*. I do not believe that *Urceolina* and *Caliphruria* necessarily share an immediate common ancestor—the three apomorphies that define their sister group relationship in Figure 65 (reversal to straight tubes, flower habit, and smaller pollen grains) are homoplasious within the *Eucharideae* as well as in other tribes of the Pancratioidinae (Meerow, 1987c; Meerow & Dehgan, 1985). Until further data allow a more accurate understanding of their relationships, I also prefer to maintain *E. lehmannii* and *E. oxyandra* as species of *Eucharis* subg. *Eucharis*, allied with the small-flowered species with numerous ovules per locule. Without study of living material, and particularly knowledge of fruit characters, I am unwilling to declare *E. oxyandra* a sister taxon to *Urceolina* and *Caliphruria*.

Ashlock (1971, 1972, 1979, 1984) has repeatedly argued for the acceptance of paraphyletic groups in evolutionary systematic classifications. He defined two subclasses of monophyletic groups: holophyletic, which contain all descendents of the stem ancestor, and paraphyletic, those which do not. Ashlock (1979: 449) rejected "the automatic conversion of the cladogram into a classification." Meacham & Duncan (1987) have elaborated on the term "convexity," first proposed by Estabrook (1978), which attempts to resolve the concepts of monophyly, holophyly, and paraphyly. Meacham & Duncan concluded that Ashlock's (1979) advocation of overall evolutionary similarity as a component of classification schemes, rather than strict cladistic topology alone, is sound, and they discussed the mitigating factors surrounding cladistic methodology (e.g., uncertainty of character state polarities, the speculative nature of phylogenetic reconstructions, among others) which compromise a direct translation of cladogram into classification. A similar argument was recently articulated by Cronquist (1987). Donoghue & Cantino (1988) and Humphries & Chappill (1988) have responded vociferously to Cronquist's (1987) critique. Donoghue & Cantino (1988: 108) assail paraphyletic higher taxa as "artificial classes created by taxonomists who wish to emphasize phenetic 'gaps', and that formal recognition of such taxa conveys a misleading picture of common ancestry and character evolution."

The enormous amount of homoplasy evident within the highly canalized Amaryllidaceae creates great difficulty in phylogenetic reconstruction (Meerow, 1985, 1987c). In the analyses of *Eucharis* and related genera, missing character state data further weaken the argument for adopting ad hoc the most parsimonious phylogeny as the basis for classification. At present, I prefer to accept a less parsimonious phylogeny as represented by the user-generated topology in Figure 66 until such time as cladograms can be generated with consistency indices greater than 0.5. Towards this end, work is continuing with careful application of selected character weighting (Neff, 1986; Wheeler, 1986).

In three neotropical lineages of the Pancratioidinae, parallel trends in the evolution of floral morphology have occurred (Meerow, 1985, 1987c). In each case, taxa with smaller, tubular or ventricose, brightly colored flowers with reduced staminal connation, and without noticeable fragrance

have apparently diverged from taxa possessing a large, white, fragrant, crateriform flower with a staminal cup (Meerow, 1985, 1987c). Each lineage appears to be a monophyletic group on the basis of vegetative and ovarian morphology, as well as chromosome number (Meerow, 1985, 1987c; Traub, 1963). A similar pattern occurs in all three lineages: 1) floral morphology of "derived" taxa suggests an ornithophilous pollination syndrome, and 2) "derived" taxa are found, entirely or in part, at higher elevations than apparent ancestral taxa. *Eucharis* and *Urceolina*, as documented in this paper, present one such case. *Pseudostenomesson* Velarde, submerged by Traub (1980) into *Hymenocallis* as section *Artema*, presents a parallel situation within the *Hymenocallis* lineage (Meerow, 1985; Meerow & Dehgan, 1985). Tribe *Stenomesseae* contains two small genera, *Pamianthe* and *Paramongaia*, with ancestral floral morphology and contains a large genus, *Stenomesson*, with derived morphology (Meerow, 1987c). In the *Hymenocallis* and *Eucharis* lineages, the pancratioid floral morphology has radiated to a far greater extent than the putatively ornithophilous divergence (*Pseudostenomesson* and *Urceolina*, respectively). In the *Pamianthe–Paramongaia/Stenomesson* lineage, the derived genus, *Stenomesson* (35–40 species), has speciated to a greater degree than taxa with the ancestral pancratioid flower (*Pamianthe*: 2 species, *Paramongaia*: monotypic).

The high level of divergence in neotropical pancratioid tribes may be primarily a factor of two causes, 1) the uplift of the Andes in the Pliocene (van der Hammen, 1974, 1979), creating much opportunity for geographic isolation, and 2) greater genetic adaptability via tetraploidy to new ecological zones. The occurrence of rare hybridization in nature between the relict complex represented by *Eucharis* subg. *Heterocharis* and both *Caliphruria* (×*Calicharis butcheri*) and *Urceolina* (×*Urceocharis edentata*) may be further indication that the evolution of these genera was geologically recent.

Taxonomic Treatment

subspecific taxa

The rank of subspecies is used once in this treatment (*E. plicata*) to designate strong morphological divergence coupled with geographical isolation that I accept within specific limits. The rank of variety is used in a case (*E. bouchei*) where both the morphological and geographic components of divergence are weaker but appear to represent the first stages of speciation within a tetraploid semispecies complex (Meerow, 1987d).

critical measurements

Measurements of vegetative and floral parts in the following species descriptions are derived from examination of dried material (floral parts after rehydration in 3% solution of Aerosol OT brought to boil) supplemented with examination of fresh or FAA-preserved material when available. I found less than 5% difference between measurements of dried and fresh or spirit-preserved material of the same collection when available.

a note on the keys

Species of *Caliphruria* and *Eucharis* subg. *Heterocharis* are separable by discrete characters very amenable to key construction. Using the keys to these two groups, any worker should be able to identify material referable to described taxa whether in the field or the herbarium. The enormous degree of variation exhibited by species of subg. *Eucharis*, however, made key construction difficult. A number of the species overlap to at least some degree with one or more other species in virtually all quantitative morphological characters. As a consequence, sometimes I have had to rely on characters observable only with living material. With perseverance, it should be possible to key out all but the most depauperate herbarium specimens of subg. *Eucharis*. Collectors should note such characters as leaf plication and undulation, floral fragrance, tepal habit, and pigmentation and plication of the staminal cup in their notes when preparing specimens of *Eucharis*.

key to *Eucharis* and *Caliphruria*

1a. Leaf margins usually undulate; flowers declinate to pendulous via the curving of the tube; perianth funnelform-campanulate or crateriform; tube cylindrical, at least below middle, abruptly dilating at or above the midpoint of its length, curved, 25–50 mm long; staminal cup conspicuous, basally pigmented green or yellow, exserted from the throat of the perianth or adnate to the dilated portion of the tube; stigmatic papillae unicellular ..... *Eucharis*

1b. Leaf margins nonundulate; flowers declinate to subpendulous via the curving of the pedicel; perianth funnelform; tube funnelform, dilating gradually from base (rarely subcylindrical), straight or only slightly cernuous, 25 mm or less long; staminal cup inconspicuous and unpigmented, reduced to a membranous, basal

connation of the filaments; stigmatic papillae multicellular ..... *Caliphruria*

Eucharis Planchon et Linden, Linden's Ann. Cat. Hort. 8: 3. 1852; Fl. des Serres Jard. Eur. Ser. 1, 8: 107. 1853. TYPE: *Eucharis candida* Planchon et Linden. *Urceolina* subg. *Eucharis* (Planchon & Linden) Traub, Pl. Life 27: 57–59. 1971.

Evergreen, bulbous geophytes of rain forest understory. Bulb tunicate, usually offsetting vigorously. Leaves petiolate, persistent, glabrous; petiole subterete, somewhat concave adaxially proximal to the sinus, convex abaxially, light green, winged distally by attenuation of the lamina; lamina ovate, elliptic, ovate- or elliptic-lanceolate, usually thin, predominantly hypostomatic, usually lustrous, dark green adaxially, light or silvery green abaxially, smooth or plicate between the parallel veins, cuticle of the abaxial epidermis variably striate, margins frequently undulate, apically acute or acuminate, basally attenuate to the petiole, rarely appearing subcordate. Inflorescence scapose, umbellate (composed of 1 to several reduced helicoid cymes); scape solid, terete or slightly compressed, glaucous, terminating in 2 green or greenish white, ovate-lanceolate, valvate-imbricate, marcescent bracts enclosing the flowers and several secondary bracts before anthesis. Flowers 2–10(–12), pedicellate (rarely subsessile), each subtended by a lanceolate bracteole, pendent or declinate, sometimes fragrant, white, usually protandrous; perianth crateriform or campanulate; tube cylindrical, dilating abruptly above its midpoint, sometimes stained green proximally; limb of 6 tepals in 2 series spreading widely from the throat or imbricate for half their length, the outer series usually longer, narrower and apiculate; the inner series acute, obtuse, or minutely apiculate. Stamens 6, variously connate below, pigmented yellow or green proximally; free filament linear, subulate, or otherwise petaloid; anthers oblong to linear, sub-basifixed or dorsifixed, eventually becoming versatile, introrse, dehiscing longitudinally; pollen grain boat-shaped elliptic, monosulcate, the exine reticulate. Style filiform, included within, equal to, or exserted from the staminal cup; stigma obtusely 3-lobed, papillose. Ovary inferior, green or white, globose-ellipsoid, oblong, occasionally trigonous, 3-locular; septal nectaries present; ovules 2–20 per locule, placentation axile, globose, anatropous. Fruit a 3-lobed, loculicidal capsule, thin-walled or leathery, green or bright orange; seed globose or ellipsoid, sometimes angled by pressure, turgid, with copious endosperm, few per locule; testa thin, phytomelanous, lustrous (rarely dull) black, dark brown or blue, usually smooth. Chromosome numbers: $2n = 46$, 68, 92, 138.

KEY TO THE SUBGENERA OF *EUCHARIS*

1a. Flowers 3–7 cm long, usually pendulous, only rarely and mildly fragrant, crateriform (rarely somewhat campanulate); perianth tube cylindrical below, dilated abruptly just below the throat (rarely in the upper ¼), usually strongly curved, white; limb segments usually spreading widely (ca. 90°) at perianth throat; staminal cup inserted at throat of tube, proximally spotted or stained yellow, green, or yellow-orange equally on the exterior and interior of the cup; distal portion of filament usually widely subulate (> 1.5 mm wide) or otherwise petaloid; anthers ± erect at anthesis; ovules 2–9(–10) per locule; capsule leathery and bright orange (rarely green, in which case tardily dehiscent) ..... *Eucharis* subg. *Eucharis*

1b. Flowers 7–8 cm long, declinate or subpendulous, strongly fragrant, funnelform-campanulate to crateriform; perianth tube cylindrical below, dilated abruptly at ⅓–½ its length, green (at least proximally); limb segments usually imbricate for half their length; staminal cup partially adnate to upper portion of tube, sometimes reduced, flushed (yellow-)green, particularly along the filamental traces, with the pigmentation most intense on the interior of the cup; distal portion of the filament usually narrowly subulate (≤ 1 mm wide); anthers versatile at anthesis; ovules (7, 9–)16–20 per locule ..... *Eucharis* subg. *Heterocharis*

Eucharis subg. **Eucharis**

Leaves glabrous, petiolate, persistent; lamina ovate, elliptic, or lanceolate, mostly thin, margins usually undulate, variably plicate between the parallel veins, apically acute or acuminate, basally attenuate to the petiole or rarely subcordate, mostly dark green and lustrous adaxially, light or silvery green abaxially, the abaxial epidermis variously striate; petiole subterete, somewhat channeled adaxially proximal to the sinus. Inflorescence scapose, umbellate, terminating in 2 greenish white marcescent bracts. Flowers pedicellate, (3–)5–10, only rarely with noticeable fragrance, mostly pendulous, 3–7 cm long, crateriform (rarely slightly campanulate); perianth tube usually strongly curved, cylindrical below, dilated just below the throat or rarely at ⅓ length, white; limb of 6 white, ovate to ovate-lanceolate tepals usually spreading widely from the throat, often recurved above the middle, the outer 3 usually longer, narrower, and apically apiculate, the midvein often faintly yellow in strong light. Stamens connate into a conspicuous

or rarely reduced staminal cup, usually exserted from the rim of the throat; staminal cup apically white, marked green or yellow (rarely yellow-orange) basally, variously toothed, lobed or entire; distal portion of the filaments petaloid and variously shaped; anthers oblong or linear, subdorsifixed or sub-basifixed, ± erect at anthesis, finally becoming versatile; pollen grain 45–60 μm (polar axis), 55–86 μm (longest equatorial axis), the exine coarsely reticulate. Style filiform, white; stigma obtusely trilobed, glandular pubescent. Ovary globose, elliptic or trigonous, green or white; ovules globose to ellipsoid, axile, superposed, 1–12 per locule, most often 2–4. Fruit a loculicidal capsule, orange and leathery when ripe (rarely remaining green); seeds 1–3(–4) per locule, ca. 1 cm long, turgid, ellipsoid (rarely somewhat compressed), with a lustrous black or blue testa.

Distribution. Fourteen species, (Guatemala) Costa Rica to Bolivia, concentrated on the lower slopes of the northeastern Andes and western Amazonas, usually below 1,000 m.

KEY TO THE SPECIES OF *EUCHARIS* SUBG. *EUCHARIS*

1a. Perianth tube 25 mm or more long.
  2a. Flowers (7–)8–10 (or very rarely 5); ovules 3–9 per locule (or very rarely 2).
    3a. Flowers not fragrant; perianth tube (25–)30–35 mm long; outer tepals (20–)25–30(–33) mm long; staminal cup 8–11 mm long to apex of teeth or lobes; ovules (2–)3–5(–7) per locule ..... 1. *E. candida*
    3b. Flowers mildly fragrant; perianth tube 35–45(–50) mm long; outer tepals (28–)32–45(–47) mm long; staminal cup 10–16 mm long to apex of teeth or lobes; ovules (2–4)7–9 per locule.
      4a. Floral fragrance slightly fetid; flowers pendent; staminal cup less than 15 mm long to apex of teeth or lobes, cleft 3–5 mm between each stamen, nonplicate; staminal teeth (if present) much less than half the length of the subulate portion of the filament; style exserted ca. 1 cm beyond the anthers ..... 2. *E. formosa*
      4b. Floral fragrance sweet; flower perpendicular to vertical axis of scape; staminal cup more than 15 mm long to apex of teeth, cleft very shallowly (less than 2 mm) between each stamen, plicate; staminal teeth half the length of the subulate portion of the filament; style exserted less than 0.5 cm beyond the anthers ..... 3. *E. bakeriana*
  2b. Flowers 2–5(–7); ovules 2–3(–5) per locule.
    5a. Leaves nonplicate, somewhat succulent, margins nonundulate, length-to-width ratio usually less than 3; petiole usually shorter than the lamina; plants of central and western Colombia or Central America.
      6a. Leaves slightly glaucous adaxially; abaxial cuticle densely striate; perianth tube 25–33 mm long; staminal cup irregularly toothed, proximally pigmented pale yellow; stamens always constricted distally into a narrow subulate portion; style exserted less than 0.5 cm beyond anthers; ovary not trigonous; plants of Colombia ..... 4. *E. bonplandii*
      6b. Leaves not glaucous; abaxial cuticle largely devoid of striations; perianth tube (25–)33–45 mm long; staminal cup most frequently edentate, proximally pigmented green; stamens often dilating gradually from apex to base; style exserted 0.5–1 cm beyond anthers; ovary often trigonous; plants of Central America ..... 5. *E. bouchei*
    5b. Leaves plicate, thin, margins undulate, lamina length-to-width ratio usually greater than 3; petiole usually equal to or longer than the lamina; plants of western Ecuador, Colombia, or Amazonas.
      7a. Leaves bullate-pustulate in texture, nonlustrous; staminal cup pigmented yellow-orange proximally; stamens deltoid, dilating gradually from apex to base; ovary white; plants of western Ecuador ..... 6. *E. astrophiala*
      7b. Leaves not bullate-pustulate in texture, lustrous; staminal cup pigmented yellow or green; stamens not deltoid, constricted distally into a narrow (less than 2 mm wide) subulate portion; ovary green; plants of western Colombia or Amazonas.
        8a. Perianth funnelform-campanulate, tube dilated distally at approximately ⅓ its length; staminal cup inconspicuous; filaments connate proximally for 3 mm or less; plant of western Colombia ..... 7. *E. caucana*
        8b. Perianth crateriform, tube dilated abruptly just below the throat; staminal cup conspicuous; filaments connate proximally for 8 mm or more; plants of Amazonas.
          9a. Perianth tube curved gradually throughout the proximal half; staminal cup usually bidentate but sometimes obtusely lobed (rarely one to several stamens quadrate); ovary globose-elliptic at anthesis; testa lustrous black ..... 8. *E. ulei*
          9b. Perianth tube usually curved abruptly above the ovary, then more or less straight for the rest of its length; staminal cup usually quadrately lobed, but one or several stamens occasionally toothed; ovary deeply trigonous at anthesis; testa lustrous blue ..... 9. *E. cyaneosperma*
1b. Perianth tube equal to or less than 25 (or very rarely to 30) mm long.
  10a. Staminal cup usually less than 1 cm long to apex of teeth or lobes, but connate portion of filaments always much shorter than free, subulate portion.

11a. Teeth of the staminal cup acutely long-lanceolate, as long as the subulate portion of the filament; ovules 10 per locule, plants of western Colombia ..... 10. *E. lehmannii*

11b. Teeth of the staminal cup (when present) obtuse, much shorter than the subulate portion of the filaments; ovules fewer than 10 per locule; plants of the Peruvian east Andes.

12a. Staminal cup 3.5 mm long (to apex of teeth), obtusely bidentate between each stamen; free filaments club-shaped (appearing elliptic-lanceolate in dried material), 1.8–2 mm wide, ovules 4–6 per locule ..... 11. *E. corynandra*

12b. Staminal cup reduced to a basal connation of the filaments 0.8–1.5 mm long, edentate or obtusely bidentate; free filaments narrowly subulate, ca. 1 mm wide; ovules 6–8 per locule ..... 12. *E. oxyandra*

10b. Staminal cup usually greater than 1 cm long to apex of teeth or lobes, but connate portion of filaments always longer than the free, subulate portion.

13a. Leaves 7–12(–14) cm wide; staminal cup campanulate, gradually dilating distally, plicate along the filamental traces; ovary green; capsule leathery, bright orange, dehiscent; seeds ellipsoid, with a lustrous, smooth black testa ..... 13. *E. plicata*

13b. Leaves 3–6 cm wide; staminal cup funnelform-cylindrical to cylindrical, often abruptly dilated distally at ½–⅔ length, plicate between the filamental traces; ovary whitish; capsule green, thin-walled, often tardily dehiscent; seeds wedge-shaped, with a dull, rugose black testa ..... 14. *E. castelnaeana*

1. Eucharis candida Planchon et Linden, Linden's Ann. Cat. Hort. 8: 3. 1852; Fl. des Serres Jard. Eur. Ser. 1, 8: 107. 1853. TYPE: ex hort. Linden, supposedly imported from Colombia, no other data, *Planchon s.n.* (MPU). *Urceolina candida* (Planch. & Lind.) Traub, Pl. Life 27: 57–59. 1971. Figures 67–69, 70A.

Bulb subglobose, 3–5(–6) cm long, 3–4(–5) cm diam., neck 1–2.5(–4) cm long, 1–2.5 cm wide; tunics brown. Leaves 1–2, petiole (15–)18–30(–35) cm long, ca. 7 mm thick proximally, ca. 3–4 mm thick distally; lamina elliptic, (18–)30–35 cm long, (7–)8.5–11.5(–12) cm wide; acuminate, deeply plicate, dark green but only slightly lustrous adaxially, light green abaxially, abaxial cuticle striate, the margins coarsely undulate. Scape (4–)5–6 dm tall, 8–10 mm diam. proximally, 4–5 mm diam. distally; bracts 25–45(–50) mm long, ca. 5–6 mm wide, ovate-lanceolate. Flowers (7–)8–10, rarely as few as 5, without noticeable fragrance; pedicels (9–)15–20(–35) mm long; tube (25–)30–35 mm long, ca. 2 mm diam. for most of its length, abruptly dilated to (7–)10(–11.5) mm at the throat; limb spreading to 4.5–6 cm wide; tepals sometimes recurved distally, outer tepals (20–)25–30(–33) mm long, (9–)10.5–14(–15) mm wide, ovate-lanceolate, apiculate, the apiculum only slightly or obscurely tufted adaxially; inner series (20–)22–28(–32) mm long, (10–)12–15(–20) mm wide, ovate, acute to minutely apiculate. Staminal cup funnelform-cylindrical to slightly campanulate, rarely widely ampliate distally, (7–)8–11 mm long (to apex of teeth or lobes), (10–)13–16(–18) mm wide, most frequently edentate and lobed between each stamen, at times bidentate or irregularly toothed, widely spotted green to greenish yellow below each stamen; teeth, when present, 1–2 mm long, < 1 mm wide, acute or obtuse; cup cleft for (2.5–)3–5(–6) mm between each stamen; stamens (3.5–)4.5–5.5(–6) mm wide proximally; distal subulate portion (3.5–)4.5–6(–6.5) mm long, 1.5–2 mm wide at the base; anthers (3.5–)4–5(–6) mm long, oblong; pollen grain 46.8–50 μm polar diam., 68.7–73 μm longest equatorial diam. Style (38–)45–55 mm long, exserted 0.5–1 cm beyond the anthers; stigma 2—d3 mm wide. Ovary globose-ellipsoid, green, 5–7(–8) mm long, 4–6(–7) mm diam.; ovules (2–)3–5(–7) per locule. Capsule (1.5–)1.8–2.4 cm long, (2–)2.5–2.9 cm wide, bright orange, leathery; pedicel 2–4 cm long; seeds 1–2(–3) per locule, ellipsoid, ca. 1 cm long, ca. 0.5 cm diam., with a lustrous, smooth black testa. Chromosome number: $2n = 46$.

Distribution. Understory of primary rain forest chiefly in the Oriente of Ecuador, particularly the Río Napo valley, occasional in north Peru and southeast Colombia (Figs. 71, 72) at (100–180)240–550(1,000–1,600) m. Flowering at any time of the year, most frequently in February, March, and August.

Vernacular name. Cebolleta.

Additional specimens examined. COLOMBIA. AMAZONAS: Puerto Nariño, 24 Jul 1965, *Lozano et al. 594* (COL); Trapecio amazonica, Loretoyacu River, ca. 100 m, Oct. 1946, *Schultes & Black 8478* (US). META: sabanas de San Juan de Arama, margen izquierda del Río Güejar, alrededores del aterrizaje "Los Micos," 500 m, 22 Jan. 1951, *Idrobo & Schultes 1208* (COL, GH, NY, US). PUTUMAYO: vicinity Mocoa, Río Rumiyaco, 1,100 m, 8 Oct. 1959, *Barclay & Juajibioy 9461* (MO). ECUADOR. NAPO: Tena, wet forest, 27 Sep. 1939, *Asplund 8853* (S); El Napo, 1931, *Benoist 4717* (P); Río Yasuni, 12 km from mouth at Río Napo, 0°57′S, 75°25′W, 200 m, 25–26 Aug. 1982, *Balslev & Alarcon 2966* (QCA);

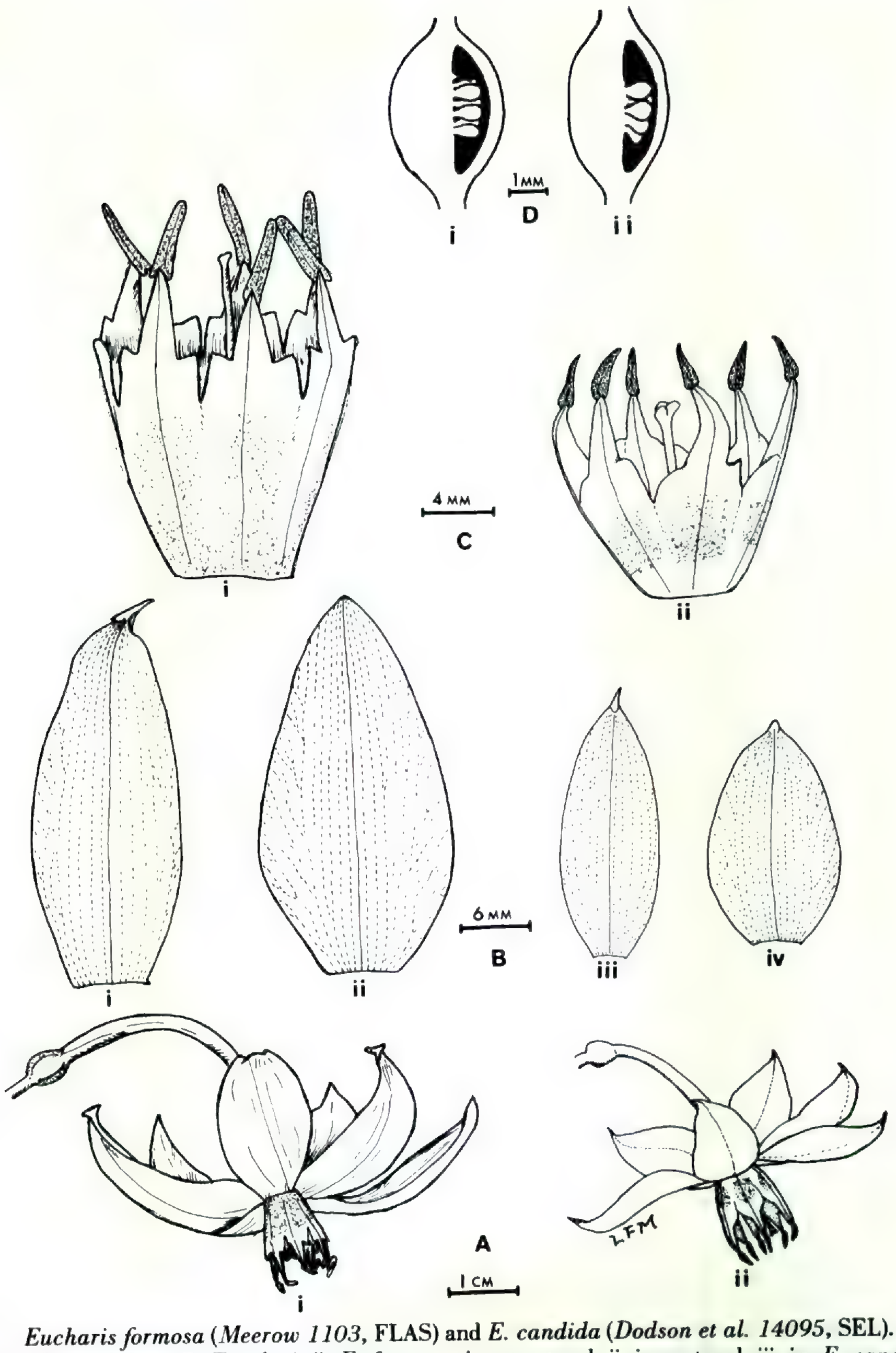
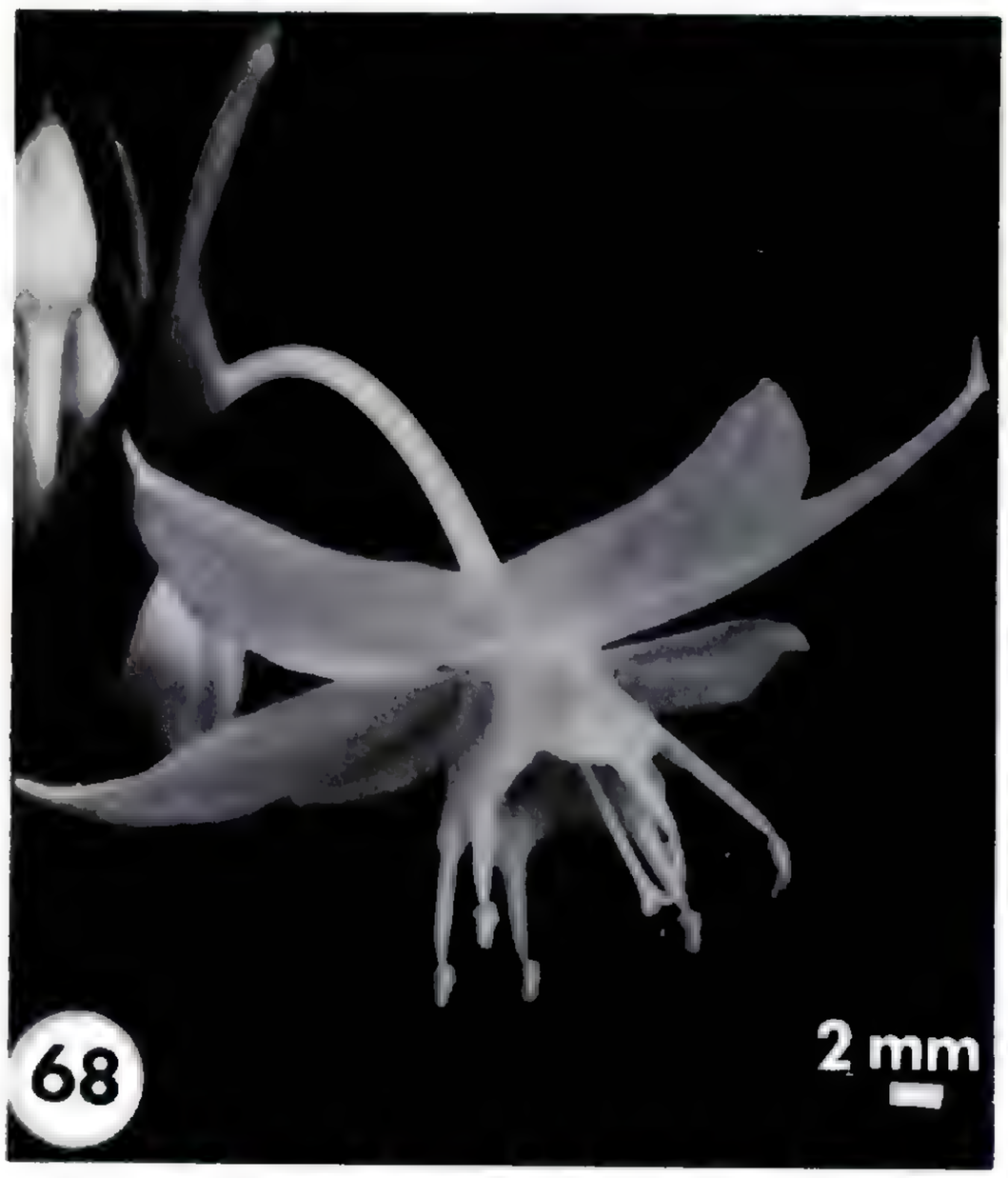
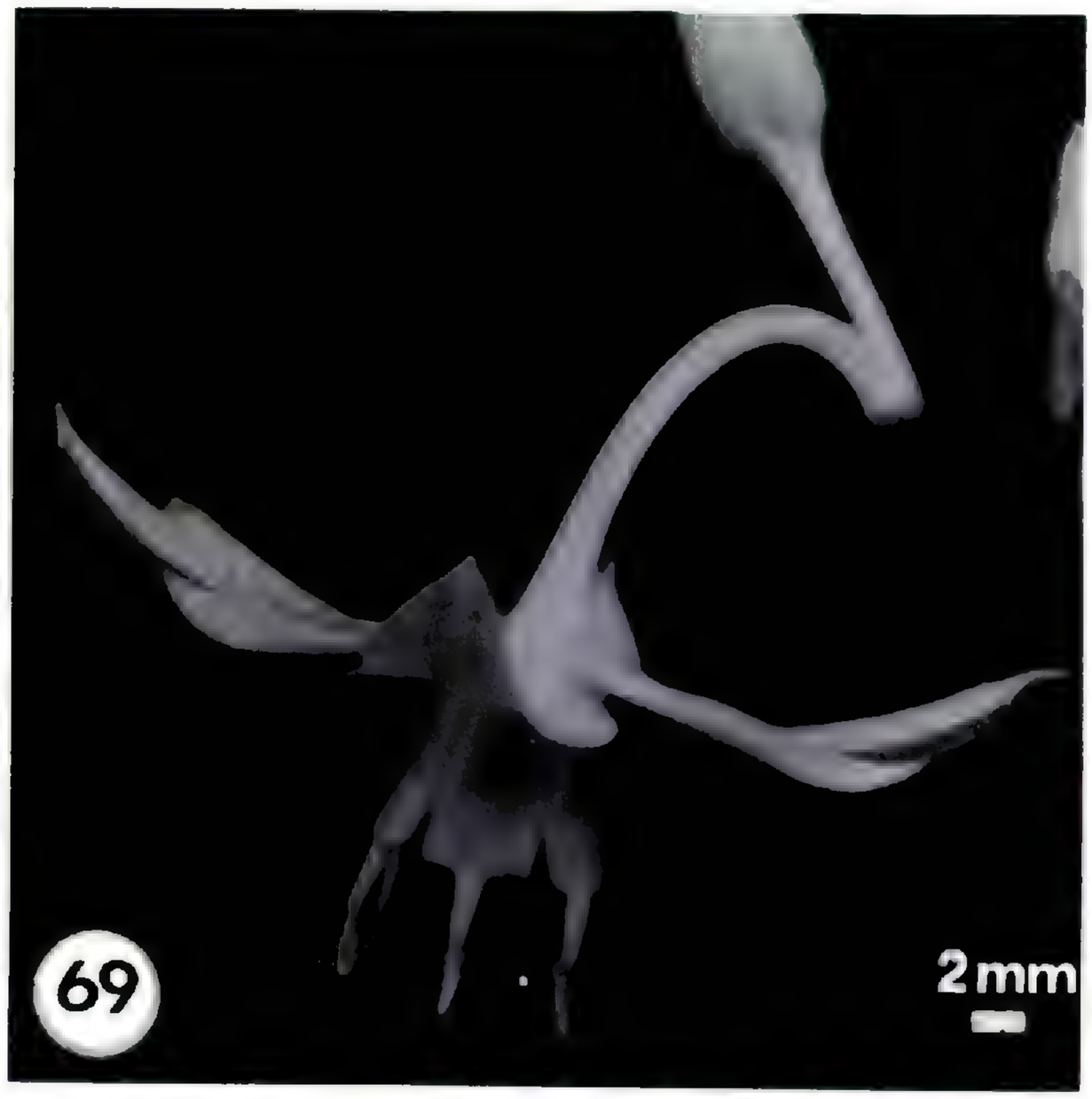


FIGURE 67. *Eucharis formosa* (*Meerow 1103*, FLAS) and *E. candida* (*Dodson et al. 14095*, SEL).—A. Flowers. i, *E. formosa*; ii, *E. candida*.—B. Tepals. i, ii. *E. formosa*. i, outer tepal; ii, inner tepal. iii, iv. *E. candida*. iii, outer tepal; iv, inner tepal.—C. Staminal cups. i, *E. formosa*; ii, *E. candida*.—D. Ovaries, longitudinal section. i, *E. formosa*; ii, *E. candida*.

70 km downstream from Coca at Anangu, 260 m, 8–11 Aug. 1982, *Besse et al. 1598* (SEL); Tena–Puyo road, 550 m, Aug. 1982, *Besse et al. 1643* (SEL); Coca–Lago Agrio road, 45 km north of Coca, Río Palanda Yacu, 7 June 1983, *Bohlin & Bohlin 319* (GB); Isla Pompeya, 19 Apr. 1983, *Dinua 42* (QCA); km 5, Cotunda-Coca, 1,130 m, 19 June 1963, *Dodson et al. 14095* (SEL); orilla izquierda del Río San Miguel, Puerto Nuevo, 26 Mar. 1953, *Gutierrez V. 2687* (COL); Santa Rosa at Río Napo, ca. 400 m, 29 Feb. 1972, *Harling 11090* (GB); Hacienda Cotapino (Concepción), 550 m, 19–20 Feb. 1968, *Harling et al. 7121* (FLAS, GB); lower Río Aguarico (above Puesto militar Puerto Loja, 7 Mar. 1968, *Harling et al. 7400* (GB); Coca, potreros and rastrojos near the village along road to Lago Agrio, ca. 250 m, 2 Feb. 1974, *Harling & Andersson 11682* (GB); Cañon de los Monos, ca. 12 km north of Coca, 250 m, 4 Feb. 1974, *Harling & Andersson 11719*, FLAS specimen (FLAS); Misahualli at Río Napo, 28 Mar. 1969, *Holguer 925* (FLAS, GB); environs of Limoncocha, 240 m, June 1978, *Madison et al. 5326* (F, SEL); between Río Napo and Río San Miguel, 0°30′S, 76–77°W, 300 m, Aug.–Sep. 1978, *Navarrete 78*. PASTAZA: Mera, forest on shore of Río Pastaza, ca. 1,000 m, 30 Jan. 1956, *Asplund*





FIGURES 68, 69. Variation in a single Peruvian population of *Eucharis candida* (*Schunke 14155-B*, FLAS).—68. Flower with wide-spreading staminal cup.—69. Flower with cylindrical staminal cup.

19120 (S); Puyo–Arajuno Road, 1–5 km SW Diez ed Agosto, ca. 900 m, 4 Feb. 1980, *Harling & Andersson 16862* (GB); 68 km north of Puyo on road to Tena, along creek, ca. 500 m, 26 July 1982, flowered in cultivation, 15 Jan. 1985, *Meerow 1144* (FLAS). MORONA-SANTIAGO: Huamboya, 1,500–1,600 m, 15 Feb. 1944, *Acosta-Solis 7469* (F). PERU. AMAZONAS: 400 m atras de La Poza, Río Santiago, 180 m, 23 Aug. 1979, *Huashikat 164* (MO). LORETO: Maynas, Río Ampiyacu, Pebas and vicinity, approx. 3°10′N, 71°49′W, behind Pebas on trail north of town, 10 Apr. 1977, *Plowman et al. 6724* (F); Maynas, Santa María de Nanay, Colonia San Fransisco de Indies Yaguas, 1.5 km del Fundo Balcon, Río Momen, 106–110 m, 15 Nov. 1984, *Schunke 14155-B* (F, FLAS).

Putative hybrids with E. formosa*:* ECUADOR. NAPO: km 23 Lago Agrio–Baeza road, 350 m, July 1982, *Besse et al. 1558* (SEL); 35 km south of Río Aguarico, Lago Agrio–Coca road, July 1982, *Besse et al. 1563* (SEL); Río Coca, 10 km upstream from ferry crossing, 250 m, 28 Nov. 1983, *Besse et al. 1949* (SEL).

Eucharis candida was originally described from cultivated material supposedly originating from Colombia, a country in which it has been encountered only rarely. The species previously has been delimited by the absence of staminal dentation; however, this character varies considerably throughout the range of *E. candida* (Fig. 70A), as in the related species *E. formosa* and *E. ulei*. Peruvian populations of *E. candida* are variable in the shape of the staminal cup (Figs. 68, 69), even among flowers of the same inflorescence.

Eucharis candida is most common throughout the upper Napo Valley in eastern Ecuador and is very often sympatric with the larger-flowered and more widely distributed *E. formosa* (Figs. 71, 72). In one instance, two specimens (*Harling & Andersson 11719*), one each of the two species, were collected under the same number. To date, no species of *Eucharis* other than these two have been collected north of the Pastaza valley in eastern Ecuador. On the basis of herbarium study alone, Ecuadorean populations of these two taxa form a mosaic that seemed taxonomically insoluble until living material of both species from several populations was collected and flowered. Phenetic and karyotype analyses (Meerow, in press) support their recognition as distinct species and suggest that *E. candida* and *E. formosa* have hybridized in at least one area of sympatry.

Eucharis candida may be separated from *E. formosa* by its smaller leaves and flowers, complete absence of fragrance (*E. formosa* produces a mild, "sour" odor), and generally fewer ovules per locule (though both species are variable in ovule number). On the basis of known collections, *Eucharis formosa* is slightly better represented in the Pastaza valley than *E. candida*.

2. Eucharis formosa Meerow, Sida 21: 29–49. 1987. TYPE: Ecuador. Morona-Santiago: Road Limón–Macas, ca. km 20 from Limón, primary rain forest and rastrojos, 700–900 m, 26 Mar. 1974, *Harling & Andersson 12915* (holotype, GB; isotype, FLAS). Figures 67, 70B, 73–78.

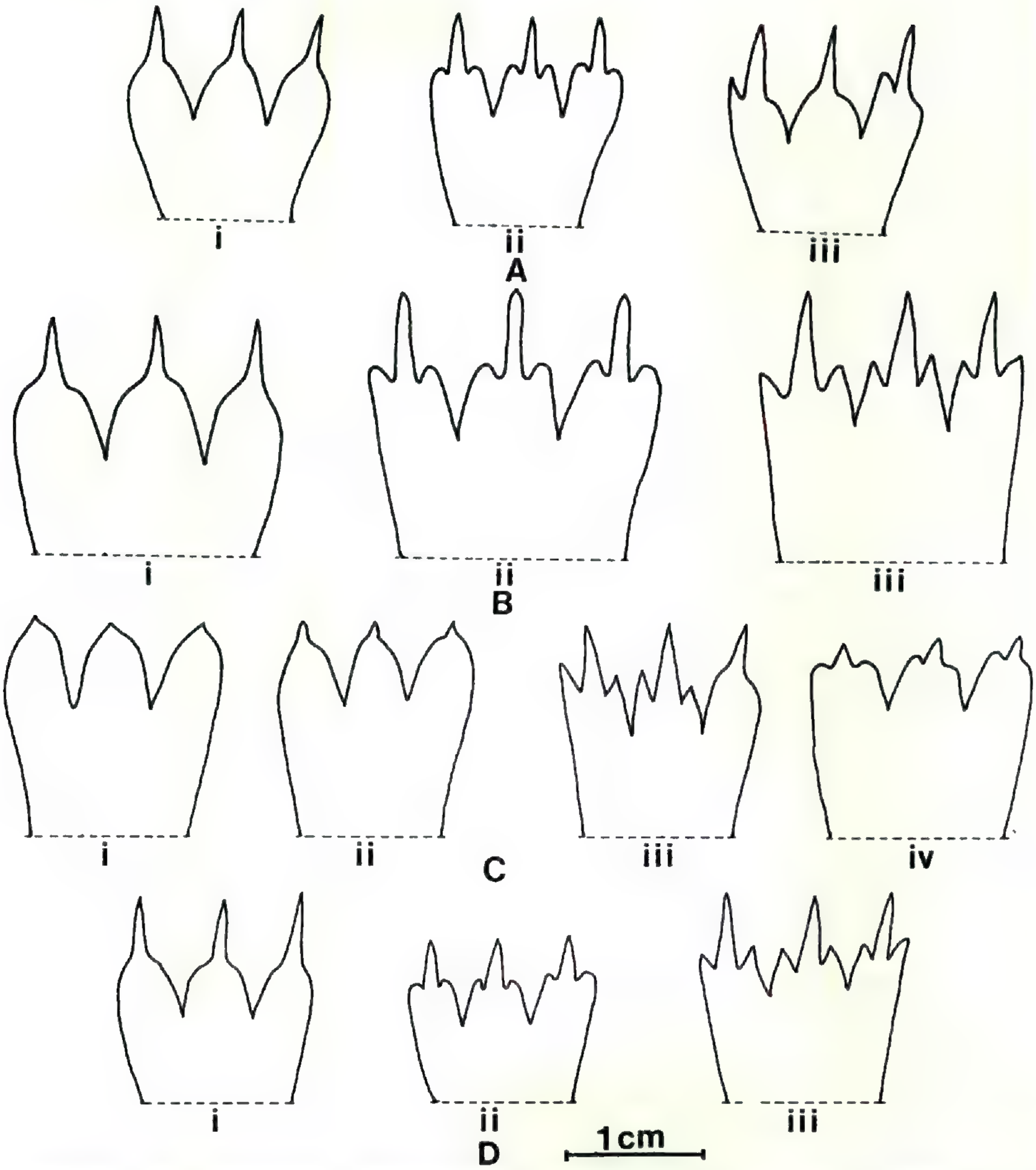


FIGURE 70. Staminal cup variation in four species of *Eucharis*.—A. *E. candida*. i, *Besse et al. 1598* (SEL); ii, *Harling et al. 7400* (GB); iii, *Schultes & Black 8476* (US).—B. *E. formosa*. i, *Penland 142* (US); ii, *Holguer 2655* (GB); iii, *Harling et al. 7201* (GB).—C. *E. bouchei*. i, ii. Variety *bouchei*. i, *Lewis et al. 2617* (MO); ii, *Allen 120* (US). iii. Variety *dressleri* (*Meerow 1107*, FLAS). iv. Variety *darienensis* (*Gentry & Mori 13945*, MO).—D. *E. ulei*. i, *Plowman & Kennedy 5811* (GH); ii, holotype, *Ule 5737A* (B); iii, *Schunke 1887* (F).

Bulb subglobose, 4–7 cm long, 3–5 cm diam., neck 2–5 cm long, ca. 1 cm thick, tunics brown. Leaves 1–2(–3); petiole 25–38(–42) cm long, 8.5–1 mm thick proximally, 5–6 mm thick distally; lamina elliptic, (21–)30–45(–52) cm long, (8–)11–15(–16) cm wide, usually conspicuously plicate, dark green and only slightly lustrous adaxially, light green abaxially, abaxial cuticle striate, margins coarsely undulate. Scape (5–)6–7(–8) dm tall, ca. 1 cm diam. proximally, 5–6 mm diam. distally; bracts ovate-lanceolate, (36–)43–60(–85) mm long, 10–15 cm wide at the base. Flowers 8–10, very rarely fewer, pendent, emitting a mild "sour" odor; pedicels (8–)12–18(–30) mm long; tube 35–45 (–50) mm long, ca. 2–2.5 mm wide for most of its length, abruptly dilated to (9–)10–13(–14) mm at the throat; limb spreading to (55–)60–70(–80) cm; tepals sometimes recurved distally; outer tepals narrowly ovate, (30–)35–45(–47) mm long, (10–)15–18(–20) mm wide, apiculate, apiculum conspicuously horned adaxially (Ecuadorean populations); inner tepals ovate, (28–)31–40(–45) mm long, (15–)18–22(–25) mm wide, acute to minutely apiculate. Staminal cup funnelform-cylindrical, 10–13(–15) mm long (to apex of teeth or lobes), (15–)17–20(–22) mm wide; flushed greenish yellow proximally, with the greatest concentration of pigment below each free filament, rarely only widely punctate; bidentate, irregularly toothed, lobed or quadrate between the distal portion of the filament; cup cleft between each stamen for 3–5 mm; teeth when present acute or obtuse, ≤ 2 mm long; each stamen (5–)6–7(–7.5) mm wide tooth to tooth or lobe to lobe; distal portion of filament subulate, (4.5–)5–6.6(–7) mm long, (1.8–)2–2.5 (–3) mm wide at point of dilation; anthers oblong,

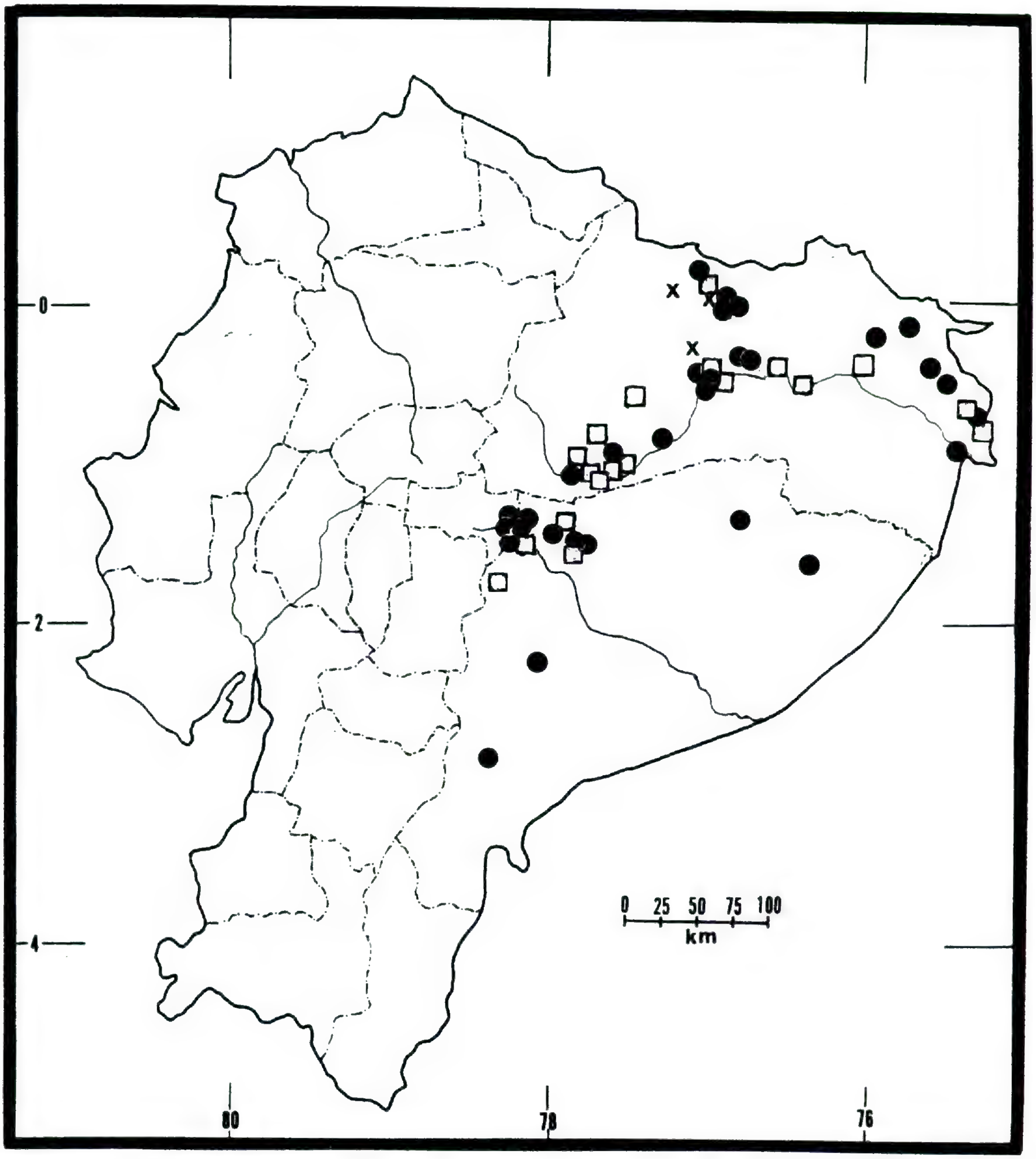


FIGURE 71. Distributions of *Eucharis candida* (squares) and *E. formosa* (circles) in Ecuador. X = *E. candida* × *E. formosa*.

4.5–5.5(–6) mm long, gray-brown; pollen grain 47.7–53.4 μm polar diam., 65.5–73.8 μm longest equatorial diam. Style 5.5–6(–6.5) cm long, exserted ca. 1 cm beyond the anthers; stigma ca. 2–3 mm wide. Ovary globose-ellipsoid, 6–8.5(–10) mm long, (4.5–)5.5–7(–7.5) mm diam., green; ovules (2–)5–7(–8). Capsule 1.5–2 cm long, 2–3 cm wide, bright orange, leathery; pedicels 3–4 cm long; seeds (1–)2–4 per locule, ellipsoid, 8–10 mm long, 5–6 mm diam., with a lustrous, smooth black testa. Chromosome number: $2n = 46$.

Distribution. Rich, moist soil in the understory of premontane and lower montane rain forest, chiefly in the Napo and Pastaza drainage of Ecuador (Fig. 71); less frequent in Amazonian Peru and Colombia, the lower "ceja de la selva" of north-central Peru, and upper Huallaga valley of Peru (Fig. 72); rare in central Colombia (a single, poorly documented, and very disjunct collection (*Killip s.n.*, COL) from near Popayan may be of cultivated origin), 100–1,800 m. Flowering most commonly January–March.

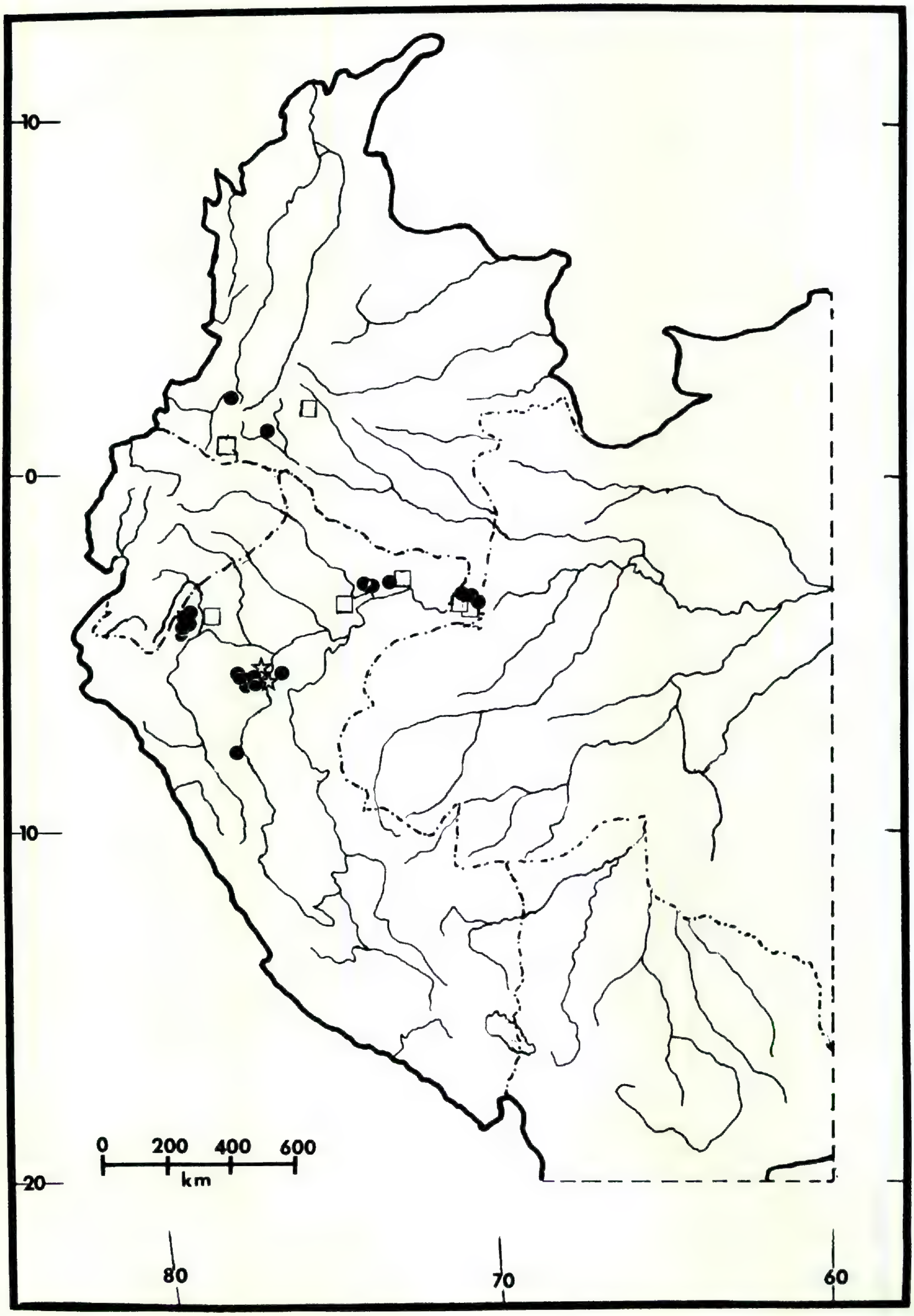


FIGURE 72. Distributions of *Eucharis bakeriana* (stars), *E. candida* (squares), and *E. formosa* (circles) in northwestern-central South America exclusive of Ecuador.

FIGURES 73–78. Variation in *Eucharis formosa*.—73, 74, 76. *Meerow 1103* (FLAS).—75, 77. *Schunke 14171* (FLAS).—78. *Schunke 14174* (FLAS).

Vernacular names and uses. Cebolla de la selva, sugkip, sacha cebolla. A poultice of the bulbs is used to treat tumors (*Lawesson et al. 39632*).

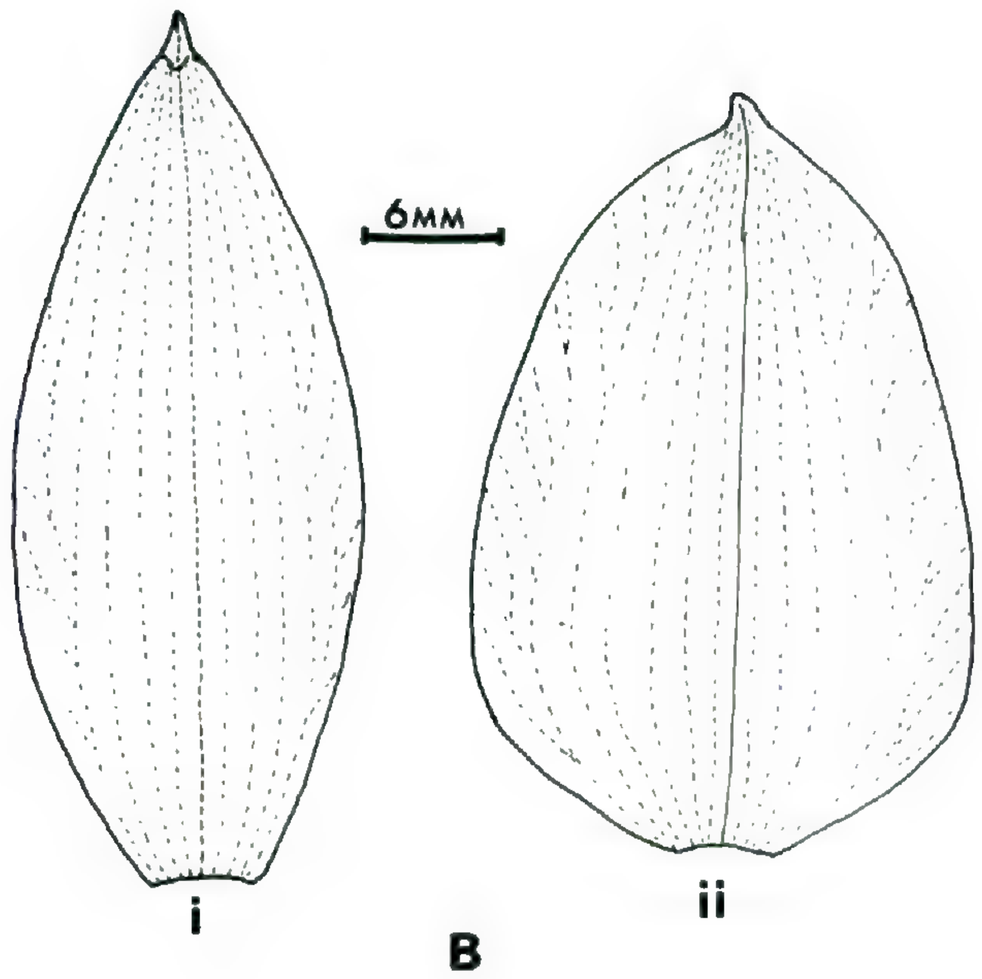
Additional specimens examined. COLOMBIA. AMAZONAS: confluencia de los ríos Amazonas y Loretoyacu, 12 Apr. 1975, *Cabrera 3336* (COL); Trapecío amazonico, Loretoyacu River, ca. 100 m, Sep. 1946 (fr), *Schultes & Black 8342* (US); same locality as preceding, Oct. 1946, *Schultes & Black 8410* (GH, US). CAQUETA: Morelia, 150 m, 5 Oct. 1941 (fr), *von Sneidern s.n.* (S). CAUCA: Popayan, 25 Jan. 1935, *Killip s.n.* (COL). ECUADOR. MORONA-SANTIAGO: 15 km N of Macas on road to Río Upano, 2°7′S, 78°8′W, 1,250 m, 20 Feb. 1987, *Bohlin et al. 1498* (GB); road Limón–Macas, ca. km 20 from Limón, primary rain forest and rastrojos, 700–900 m, 26 Mar. 1974, *Harling & Andersson 12915* (FLAS, GB). NAPO: Nuevo Rocafuerte, Río Napo, W of Río Yasuni, Laguna Jatuncocha, *Alarcon 106* (QCA); Misahualli, Guacamayos, Puerto Francisco de Orellana, *Alarcon 19509* (QCA); Napo, forest, 6 Oct. 1939, *Asplund 9122* (S); Tena, marshy forest, 21 Oct. 1939, *Asplund 9488* (S); Limoncocha, 300 m, 22 Jan. 1977, *Dodson 6636* (SEL); 45 minute walk by trail from Santa Cecilia up Río Aguarico, ca. 350 m, 28 Mar. 1972 (fr), *Dwyer*

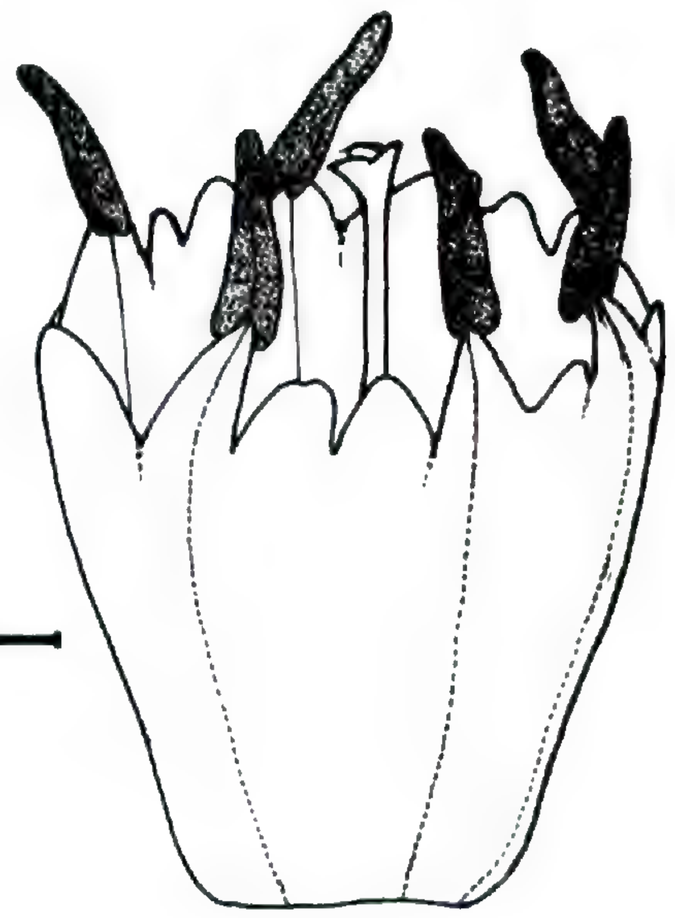
& MacBryde 9699 (MO, QCA); Santa Cecilia, rain forest off runway, 340 m, 30 Mar. 1972 (fr), *Dwyer & Simmons 9743* (MO); Cañon de los Monos, ca. 12 km north of Coca, 250 m, *Harling & Andersson 11719* (GB); path from Río Bueno to Santa Rosa, *Harling et al. 7201* (GB); Río Jivino, Limoncocha, 13–15 Mar. 1968, *Harling et al. 7673* (FLAS, GB); Armenia Vieja at Río Napo, ca. 12 km SW of Coca, 12 Jan. 1973, *Holguer 2655* (FLAS, GB); Cañon de los Monos, road Coca–Lago Agrio, ca. 12 km north of Coca, 24 Jan. 1973, *Holguer 2960* (GB); Santa Cecilia, Lago Agrio–Baeza, ca. 16 km west of Lago Agrio, 27 Feb. 1973, *Holguer 3532* (FLAS, GB); Río Aguarico W of Detacamento Zancudo at entrance of Río Zancudo, 320 m, very rich soil, 29 Aug. 1979 (fr), *Holm-Nielsen et al. 20168* (AAU); Río Aguarico, Sarayacu, 29 June 1980, *Jaramillo & Coello 2145* (QCA); Coca, km 15 from road to Las Yucas, 300 m, 31 Jan. 1980, *Jaramillo & Coello 2191* (QCA); Río Cuyabeno, Puerto Bolivar, 6 July 1980, *Jaramillo & Coello 2852* (QCA); Dureno, right bank of Río Aguarico, 10 July 1980, *Jaramillo & Coello 2962* (QCA); Anañgu, Río Napo, 76°23′W, 0°32′S, 260–350 m, 27 June 1983, *Lawesson et al. 39632* (AAU); 4.2–7.5 km west of Lago Agrio (5–8.2 km east of Río Conejo) near Lago Agrio–Baeza Road, ca. 340 m, 31 Mar. 1972, *MacBryde & Dwyer 1387* (MO); ex hort., voucher of SEL Acc. 78-1099, collected vicinity Limoncocha, 240 m, 15 Dec. 1982, *Meerow 1103* (FLAS). PASTAZA: Mera, ca. 1,100 m, 3 Mar. 1956, *Asplund 19571* (S); 3 km NW of Mera on road from Mera–Río Anzu, Hacienda San Augustin, 900–1,300 m, *Dodson et al. 15717* (MO); Curaray (Jesús Pitishka), virgin rain forest near the posto militar, ca. 200 m, 18 Mar. 1980, *Harling & Andersson* 17374 (FLAS, GB); between Nalpi and Canelo, 26 Feb. 1971, *Holguer 1504* (FLAS, GB); trail from Indillama to Canelos, 400 m, occasional, 5 Feb. 1935, *Mexia 6855* (UC, US); Río Curaray, mouth of Río Querano, 1°30′S, 76°32′W, 230 m, 3 Sep. 1985, *Neill & Palacios 6828* (MO); 2 km NE of Mera, Hacienda San Antonio del Baron von Humboldt, 1°27′S, 78°6′W, 1,300 m, 27 Feb.–19 Mar. 1985, *Palacios et al. 75* (MO); Napo road north of Puyo, 16 Feb. 1953, *Prescott 438* (NY). TUNGURAHUA: valley of Pastaza River, between Baños and Cashurco, 8 hours east of Baños, 1,300–1,800 m, *Hitchcock 21891* (GH, NY, US); vicinity of Río Margarjitas on Canelos trail, 1,225 m, 19 Mar. 1939, *Penland & Summers 142* (US). PERU. AMAZONAS: Quebrada Huampami, lugar tseasim, monte al lado nayumpin, 800 ft., 3 Apr. 1973, *Ancuash 161* (MO); Quebrada de Apigkagentsa, Río Cenepa, 720 ft., *Kayap 597* (F, MO); Quebrada Cunup, monte cerca a la chacra, 800–850 ft., 24 July 1974 (fr), *Kayap 1298* (MO); Río Cenepa, vicinity of Huampami, ca. 5 km E of Chavez Valdivia, ca. 78°30′W, 4°30′S, 3 Aug. 1978, *Kujikat 154* (MO); Río Cenepa, vicinity of Huampami, ca. 5 km east of Chavez Valdivia, ca. 78°30′W, 4°30′S, Quebrada Aintami, 17 Aug. 1978, *Kujikat 415* (MO). LORETO: Maynas, Yanamono, Explorama Tourist Camp, Río Amazonas, between Indiana and mouth of Río Napo, 72°48′W, 3°28′S, 120 m, 18 Aug. 1980, *Gentry et al. 29867* (MO); same locality, 130 m, 18 Feb. 1981, *Gentry et al. 31418* (MO); Maynas, Iquitos, Río Ampiyacu, 4 vueltas de Monona Cocha, 4 Aug. 1976, *Revilla 990* (MO); Alto Amazonas, Yurimaguas, Camino a "Shunguyco," al sur-este de Puerto Arturo, cerca a Yurimaguas, 150–200 m, 1 Dec. 1984, *Schunke 14157* (FLAS). SAN MARTÍN: road between Moyobamba and Chachapoyas near km marker 415, 13.5 km W of Naranjos, 5°38′S, 77°25′W, 700 m, 12 Apr. 1984, *Croat 58172A* (MO); Mariscal Caceres, Tocache Nuevo, Camino a Shunté, 12 Mar. 1970, *Schunke 3856* (F); Lamas, Alonso de Alvarado, San Juan de Pacaizapa, km 72, carretera Tarapoto–Moyobamba, 1,000–1,050 m, 9 June 1977, *Schunke 9675* (F); Lamas, Alonso de Alvarado, Fundo Las Malvinas, carretera Moyobamba–Tarapoto, km 43, 850 m, 6 Dec. 1984, *Schunke 14174* (FLAS); San Roque, in humid loam, 1,350–1,500 m, 5 Feb. 1930, *Williams 7748* (F).

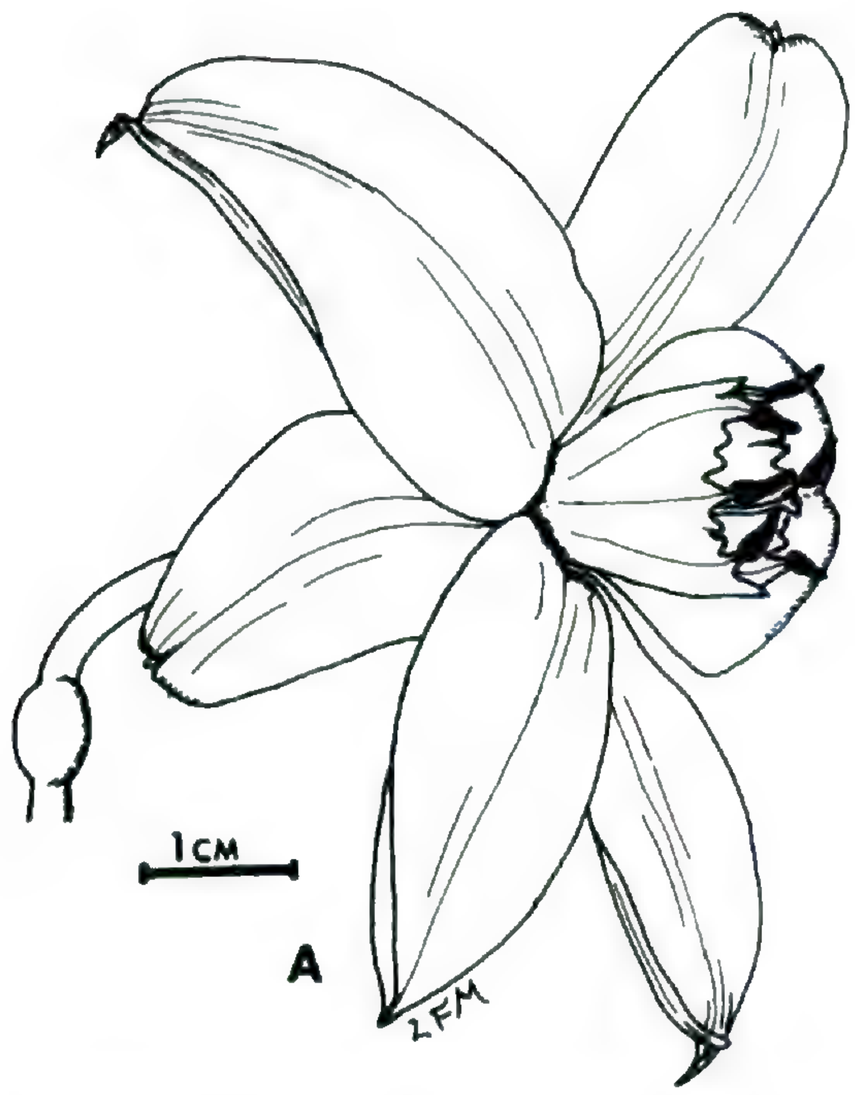
Eucharis formosa is the most commonly encountered species in eastern Ecuador (Fig. 71). It extends into Amazonian Peru and Colombia and occurs in the lower "ceja de la selva" forests of north-central Peru (Fig. 72). Like the closely related *E. candida*, *E. formosa* has a wide elevational range, possibly in part from cultivation (Meerow, 1987e). The flowers emit a mild and unpleasant "sour" odor. *Eucharis formosa* is larger in all parts than *E. candida* and generally has more ovules per locule. The conspicuous horn on the apiculum of the outer tepal is characteristic of Ecuadorean populations of *E. formosa* (Fig. 67Ai); this character is not obvious in Peruvian collections. Forms with toothed or edentate staminal cups occur throughout the range of this species without any observable geographic pattern (Fig. 70B). Flowers of the same inflorescence can vary for this character. A Peruvian collection (*Schunke 14174*) shows some karyotypic and allozyme divergence from Ecuadorean populations (Meerow, in press). In floral morphology (Fig. 78), however, it is indistinguishable from other Ecuadorean material. A second collection (*Schunke 14171*), from the same general vicinity of Peru as *Schunke 14174*, has only shallowly plicate leaves and reduced pigmentation of the staminal cup (Figs. 76, 77). At present, too little is known about *E. formosa* in Peru to justify recognition of subspecific taxa.

3. Eucharis bakeriana N. E. Brown, Gard. Chron. 7: 416, fig. 61. 1890. TYPE: Colombia (?): no other data, ex hort. Sander and Co., 1890, *s.n.*, in part (holotype, K). *Urceolina bakeriana* (N. E. Brown) Traub, Pl. Life 27: 57–59. 1971. Figure 79.

Bulb to ca. 5 cm diam., the tunics brown. Leaves 2–4; petiole 15–17, 25–30 cm long, (5–)10–11 mm wide; lamina elliptic, 24–29.5, 44–55 cm long, (10–)17–20 cm wide, somewhat succulent, smooth. Scape 6–8 dm tall, ca. 1 cm diam. proximally, 5–7 mm diam. distally; bracts ovate-lanceolate, 30–38 mm long, ca. 10 mm wide at the base. Flowers (5–)10, with a mild, sweet fragrance, pedicels 10–30 mm long; tube 35–40 mm long,







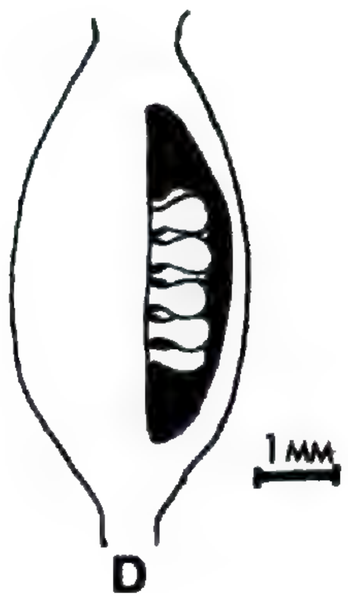


FIGURE 79. *Eucharis bakeriana* (*Meerow 1108*, FLAS).—A. flower.—B. Tepals. i. Outer tepal. ii. Inner tepal.—C. Staminal cup.—D. Ovary, longitudinal section.

2–3 mm wide for most of its length, abruptly dilated near the throat to 9–9.7 mm wide, curved abruptly just above the ovary and straight for the rest of its length, thus perpendicular to the vertical axis of the scape; limb spreading to 50–60 mm wide; outer tepals 28.5–32 mm long, ca. (10–)16.8 mm wide, ovate-lanceolate to ovate, apiculate; inner tepals 26–30 mm long, (14–)20–22 mm wide, ovate, acute to minutely apiculate. Staminal cup subcylindrical to campanulate, ca. 16 mm long (to apex of teeth), 13–15 mm wide, slightly plicate between the filamental trace, very shallowly cleft between each stamen (< 1 mm), proximally marked green, obtusely bidentate between each free filament; teeth 2–3 mm long, half the length of the subulate portion of the free filament; each stamen 5–6.4 mm wide tooth to tooth; subulate portion of the filament 3–4.5 mm long, 1.5–1.7 mm wide; anthers oblong, 5.4–6 mm long; pollen grain ca. 50.7 μm polar diam., ca. 76.9 μm longest equatorial diam. Style 45–54.5 mm long, exserted just slightly past the anthers; stigma 2.4–2.8 mm wide. Ovary ellipsoid, 6.5–7 mm long, 5.3–6.5 mm diam.; ovules 2–3, 8–9 per locule. Capsule ca. 1.5–2 cm long, 2.5–3 cm wide, bright orange, leathery; seeds ellipsoid, ca. 1 cm long, 0.5 cm diam., with a lustrous, smooth black testa. Chromosome number: $2n = 46$.

Distribution. Very rare in the understory of lower montane rain forest in the middle Río Huallaga valley of Peru, 800 m (Fig. 72). Living material

from which the type specimen was prepared was reportedly collected in Colombia, but I have seen no Colombian material. Flowering season not known.

Additional specimens examined. PERU. SAN MARTÍN: 17 km NE of Tarapoto on road to Yurimaguas, trail along stream to waterfall, wet premontane forest on rocky hills, 6°30′S, 76°20′W, 800 m, 21 July 1982 (fr), *Gentry et al. 37852* (MO); vicinity of Tarapoto, no other data, flowered in cultivation from material collected by L. Besse, *Meerow 1108* (FLAS).

The type of *E. bakeriana* was prepared from living material supposedly collected in Colombia. When I examined the type specimen, only the several large flowers present in the fragment packet resembled the figure that accompanied Brown's (1890) description of *E. bakeriana*. The mounted material was referable to the smaller-flowered *E. candida*. At the time, I thought that *E. bakeriana* might represent an aberrant form of *E. candida*. Several years later I received a bulb of a *Eucharis* collected near Tarapoto, Peru, by Libby Besse of SEL. The flowers that grew from the bulb bore an exact resemblance in habit and staminal cup morphology to *E. bakeriana*, though with considerably more ovules per locule. At present, *E. bakeriana* is known only from the type, the Besse material, and a fruiting specimen referred to this species on the basis of leaf size.

Eucharis bakeriana is distinct from *E. formosa*, its closest phenetic relative, by its nonpendent flowers that are perpendicular to the vertical axis of the scape, very shallowly cleft staminal cup (< 1 mm, vs. 2 mm in *E. formosa*), short subulate portion of the stamen, and sweet floral fragrance (slightly fetid in *E. formosa*). In leaf size and karyotype, *E. bakeriana* is very similar to Peruvian material of *E. formosa* (*Schunke 14174*) but differs by its greater number of subtelocentric chromosomes and the submetacentric morphology of the second-largest pair (Meerow, 1987b). The leaves are only shallowly, if at all, plicate and are thicker.

FIGURE 80. *Eucharis bonplandii* (*Meerow 1098*, FLAS).

4. Eucharis bonplandii (Kunth) Traub, Pl. Life 7: 40. 1951. *Hymenocallis bonplandii* Kunth, Enum. Pl. 5: 666. 1850. TYPE: Colombia. Cundinamarca: Río Magdalena, near Nares, *Bonpland 1657* (holotype, P, photo of type, NY). *Caliphruria bonplandii* (Kunth) Baillon, Bull. Mens. Soc. Linn. Paris 143: 1136. 1894. *Urceolina bonplandii* (Kunth) Traub, Pl. Life 27: 57–59. 1971. Figure 80.

Bulb subglobose, 41–46 mm long, 29–32 mm wide, neck ca. 18 mm long and wide, tunics brown. Leaves 2, somewhat succulent; petiole 8–14(–18) cm long, 6–8 mm thick proximally, 3–4 mm distally, always shorter than the lamina; lamina elliptic, (16–)18–24(–26) cm long, 8.5–11.5 cm wide, bluish green, especially in strong light, slightly glaucous adaxially; lighter green abaxially, the abaxial cuticle densely striate; apex acute to shortly acuminate; attenuate at the base. Scape 4.5–5.8 dm tall, 6–8 mm diam. proximally, 3–4 mm diam. distally; bracts (25–)33–40 mm long, ovate-lanceolate, greenish white. Flowers 5–7, nonfragrant, pendent; pedicels 18–25 mm long; tube 25–33 mm long, 1.8–2.5 mm wide for most of its length, abruptly dilated at the throat to 7–9(–10) mm wide; limb spreading to 47–55 mm wide; outer tepals ovate-lanceolate, 25.7–30.5 mm long, 8–10 mm wide, apiculate; inner tepals 23–28 mm long, 11.5–14 mm wide, acute to minutely apiculate. Staminal cup subcylindrical, (11.5–)12.5–14.3 mm long (to apex of teeth), 11.5–13 mm wide, stained pale yellow proximally, irregularly bidentate between each free filament, one stamen occasionally only lobed or quadrate, cleft 2.6–4 mm between each stamen; teeth variously acute or obtuse, 1–2 mm long; each stamen 3.6–4.5 mm wide tooth to tooth; free portion narrowly subulate, (3.8–)4.5–5.8 mm long, ca. 1.8 mm wide; anthers 4–4.8 mm long, oblong, grayish-brown; pollen grain ca. 43.5 μm polar diam., ca. 63 μm longest equatorial diam. Style 50–60 mm long, exserted just beyond the

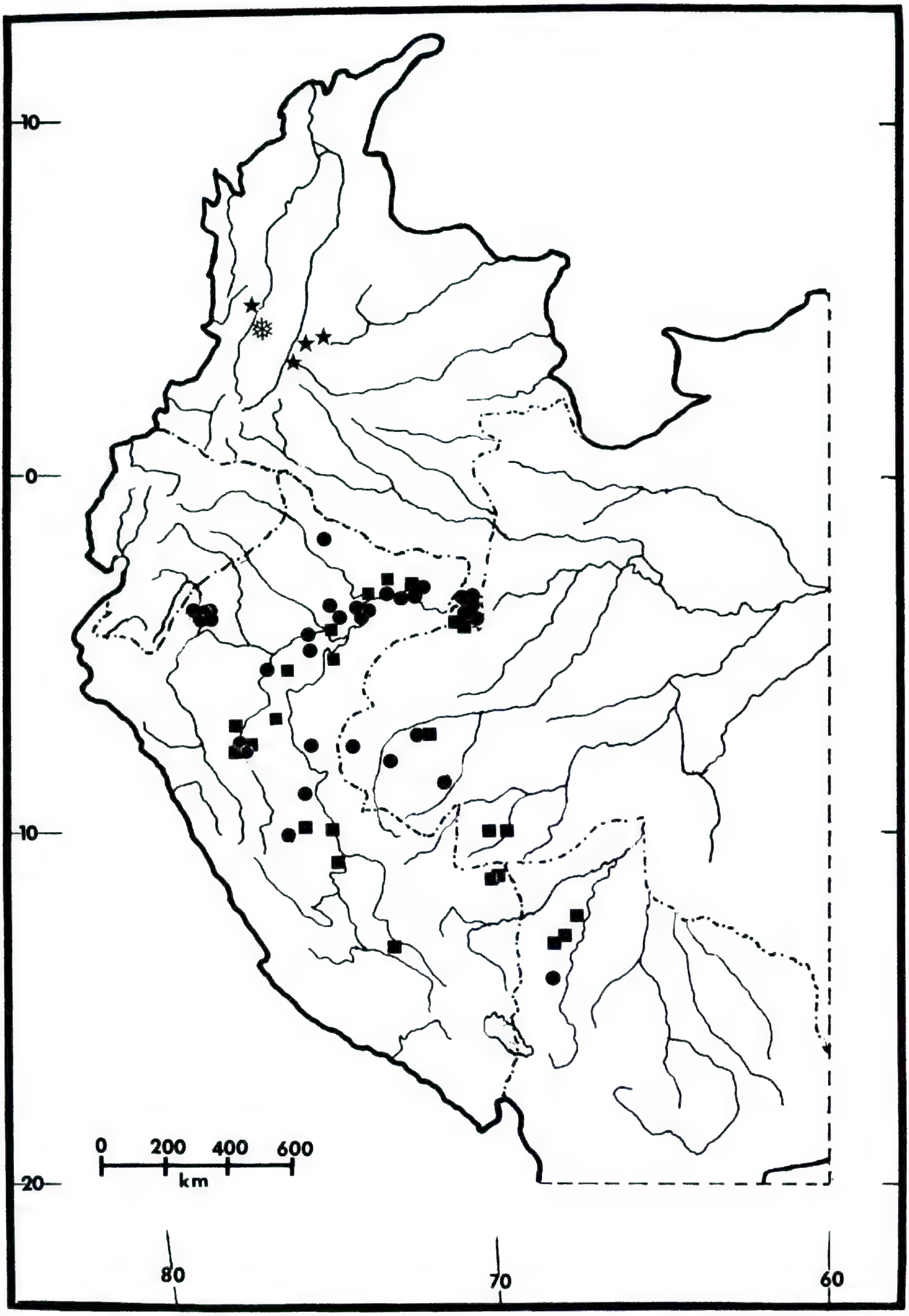


FIGURE 81. Distributions of *Eucharis bonplandii* (stars), *E. caucana* (snowflake), *E. cyaneosperma* (squares) and *E. ulei* (circles) in northwestern-central South America.

anthers; stigma 2–2.7 mm wide. Ovary subglobose, ca. 5–6 mm diam.; ovules 2–3 per locule. Capsule ca. 1 cm long, 2 cm wide, bright orange, leathery; seeds 1–2 per locule, ellipsoid, ca. 1 cm long, ca. 0.5 mm diam., with a lustrous black testa. Chromosome number: $2n = 92$.

Distribution. Rare in central and western Colombia (Fig. 81), in the understory of lower montane rain forest, 400–600(–1,300 m). Flowering February–March, May–June, August.

Additonal specimens examined. COLOMBIA. Department unknown: La Mejita (?), June 1844, *Goudot s.n.* (K, P). CALDAS: Cauca Valley, Tabeja, west of Armenia, 1,100–1,300 m, 23 July 1922, *Pennell et al. 8604* (GH, NY, US). CUNDINAMARCA: Viotá, Quebrada Cachinibulo, 550 m, 18 Feb. 1876, *Andre 1583* (K); same locality as preceding, 600 m, 19 Feb. 1876, *Andre 1721* (K); ex hort. originally collected by J. Paxton near Bogotá, ca. 650 m, received from Foster Gardens, Hawaii, 14 May 1982, *Meerow 1098* (FLAS). TOLIMA: valle del Alto Magdalena, vereda La Chamba (municipio del Guamo), 400 m, 3 Mar. 1963 (fr), *Uribe 4218* (COL).

Eucharis bonplandii is one of only two tetraploid ($2n = 92$) species so far known in the genus. The species is known only from Colombia, and has been rarely collected. Among Amazonian species, *E. bonplandii* has the greatest phenetic relationship to *E. ulei*, with five similarly sized flowers and two ovules per locule in common. It may be separated from *E. ulei* by having succulent, glaucous leaves and short petioles. The staminal cup of *E. bonplandii* is pigmented pale yellow at its base; that of *E. ulei* is marked green. *Eucharis bonplandii* and *E. bouchei* are the northernmost species of subg. *Eucharis*, and thus may form a monophyletic, tetraploid group (Meerow, 1987d). Both species have relatively short petioles. From *E. bouchei*, *E. bonplandii* differs primarily by its leaf glaucousness and longer pedicels.

5. Eucharis bouchei Woodson & Allen, Ann. Missouri Bot. Gard. 24: 181. 1937. *Urceolina bouchei* (Woodson & Allen) Traub, Pl. Life 27: 57–59. 1971. TYPE: Panama. Coclé: El Valle de Antón, 500–700 m, 23–27 July 1935, *Seibert 466* (holotype, MO). Figure 82.

Bulb subglobose, 30–45(–85) mm long, (25–)30–40(–50) mm diam.; neck short, to 25 mm long, 10–20 mm wide; tunics brown. Leaves 1–3(–4); petiole (9–)15–25(–28) cm long, 7–8 mm wide proximally, 5–6 mm wide distally; lamina widely (ovate-)elliptic, (17–)20–25(–40) cm long, (7–)8–10(–14) cm wide, shortly acuminate, slightly succulent, lustrous bright green adaxially, dull pale green abaxially, smooth, margins mostly nonundulate; abaxial cuticle largely devoid of striation. Scape ca. (4–)5.5 dm tall, ca. 1 cm diam. proximally, ca. 5 mm diam. distally; bracts ovate-lanceolate, 25–36(–47) mm long, (5–)7–10 mm wide at the base. Flowers (3–)5(–6); usually pendent, sometimes only declinate, not fragrant; pedicels 5–10(–20) mm long, very rarely less than 5 mm; tube (25–)33–45 mm long, cylindrical and (1.5–)2–2.5(–3) mm for most of its length, abruptly dilated near the throat to (7–)8–10(–12) mm wide, usually curved gradually, but sometimes only curved abruptly at the base, in which case nearly straight for most of its length; tepals spreading widely from the throat (ca. 90°) or sometimes only at an angle of 45–60°; outer tepals ovate-lanceolate, (18–)21–28(–32) mm long, 8–11(–15) mm wide, apiculate; inner tepals ovate, (16–)20–26(–32) mm long, (10–)12–15(–17) mm wide, obtuse to acute. Staminal cup subcylindrical, 9–12(–15) mm long to apex of filament, (10–)12–15(–18) mm wide, deeply cleft between each stamen to 3–5 mm, usually edentate but variably lobed, acutely or obtusely bidentate, or irregularly toothed between each stamen, marked pale green to greenish yellow proximally; each stamen (3.5–)4–5 mm wide at the base, 4–6(–7) mm long, either trapezoidal in shape (in which case dilating gradually from apex to base), or abruptly dilated at ½–¼ of its length (in which case the upper portion narrowly subulate and 2–3 or 3–4 mm long, 1.5–2 mm wide); anthers oblong, 3.5–4.5 mm long; pollen grain 45.7–49.65 μm polar diam., 66.8–68.43 μm longest equatorial diam. Style (30–)45–60 mm long, exserted 0.5–1 cm beyond anthers; stigma 2–3 mm wide. Ovary globose or ellipsoid and deeply trigonous, rarely not trigonous, 5–8 mm long, 4–6(–6.5) mm diam., usually wider than long when deeply trigonous; ovules 2–3(–4, very rarely 5) per locule, superposed in the lower half of the cell. Capsule 1.5–2 cm long, 2–3 cm wide, bright orange, leathery; pedicels 15–27 mm long; seeds 1–2 per locule, ellipsoid, ca. 1 cm long, 0.5 cm diam., with a lustrous, smooth, black testa. Chromosome number: 2n = 92.

KEY TO THE VARIETIES OF *E. BOUCHEI*

1a. Staminal cup edentate, or occasionally with one obscure tooth at the base of one stamen; stamens trapezoidal and gradually dilated from apex to base or, if obscurely constricted distally, subulate portion more than 2 mm wide; Coclé and Colón provinces of Panama, rare in Panamá Province and in Costa Rica and Guatemala ..... 5a. *E. bouchei* var. *bouchei*

1b. Staminal cup lobed or toothed; stamens abruptly

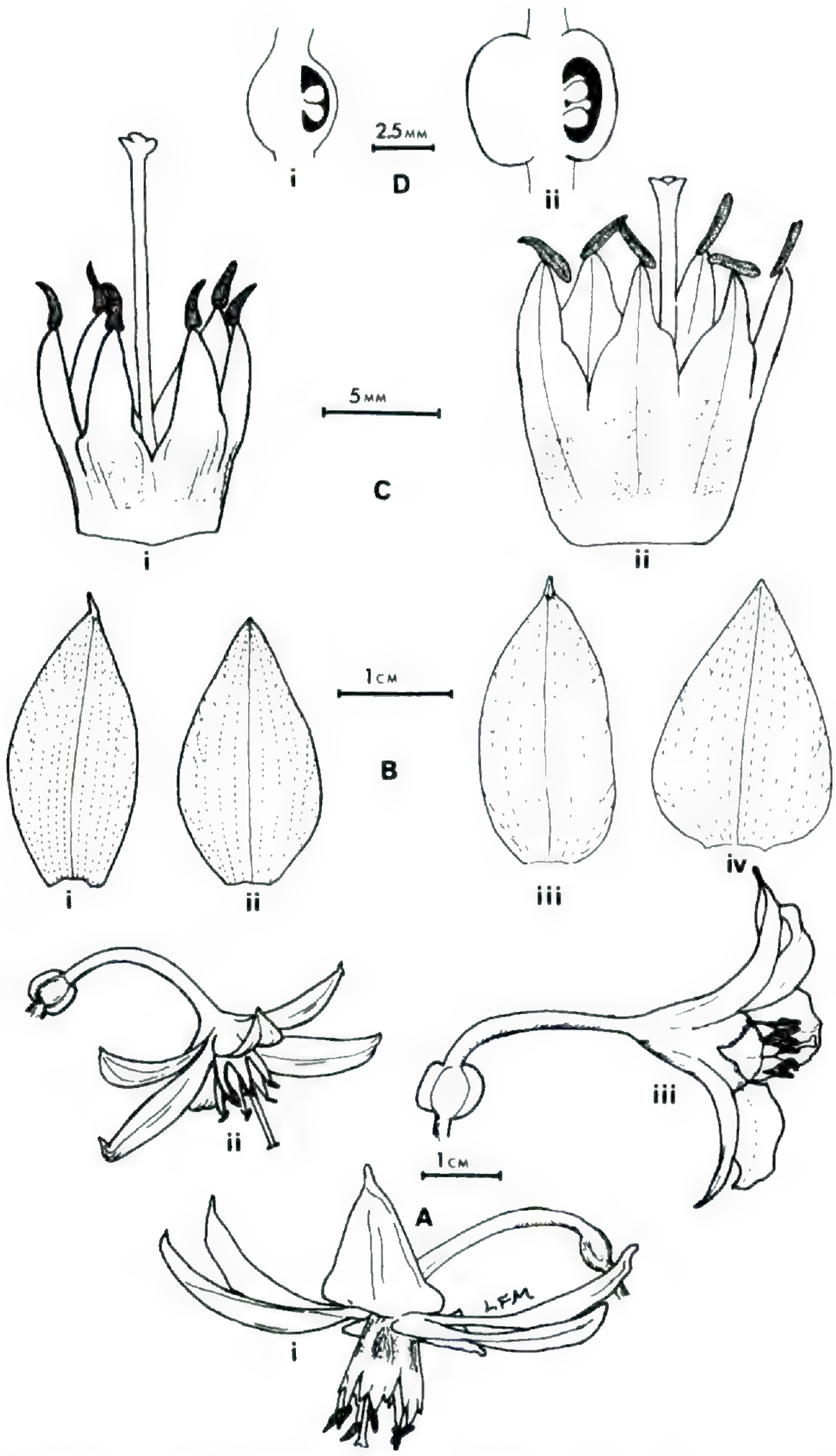


FIGURE 82. *Eucharis bouchei*.—A. Flowers. i. Variety *dressleri* (holotype, *Meerow 1107*, FLAS). ii, iii. Variety *bouchei*. ii, *Meerow 1125* (FLAS); iii, *Meerow 1157* (FLAS).—B. Tepals, variety *bouchei*. i, ii. *Meerow 1125*. i, outer tepal; ii, inner tepal. iii, iv. *Meerow 1157*. iii, outer tepal; iv, inner tepal.—C. Staminal cups, variety *bouchei*. i, *Meerow 1125*; ii, *Meerow 1157*.—D. Ovaries, variety *bouchei*, longitudinal section. i, *Meerow 1125*; ii, *Meerow 1157*.

constricted distally at ½–¼ length into a subulate portion 1.5–2 mm wide 2

2a. Outer tepals 26–32 mm long; staminal cup irregularly toothed, the teeth acute; subulate portion of filament 3.5–4.5 mm long; ovary not deeply trigonous; ovules 2–4 per locule; Coclé Province of Panama near El Valle ..... 5b. *E. bouchei* var. *dressleri*

2b. Outer tepals 20–26 mm long; staminal cup obtusely bidentate or lobed; subulate portion of filament up to 3.5 mm long; ovary deeply trigonous; ovules 2–5 per locule; Panamá and Darién provinces of Panama, rare in Guatemala ..... 5c. *E. bouchei* var. *darienensis*

5a. Eucharis bouchei var. **bouchei**. Figures 70Ci–ii, 82Aii–iii, B.

Perianth tube (30.8–)34–45 mm long; outer tepals (18–)24–28(–35) mm long, (8.8–)9.4–15.5 mm wide; inner tepals 21–26(–31) mm long, 11–17.5 mm wide. Staminal cup (8, 9–)11.5–15(–16.7) mm long (to apex of filaments), (9–)12–15.5(–16, 18) mm wide, edentate or rarely with a single obscure tooth between one or several stamens; each stamen trapezoidal in shape, dilating gradually from apex to base, or, if obscurely constricted in the distal 2–3 mm, then the subulate

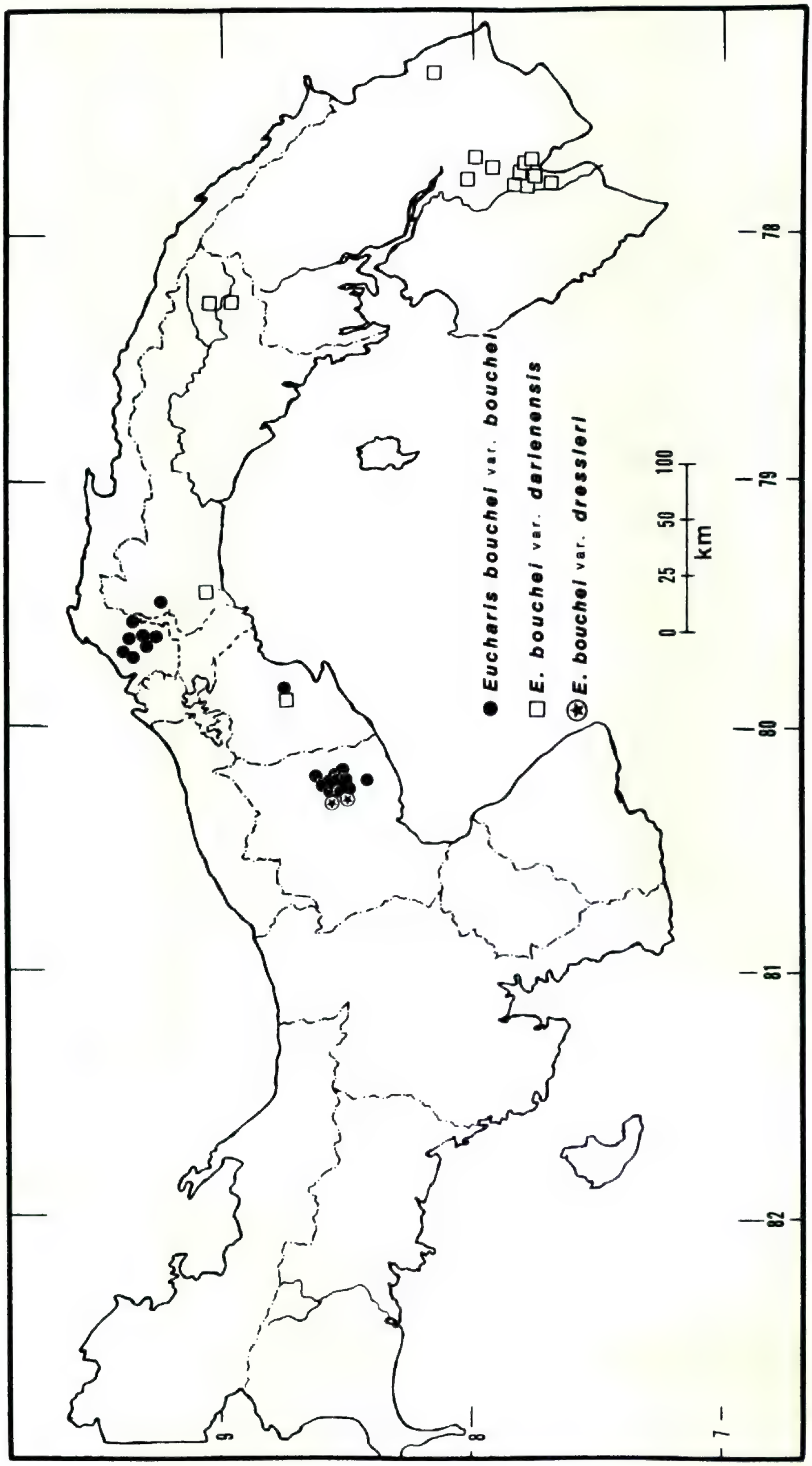


FIGURE 83. Distribution of *Eucharis bouchei* in Panama.

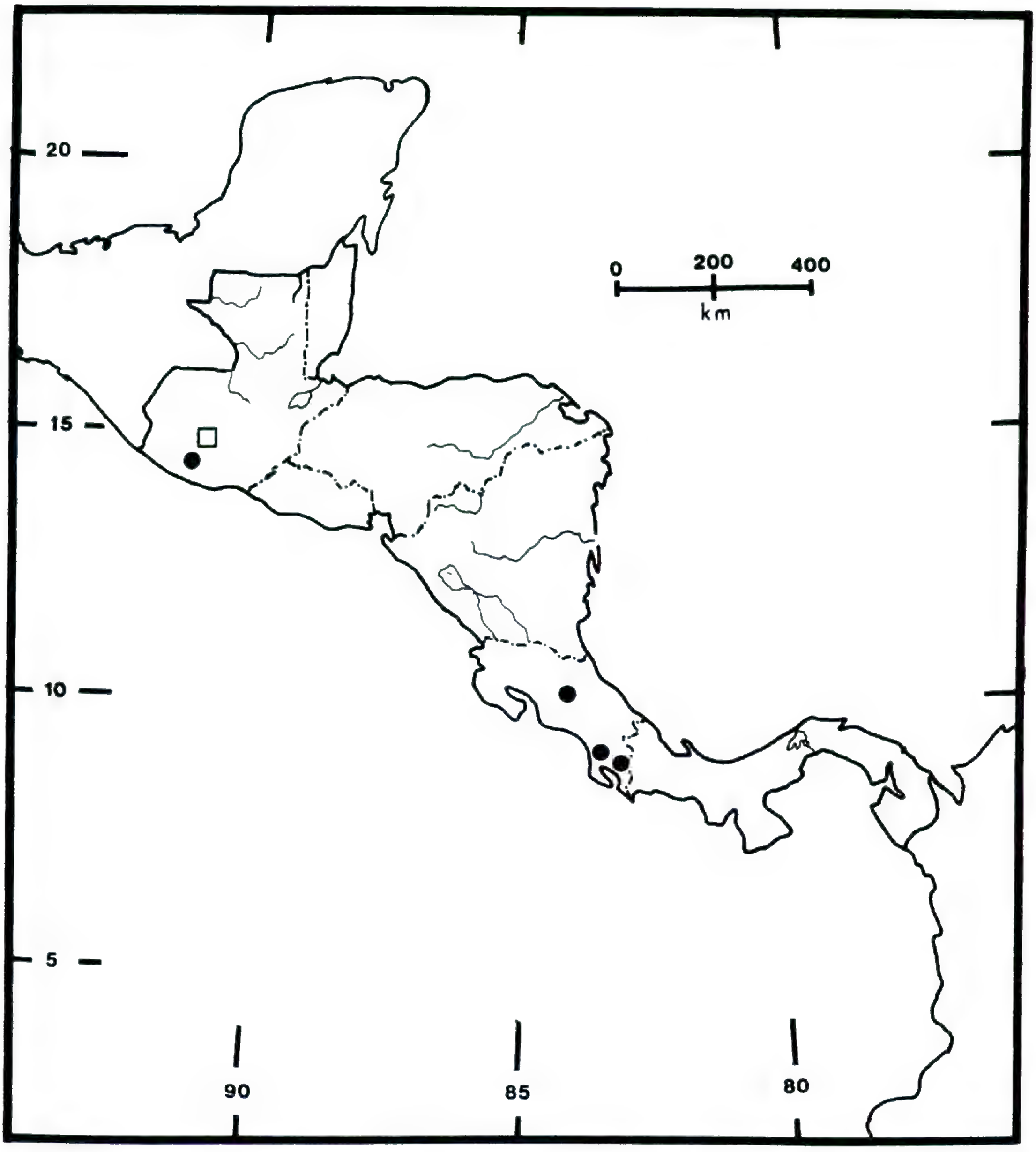


FIGURE 84. Distribution of *Eucharis bouchei* in Central America exclusive of Panama. Circles = *Eucharis bouchei* var. *bouchei*; square = *E. bouchei* var. *darienensis*.

portion wider than 2 mm. Style exserted ca. 1 cm beyond the anthers. Ovary trigonous; ovules 2–3(–4) per locule.

Distribution. Understory of primary, premontane and lower montane rain forest in Coclé and Colón provinces of Panama (Fig. 83), particularly in the vicinity of El Valle de Antón and the Río Guanche valley; rare in Panamá Province, Costa Rica, and Guatemala (Fig. 84); frequently on steep slopes; (200–)500–1,000 m. Flowering (March) June–August, October–December.

Additional specimens examined. COSTA RICA. PUNTARENAS: Canton de Osa, hills near Palmar Norte, Río Grande de Terraba, 2,000 ft., *Allen 5347* (F, K, MO, US); cataratas de San Ramón, 26 Feb. 1931, *Brenes 13515* (F). SAN JOSÉ: El Rodeo, Mar. 1931, *Lankester s.n.* (F). GUATEMALA. SUCHITEPEQUEZ: Finca Moca, steep, bushy slope, 3,300 ft., 31 Oct. 1934, *Skutch 1585* (F). PANAMA. COCLÉ: lower Río Antón, vic. El Valle de Antón, 800–1,000 m, 30 Dec. 1936, *Allen 120* (GH, MO); vic.

of El Valle de Antón, 600–1,000 m, *Allen 1228* (GH, MO); vic. El Valle de Antón, ca. 600 m, 10 Dec. 1939, *Allen 2063* (MO); hills north of El Valle de Antón, 100 m, 14 Aug. 1940, *Allen 2182* (MO); region north of El Valle de Antón, ca. 1,000 m, 21 Aug. 1946, *Allen 3641* (G); La Mesa, above El Valle, 600–800 m, 18 Jan. 1968 (fr), *Duke & Dwyer 15180* (NY); 1–3 mi. W of Portobello, *Gentry 1750* (MO); foot of Cerro Pilón, 11 Jan. 1972 (fr), *Gentry & Dwyer 3634* (F, MO); foot of Cerro Pilón, 11 Jan. 1972 (fr), *Gentry & Dwyer 3636* (MO); El Valle de Antón, along Río Indio Trail, 500–700 m, (fr), *Hunter & Allen 338* (G, MO, P, US); el Valle de Antón, 1,000–2,000 ft., edge of cloud forest and roadside, Dec. 1967, *Lewis et al. 2617* (MO); ex hort. from bulb collected by M. Whitten & M. Elliot, vic. El Valle, flowered in cultivation, 25 July 1984, *Meerow 1125* (FLAS); Cerro Pilón, 5 km north of El Valle, 800–1,045 m, 13 June 1975, *Mori et al. 6586* (AAU); Quebrada Amarillo, north of El Valle, 17 Oct. 1975, *Witherspoon & Witherspoon* 8736 (MO). COLÓN: Río Guanche, 16 Nov. 1975, *D'Arcy 9679* (MO); hills just north of Río Guanche, 1–200 m, 16 Nov. 1975 (fr), *Davidse & D'Arcy 10096* (MO); Cerro Brujo, ex hort., collected by R. Dressler, flowered in cultivation, July 1985, *Meerow 1157* (FLAS); trail south of Río Guanche, on ridge to Cerro Pan de Azucar, 200 m, *Mori & Kallunki 2014* (AAU); Río Guanche, 6 Nov. 1974 (fr), *Mori & Kallunki 3019* (AAU). PANAMÁ: mountains above Torti Arriba, 2 Dec. 1977, *Folsom et al. 6582* (AAU, BM, MO); near Cerro Campana, on trails radiating from end of road which passes Campana water tank, 23 Aug. 1967, *Kirkbride & Hayden 305* (MO, NY).

5b. Eucharis bouchei var. **dressleri** Meerow, var. nov. TYPE: Panama. Coclé: El Valle de Antón, from bulbs collected by R. Dressler in Panama, flowered in cultivation, 17 Mar. 1983, *Merrow 1107* (holotype, FLAS). Figure 82Ai.

Varietas haec ab varietas typica differt staminibus acute dentatis ad 1.5–2.7 mm distale concratis, ovario non trigono, et ovulis in quoque loculo aliquando plurimioribus.

Perianth tube 30–41 mm long; outer tepals 26.2–32 mm long, 6–10 mm wide; inner tepals 24–28 mm long, 9–13.5 mm wide. Staminal cup 10–16 mm long (to apex of filaments), 9.5–11.5 mm wide, irregularly toothed (some stamens lobed or quadrate), the teeth acute and 1.5–2.7 mm long; each stamen distally constricted abruptly at ½ length, the subulate portion 3.5–4.5 mm long, ca. 1.8 mm wide. Style exserted ca. 0.5 cm beyond the anthers. Ovary not trigonous; ovules 2–4 per locule.

This variety is named in honor of Robert L. Dressler, well-known tropical biologist.

Distribution. Rare rain forest understory herb in Coclé Province of Panama (Fig. 83), in the vicinity of El Valle de Antón, ca. 900 m. Flowering in June.

Additional specimens examined. PANAMA. COCLÉ: El Valle de Antón, 900 m, 4 June 1939, *Alston 8727* (BM).

5c. Eucharis bouchei var. **darienensis** Meerow, var. nov. TYPE: Panama. Darién: valley between Cerro Pirre and next most southerly peak, July 1977, *Folsom 4402* (holotype, MO). Figure 70Civ.

Varietas a *Eucharis bouchei* var. *dressleri* affinis sed differt staminibus obtuse dentatis vel lobis et parte staminea distale subulata breviore.

Perianth tube 25.5–36(–43.4) mm long; outer tepals 20–26 mm long, 8–11 mm wide; inner tepals 10.5–24 mm long, (11–)12–15(–16.5) mm wide. Staminal cup 9–10(–13, 16) mm long (to apex of filaments), 12–14.5(–18) mm wide, obtusely bidentate or lobed, the teeth when present ca. 1–1.5 mm long; each stamen distally constricted abruptly at ½–¼ length; the subulate portion ca. 1.7–3 mm long, 1.5–2 mm wide. Style exserted less than 0.5 cm beyond the anthers. Ovary trigonous; ovules 2–5 per locule.

The varietal epithet refers to Darién Province of Panama, where *E. bouchei* var. *darienensis* is most frequently collected.

Distribution. Understory of primary rain forest in Darién Province of Panama (Fig. 83); rare in Panamá Province and in Guatemala (Fig. 84); 480–1,450 m. Flowering January–February and June–August(–November).

Additional specimens examined. GUATEMALA. SOLOLA: between St. Pedro and Sta. Lucia, 20 Jan. 1857, *Wendland 207* (GOET). PANAMA. DARIÉN: La Boca de Pirre, 13 Oct. 1967 (fr), *Bristan 1285* (MO); vicinity of airstrip at Cana gold mine, 480 m, disturbed forest, 29 July 1976, *Croat 37956* (AAU); Cerro Pirre, cloud forest and/or mossy forest, 2,500–4,500 ft., Aug. 1967, *Duke & Elias 3661* (GH, MO, US); Cerro Tacarcuna, south slope, 1,250–1,450 m, 26 Jan. 1975, *Gentry & Mori 13945* (MO); 0–2 mi. E of Tres Bocas, along shortest headwaters of Río Cuasi, premontane rain forest, 28 Mar. 1968 (fr), *Kirkbride & Duke 1175* (MO); vicinity Cana, 1,750 ft., rare on forest floor, 23 June 1959, *Stern et al. 499* (GH); gold mine at Cana, 480 m, 26 July 1976 (fr), *Sullivan 626* (MO); trail northwest of Cana, 600 m, 28 July 1976 (fr), *Sullivan 718* (MO); gold mine at Cana, 480 m, 29 July 1976 (fr), *Sullivan 753* (MO); Cana–Cuasi trail, Chepigano, 2,000 ft., 12 Mar. 1940 (fr), *Terry & Terry 1533* (F). PANAMÁ: stream flowing out of Serranía de Maje, 10 Feb. 1977 (fr), *Folsom & Collins 1725* (MO); Maje, 5 mi. up Río Maje, steep forested ridge above Chocó Indian trail, 400 m, 19 Nov. 1970, *Kennedy 680* (MO, US); woods around La Eneida, 1,000 m, 5 Aug. 1970 (fr), *Luteyn & Kennedy 1761* (F); lower slopes and trail to Cerro Campana, 13 Sep. 1975, *Witherspoon & Witherspoon 8372* (MO).

Eucharis bouchei is the northernmost species of *Eucharis*, and the only species found north of the Darién Gap. It is also the most variable species in the genus, in characteristics that elsewhere justify specific delimitation. Patterns of variation in floral size and tube and limb habit form a complete mosaic throughout the range of *E. bouchei* that shows little or no geographic consistency (Meerow, 1987d). Staminal cup morphology (Fig. 70C) does, however, demonstrate a fair degree of geographical consistency, and it is chiefly on this basis that I have recognized var. *bouchei* and var. *darienensis*. Variety *dressleri*, rarely enountered mixed with var *bouchei*, presents a special case, discussed below.

Variety *bouchei*, most common around El Valle de Antón in Coclé Province, is recognized by its largely edentate staminal cup in which the trapezoidal free filament is not markedly constricted distally into a narrow subulate portion (Figs. 70Ci, ii, 82C). The staminal cup of variety *darienenis*, found both in Panamá and Darién provinces, is obtusely bidentate or lobed (Fig. 70Civ). The free filament constricts distally into a narrow (< 2 mm) subulate portion. These two varieties occur in close proximity in one location, near Cerro Campana in Panamá Province (Fig. 83).

The rare var. *dressleri* (Fig. 82Ai), with its acutely toothed staminal cup (Fig. 70Ciii) and shallowly trigonous ovary, occurs close to populations of var. *bouchei*, which is an unstable tetraploid, producing at least some cells with diploid ($2n$ = 46) chromosome number (Meerow, 1987d). This variety also does not express either heterozygous or additive banding phenotypes for isozymes of aspartate amino transferase, which otherwise characterizes electrophoretic phenotypes of *E. bouchei* (Meerow, 1987d).

The unprecedented degree of variation in *E. bouchei* is likely the result of two main factors: (1) the species is tetraploid, and (2) it probably represents a geologically recent colonization of Central America by this primarily northern Andean and Amazonian genus (Meerow, 1987d).

Northwesternmost populations representing var. *bouchei* have the most derived androecial morphology (Fig. 70Ci, ii) relative to southeasterly populations (var. *darienensis*, Fig. 70Civ). The latter have staminal cups similar to the generalized morphology characteristic of Andean and Amazonian species of subg. *Eucharis*. This suggests that general movement of *E. bouchei* in Central America has been away from the Colombian border. The occasional presence of *E. bouchei* in Costa Rica is not surprising, but the two reported collections from Guatemala (*Wendland 207* and *Skutch 1585*) represent a substantial disjunction, or two disjunctions, since the two collections represent different varieties. Given the history of cultivation of Amazonian *Eucharis* by Indian people for medicinal, ceremonial, and possibly ornamental use, the same may have held true in Central America.

6. Eucharis astrophiala (Ravenna) Ravenna, Phytologia 57: 95–96. 1985. *Urceolina astrophiala* Ravenna, Pl. Life 38: 49. 1982. TYPE: Ecuador. Cotopaxi: Quevedo–Latacunga road, km 46 from Quevedo, 79°11′W, 0°55′S, 600 m, 4 Apr. 1973, *Holm-Nielsen et al. 2851* (holotype not seen, AAU; isotype, S). Figure 85.

Bulb globose, 4–5 cm long, 3–4 cm wide, usually without an appreciable neck, tunics tannish brown. Leaves 2–4 at anthesis, elliptic- or ovate-lanceolate; petiole 10–20 cm long, 4–5.5 mm thick; lamina 15–25 cm long, 5–10 cm wide, thin, nonlustrous, deeply plicate and pustulate, adaxial surface light green, the white midrib conspicuous; abaxial surface whitish green; margin slightly undulate; apically acuminate; basally attenuate to the petiole. Scape 3–4(–5) dm tall, ca. 5 mm diam.; bracts 29–35(–40) mm long, lanceolate. Flowers 5–8(–10); pedicels 8–14 mm long; tube 28–35 mm long, ca. 2 mm wide for most of its length, dilating to (4–)5–6 mm at the throat, strongly curved; perianth limb spreading to 4–5 cm wide; outer tepals 25–30 mm long, (7–)10 mm wide, lanceolate, apiculate; inner tepals 25–28 mm long, 10–12(–14) mm wide, ovate-lanceolate to ovate, acute. Staminal cup funnelform-cylindrical, (10–)12–14 mm long, 8–12 mm wide, edentate, stained orange-yellow basally, cleft between each stamen for ½–⅔ of its length; each free filament (5–)6.4–6.9 mm long, ca. (2.5–)3.5–4.5 mm wide at the base, deltoid; anthers oblong, 5–5.5 mm long; average pollen grain 58.6–60.6 μm polar diam., 83.0–86.1 μm longest equatorial diam. Style 50–55 mm long, exserted 5–10 mm beyond the staminal cup; stigma 3-lobed, ca. 2 mm wide. Ovary globose-trigonous, 3.9–4.5 mm long, 3.2–4 mm wide, white at anthesis; ovules 2–3(–4) per locule, medially superposed. Capsule ca. 1–1.5 cm long, 2–2.5 cm wide, bright orange, leathery; seeds 1–2 per locule, ellipsoid, ca. 1 cm long, 0.5 cm diam., with a lustrous, smooth black testa. Chromosome number: $2n$ = 46.

Distribution. Endemic to the western declivity of the Andes in north-central Ecuador (Fig. 86), particularly in contiguous areas of Cotopaxi, Los

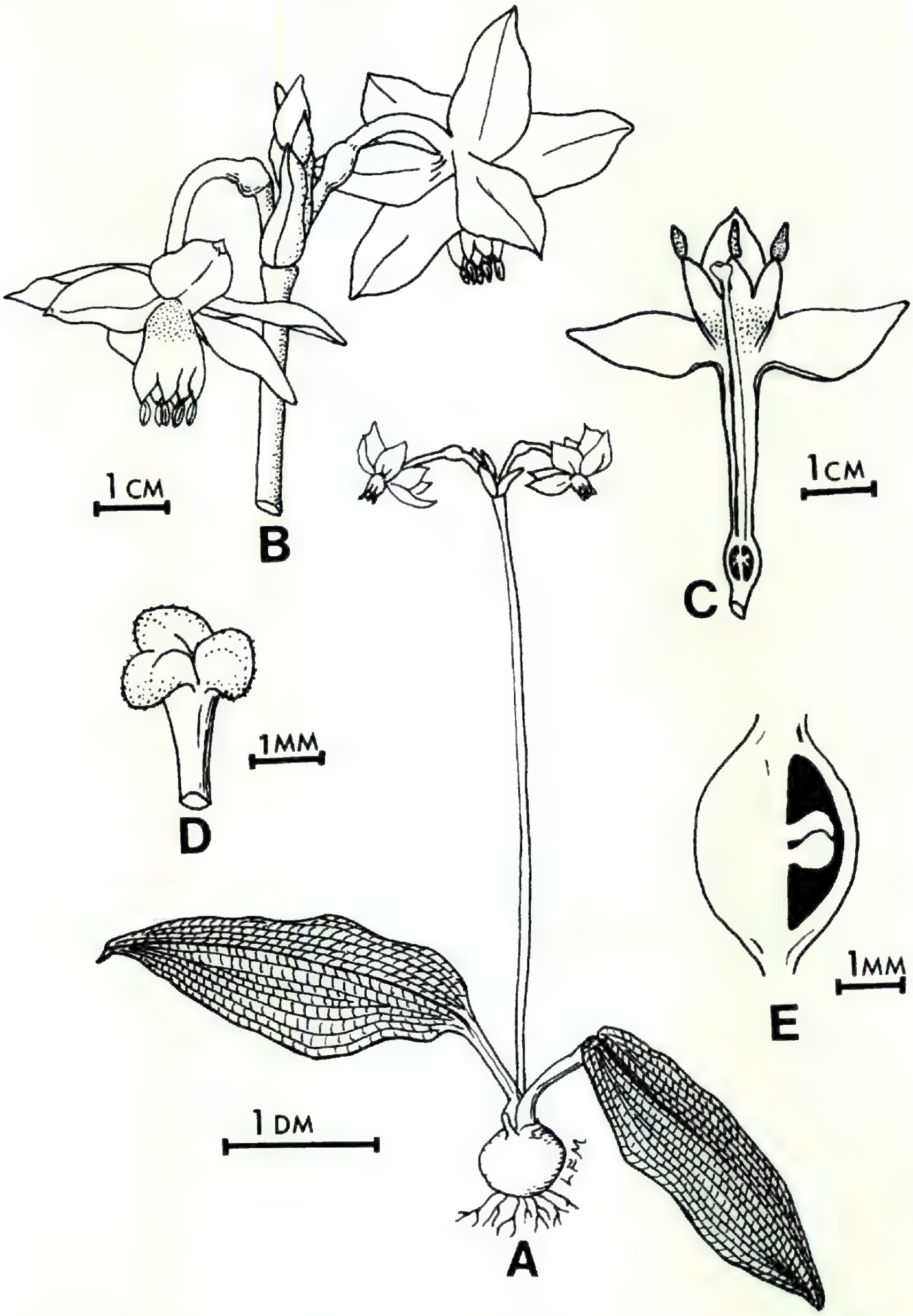


FIGURE 85. *Eucharis astrophiala*, adapted from a drawing by Boots N. Culbertson of *Dodson et al. 7122* (SEL).—A. Habit.—B. Inflorescence.—C. Flower, longitudinal section.—D. Stigma.—E. Ovary, longitudinal section.

Ríos, and Pichincha provinces, occupying the understory of lower montane rain forest (250–)400–800(–1,100) m elevation. Sporadic flowering may occur at any time but is concentrated in the wetter months of the year.

Additional specimens examined. ECUADOR. BOLÍVAR: Limón, 800–1,100 m, 14 Oct. 1943, *Acosta-Solís 6374* (F). CHIMBORAZO: km 52–53 on Quevedo–Latacunga road, Tenefuerste, Río Pilalo, Tenefuerste, 750 m, 21 Feb. 1982, *Dodson & Gentry 12815* (MO, SEL); same locality as *Dodson & Gentry 10187*, 23 May 1983, *Dodson & Gentry 13793* (MO, SEL); Puente de Chimbo, 250 m, June 1876, *Lehmann 7775* (K). COTOPAXI: km 40 on road from Quevedo to Latacunga, 600 m, 6 Mar. 1975, *Dodson 5864* (MO, SEL, US); 3 km E of El Palmar on Quevedo–Latacunga rd., 800 m, 5 Apr. 1980, *Dodson & Gentry 10187* (MO, SEL); same locality as *Dodson & Gentry 12815*, 750 m, sterile, 15 Aug. 1984, *Meerow & Meerow 1140* (FLAS). LOS RÍOS: forested hills 12 km east of Patricia Pilar, 650 m, 9 Apr. 1977, *Madison 3792* (NY). PICHINCHA: Carretera Quito–Puerto Quito, km 113, 00°05′N, 79°02′W, 10 km al norte de la carretera principal, 800 m, 27–29 Dec. 1983, *Balslev & Balseca 4695* (NY, QCA); same locality, 28 Feb. 1984, *Bravo E. 417* (QCA); Centinela, Canton Santo Domingo, km 12 E of Patricia Pilar, 600 m, 17 Aug. 1978, *Dodson et al. 7122* (MO, SEL); 2 km SE of Santo Domingo de los Colorados along Río Verde, 530 m, 5 Feb. 1979,

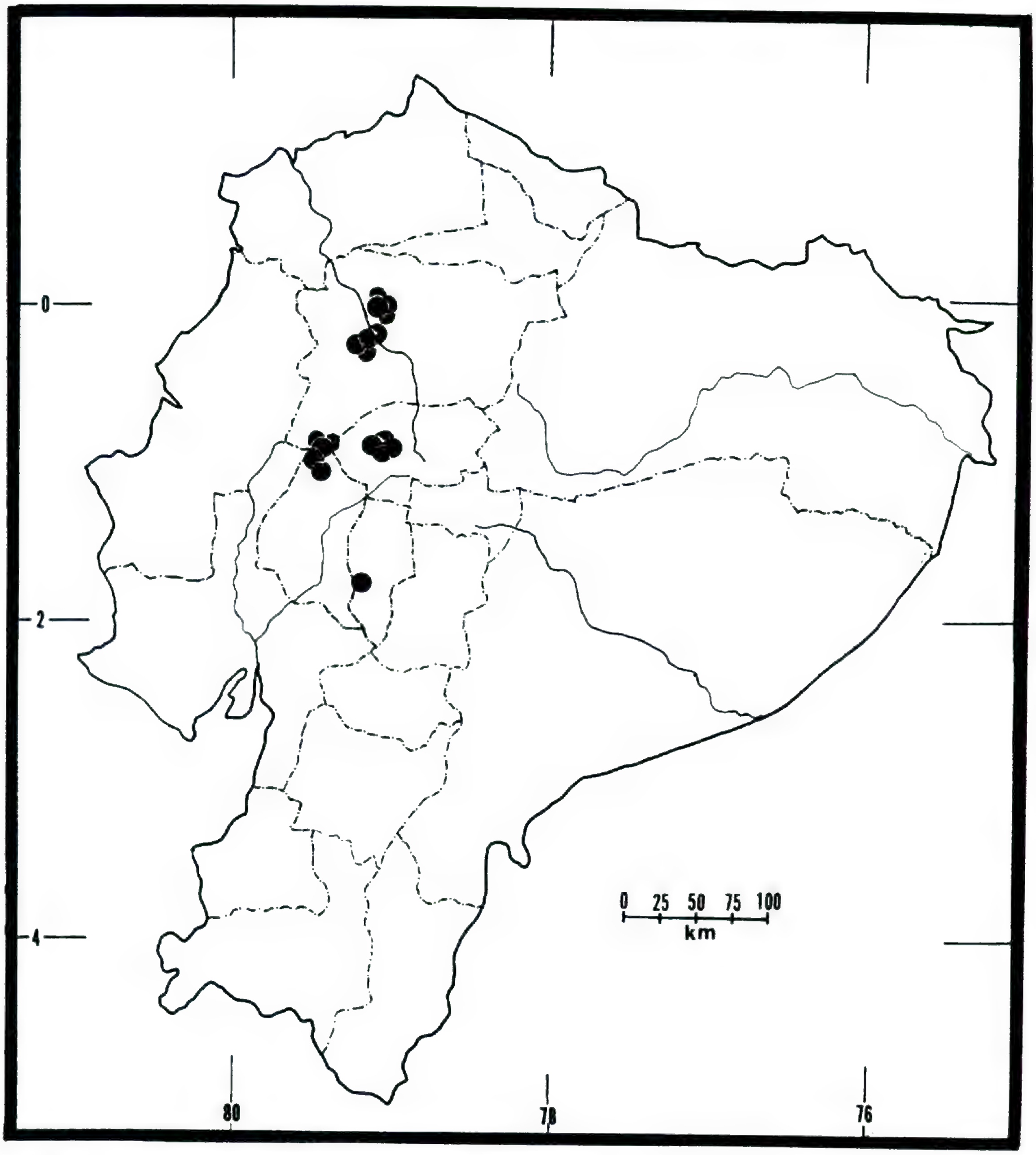
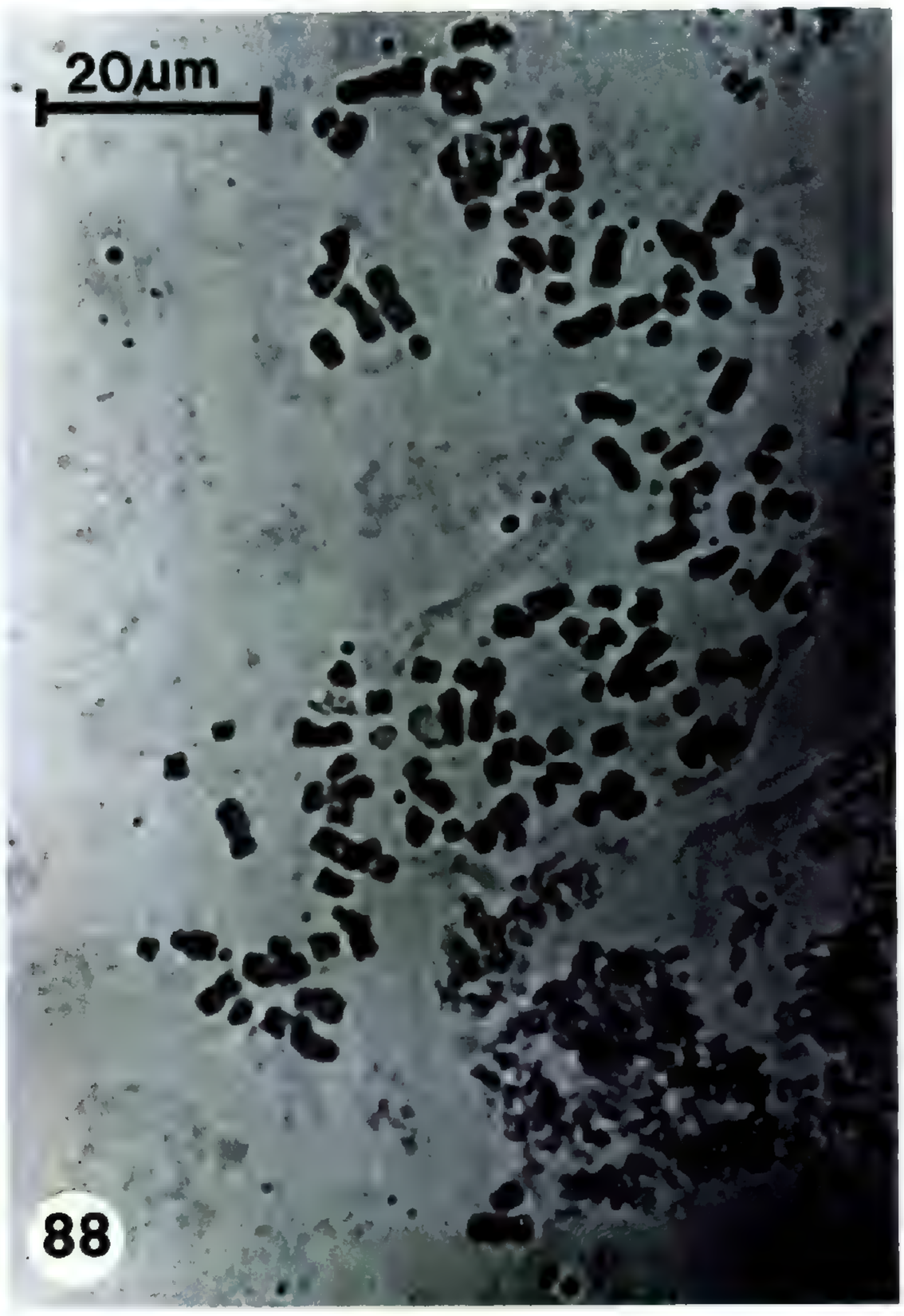


FIGURE 86. Distribution of *Eucharis astrophiala* in Ecuador.

Dodson & Duke 7714 (MO, SEL); road from Patricia Pilar to 24 de Mayo at km 12, path following ridge line at El Centinela at crest of Montañas de Ila, 600 m, 6 Apr. 1980, *Dodson & Gentry 10298* (MO, SEL); Centinela, km 12 on road from Patricia Pilar to 24 de Mayo, km 47 Santo Domingo–Quevedo, 650 m, 30 July 1984, *Dodson et al. 14666* (MO); Centinela, 12 km W of Patricia Pilar, km 45 Santo Domingo–Quevedo, 600 m, 2 Feb. 1985, *Dodson & Neill 15532* (MO); Reserva Endesa, ca. 6 km WNW of P. Vicente Maldonado, mature rain forest, ca. 800 m, 24 Mar. 1985, *Harling & Andersson 23279* (GB); Reserva Forestal Endesa, Río Silanche, km 113 Quito–Puerto Quito, 10 km N of main highway, 0°5′N, 79°2′W, 650–700 m, 25 Feb. 1984, *Jaramillo 6439* (GB); Endesa, km 113 Quito–Puerto Quito, 750 m, 23–24 Apr. 1983, *Rodriguez et al. 91, 92 & 93* (QCA); Santo Domingo de los Colorados, Rancho Brahman, ca. 10 km NW of the town on road to Esmeraldas, 400 m, 31 Mar. 1967, *Sparre 15216* (S).

Eucharis astrophiala is easily separated from the other small-flowered species of subg. *Eucharis* by its uniquely bullate-pustulate and nonlustrous ovate-lanceolate leaves; edentate and deeply cleft staminal cup with deltoid free filaments (Fig. 85B, C); and the second-largest pollen grain in the genus (the largest is that of *E. caucana*). The largest



FIGURES 87, 88.—87. *Eucharis caucana* (type collection).—88. Root-tip mitotic metaphase chromosome configuration of *E. caucana* ($2n = 138$, type collection). Thirteen chromosomes are out of the figure frame.

chromosome pair of *E. astrophiala* is submetacentric, unlike the metacentric pair of all other species of the genus I have examined (Meerow, 1987b). It is the only species of the subgenus found exclusively on the western slopes of the Andes south of Colombia. It occurs sympatrically in some localities (fide *Dodson & Gentry 12815* and *Meerow & Meerow 1140*) with *E. moorei*, though the latter grows at slightly higher elevation in these areas. *Eucharis astrophiala* is the only species of subg. *Eucharis* that enters a definite rest period during the short dry season of the northwestern and central western Ecuadorean Andes. New growth completely ceases, though one or two leaves may persist for the duration.

7. Eucharis caucana Meerow, sp. nov. TYPE: Colombia. Valle de Cauca: between La Paila and Zarzal, Hacienda El Medio, 975 m, 14 Apr. 1987, *Silverstone-Sopkin et al. 3064* (holotype, FTG; isotypes not seen, CUVC). Figure 87.

Species nova affinis *E. lehmannii* Regel sed floribus breviter pedicellatis grandioribus et paucioribus, staminibus edentatis, et ovulis paucioribus in quoque loculo differt.

Bulb subglobose, 52–60 mm long, ca. 34 mm diam., without an appreciable neck, tunics brown. Leaves 2–3; petiole 21–25 cm long, 7.2–10 mm wide; lamina ovate–elliptic, ca. 25.5 cm long, 10–11 cm wide, plicate, the margins undulate, acuminate, attenuate at the base. Scape 4–5 dm tall, ca. 1 cm diam. proximally, 5 mm diam. distally; bracts 26–27 mm long, 8 mm wide, ovate-lanceolate. Flowers 2–3, slightly declinate, funnelform-campanulate, not fragrant; pedicels ca. 6.5 mm long, ca. 2 mm diam.; tube ca. 32 mm long, 2 mm wide proximally, dilating in its distal ⅓ to ca. 9.2 mm at the throat, abruptly curved near its base, the dilated portion stained green internally; limb spreading to ca. 3.5 cm, the tepals diverging from the throat at angles of 75–90°; outer tepals ca. 20 mm long, 9.5–10.3 mm wide, ovate, apiculate; inner tepals ca. 18–19 mm long, 11.5 mm wide, ovate, acute to obtuse. Staminal cup ca. 3 mm long (to apex of lobes), edentate, stained green proximally; stamens connate only in the proximal 0.7–1 mm; each filament ca. 10 mm long, narrowly subulate and ca. 1 mm wide in the distal 4–5 mm,

then abruptly dilated proximally to 3 mm wide; anthers oblong, ca. 4 mm long, gray-brown; pollen white, the exine coarsely reticulate, 55–75 μm polar diam., 98–110 μm longest equatorial diam. Style white, ca. 50 mm long, exserted ca. 1 cm beyond the anthers; stigma ca. 2 mm wide, greenish white. Ovary globose-trigonous, 7–7.5 mm diam., ovules 4–6 per locule. Capsule leathery, orange, ca. 1.5 cm long, 2.5 cm wide; seeds 2 per locule, ellipsoid, ca. 10 mm long, ca. 5 mm wide with a smooth, lustrous black testa. Chromosome number: $2n = 138$.

Named for the Río Cauca valley of Colombia to which the species is endemic.

Distribution. Endemic to Valle de Cauca Department in the vicinity of La Paila in western Colombia (Fig. 81). The type location is a 12.5-hectare remnant of primary forest planted with cacao in which canopy trees were retained for shade (*Anacardium excelsum*, *Nectandra caucana*).

Additional specimen examined. COLOMBIA. VALLE DE CAUCA: La Paila, 30 May 1853 (fr), *Holton s.n.* (NY).

The recent receipt of material collected by Phil Silverstone-Sopkin and coworkers is the first collection of the subgenus in the largely deforested Cauca valley since 1922.

Eucharis caucana has the largest pollen grains in the genus and is the only known hexaploid species of *Eucharis*, with a somatic chromosome number of $2n = 138$ (Fig. 88). As with most other South American peripheral isolates from the Amazonian center of distribution for subg. *Eucharis* (*E. astophiala*, *E. corynandra*, *E. lehmannii*, and *E. oxyandra*), *E. caucana* exhibits some degree of morphological novelty; in this case, reduction of staminal connation, funnelform-campanulate perianth, and very large pollen grains. Nonetheless, *E. caucana* has fruit and seed morphology typical of subgenus *Eucharis*. By its reduced staminal cup *E. caucana* shows affinity with *E. lehmannii* from which it differs by having larger flowers, shorter pedicels, straighter tubes, edentate androecia, and fewer ovules per locule. By its high polyploid chromosome number, short pedicels, and flower size, *E. caucana* shows similarity to certain populations of *E. bouchei* var. *bouchei*. Some collections of the latter from Colón Province exhibit funnelform-campanulate perianth morphology and floral tube habit like *E. caucana*. The discovery of this hexaploid species in Colombia supports the hypothesis that a polyploid complex of *Eucharis* may have existed in Colombia in the recent geologic past (Meerow, 1987d).

8. **Eucharis ulei** Kränzlin, Bot. Jahrb. 50, Beibl. 111: 4–5. 1913. *Urceolina ulei* (Kränzl.) Traub, Pl. Life 27: 57–59. 1971. TYPE: Brazil. Amazonas: Juruá Miry, June 1901, *Ule 5737a* (holotype, B), non *Ule 5737b* (in fruit) (B) vel *Ule 5737* (MG). Figure 89B, C.

Eucharis ipariensis (Ravenna) Ravenna, Phytologia 57: 95. 1984. *Urceolina ipariensis* Ravenna, Pl. Life 38: 50–51. 1982. TYPE: Peru. Huánuco: Pachitea, Honoria, Bosque Nacional de Iparia, Río Pachitea, 20 km above confluence with Río Ucayali, near Miel de Abeja, 1 km from Tuernavista, 26 Apr. 1967, *Schunke 1887* (holotype not seen, NY; isotypes, F, COL, G, US).

Eucharis moana (Ravenna) Ravenna, Phytologia 57: 95. 1984. *Urceolina moana* Ravenna, Pl. Life 38: 50. 1982. TYPE: Brazil. Acre: Río Moa at Serra da Moa village, 27 Apr. 1971, *Prance et al. 12491* (holotype, NY; isotypes, K, MO, not seen: herb. Ravenna).

Eucharis boliviensis Ravenna, Phytologia 64: 218. 1988. TYPE: Bolivia. El Beni: Covendo, 600 m, 19 Aug. 1921, *White 930* (holotype, NY; isotype, K).

Bulb subglobose, (2.5–)3.5–4.5(–5) cm long, 2–3.5(–4.5) cm in diam.; neck 1–2 cm long, ca. 1.5 cm wide; outermost tunics gray-brown, inner tunics tan. Leaves 2–3; petiole (10–)18–30(–35) cm long, 5–6 mm thick; lamina (narrowly) elliptic (average length : width > 3), 18–25(–33) cm long, (5–)7–10(–12.5) cm wide, acute to shortly acuminate, attenuate at the base. Scape (35–)40–58 cm tall, 8–10 mm diam. proximally, 3–4 mm diam. distally; bracts lanceolate to ovate-lanceolate, (25–)30–37(–54) mm long, greenish white. Flowers (3–)(–7), pendent, without fragrance; pedicels (8–)11–15(–20) mm long, ca. 2 mm diam.; tube (25–)28–35(–37.5) mm long, curved gradually for most of its length, 1.5–2(–2.5) mm wide for most of its length, abruptly dilated just below throat to (6–)7–10 mm; limb spreading to 40–45(–55) mm wide; outer tepals ovate-lanceolate, 24–28(–32) mm long, (6.5–)8–10(–11) mm wide, apiculate; inner tepals ovate, 23–27(–30) mm long, (9–)10–13(–15) mm wide, acute. Staminal cup funnelform-cylindrical, 10–12 mm long (to apex of teeth or lobes), 11–13(–16) mm wide, usually bidentate between each free filament, rarely edentate, irregularly toothed, or the teeth obscure (in which case the stamens quadrately lobed), cleft between each stamen for (1.5–)2–3(–4) mm, with a ± rectangular, green zone in the proximal half of each stamen; teeth acute or obtuse, 0.5–0.7 mm long; each stamen 3.5–4.5(–5.5) mm wide from tooth to tooth; free filament subulate, (3–)4.5–6 mm long, (1–)1.5–2

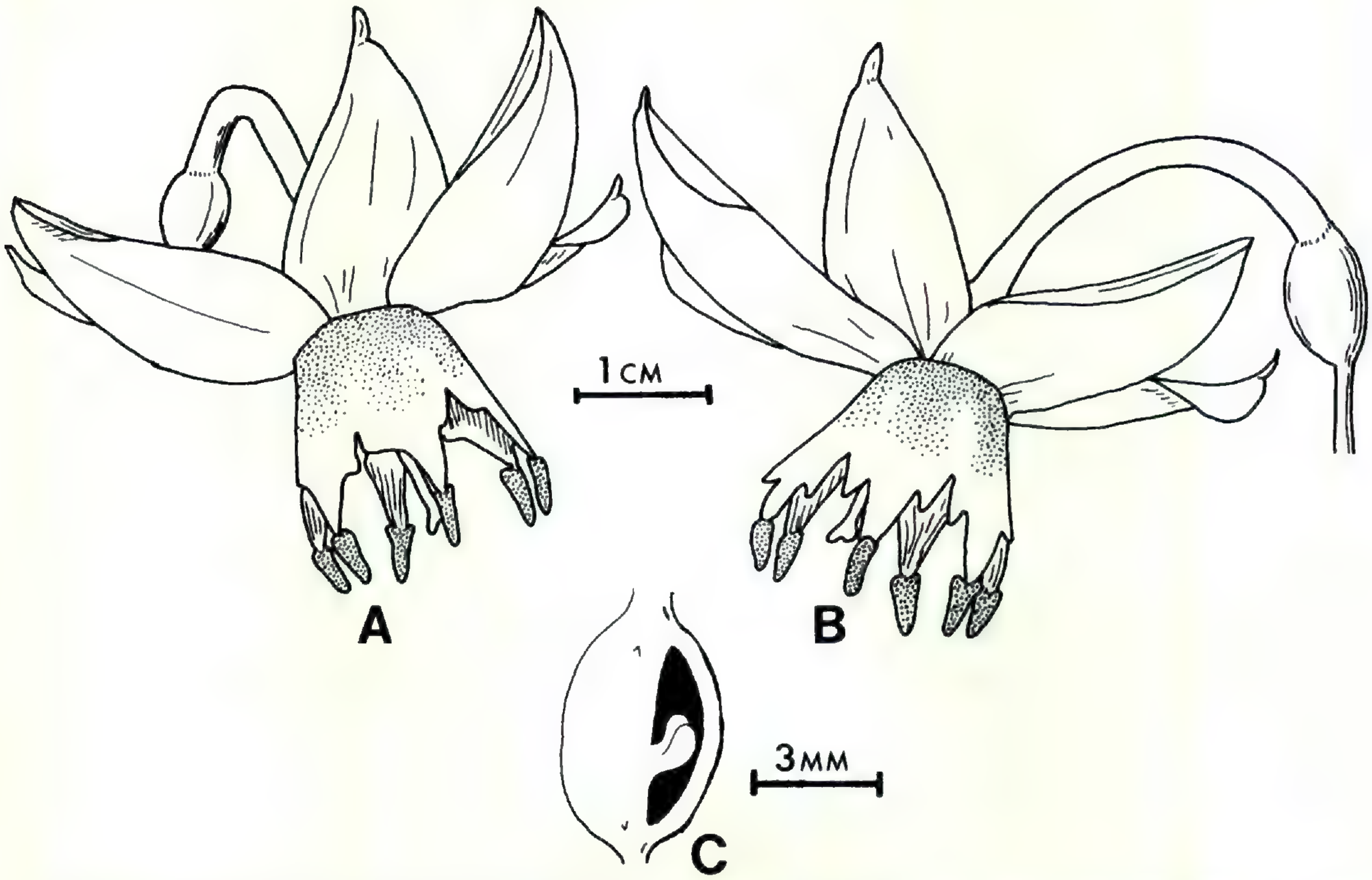


FIGURE 89. *Eucharis cyaneosperma* and *E. ulei*.—A. Flower of *E. cyaneosperma* (holotype, *Meerow 1032*, FLAS).—B. Flower of *E. ulei* (*Schunke 1887*, F).—C. Ovary of *E. ulei*, longitudinal section (*Schunke 1887*, F).

mm wide at its base; anthers oblong, 3–3.8 mm long; pollen grain ca. 49.35 μm polar diam., ca. 69.85 μm longest equatorial diam. Style (40–)45–50(–60) mm long; stigma 1.5–2.5 mm wide. Ovary globose-ellipsoid, 6–8.5(–10) mm long, 4–5.5 mm wide; ovules 2(–4) per locule, superposed in the lower half of the cell. Capsule 1.2–1.5 cm long, 2–2.5 cm wide, bright orange, leathery; pedicels 2–4 cm long; seeds 1–2 per locule, ellipsoid, 8–10 mm long, ca. 5 mm wide with a smooth, lustrous black testa.

Distribution. Understory of primary rain forest in the Amazon Basin and eastern Andean foothills, most common in Peru but sporadically encountered north to Colombia and south to Bolivia (Fig. 81), on fertile, usually noninundated, soils; 100–300(–1,000) m. Flowering at any time of the year, most frequently June–September.

Additonal specimens examined. BRAZIL. AMAZONAS: basin of Río Juruá, Foz da Tarauca, Yuma, rare, on varzea land, 1 June 1933, *Krukoff 4613* (NY); basin of Río Juruá, near mouth of Río Embira, 7°30′S, 70°15′W, 3 June 1933 (fr), *Krukoff 4637* (G, GH, K, NY, S, US); Río Purus, Río Itaxi, Seringal Jurucua, 120 km south of Labrea, 29 June 1971, *Prance et al. 13915* (MO, NY). PARA [?]: no data, *Ferreira s.n.* (P). COLOMBIA: AMAZONAS: Trapecio, confluencia de Río Loretoyacu con el Río Amazonas, Puerto Nariño, Mar. 1968, *Diaz-M 15* (COL); Trapecio amazonico, Boiauassu River, 100 m, Oct. 1946, *Schultes & Black 8608a* (US); Puerto Nariño, mouth of Río Loretoyacu, 100 m, 8 May 1972 (fr), *Plowman 3216* (COL, K). PERU. AMAZONAS: Río Santiago, canto de la Quebrada Caterpiza, 200 m, 11 Sep. 1979 (fr), *Huashicat 524* (MO); valle de Río Santiago, ca. 65 km norte de Pinglo, Quebrada Caterpiza, 2–3 km atras de la comunidad de Caterpiza, 200 m, 13 Oct. 1979 (fr), *Huashikat 930* (MO); same locality, 17 Dec. 1979, *Huashikat 1553* (MO); Monte del Isla, la isla 1 km bajo de La Poza, Río Santiago, 180 m, 8 Aug. 1979 (fr), *Leveau 7* (MO); same locality, 15 Aug. 1979 (fr), *Leveau 123* (MO); same locality, 8 Aug. 1979 (fr), *Pena 9* (MO). LORETO: Río Amazonas, SE of Iquitos, swampy forest, 17 Aug. 1972, *Croat 19289* (MO); Río Napo near Entrada de Isla Inayuga, edge of forest, 20 Sep. 1972 (fr), *Croat 20521* (MO); near Base Araguana, upper Río Mazán, ca. due north of Santa Maria de Nanay, noninundated forest, 9 July 1976 (fr), *Gentry & Revilla 16586* (MO); Maynas, Quebrada Yanomono, Explorama Tourist Camp, halfway between Indiana and mouth of Río Napo, mature noninundated forest on laterite, 4 Nov. 1979 (fr), *Gentry et al. 27438* (MO); Yanomeno, Explorama Tourist Camp, Río Amazonas above mouth of Río Napo, 72°48′W, 3°28′S, 130 m, upland forest on lateritic soil, 25 June 1982 (fr), *Gentry et al. 37204* (MO); Río Samiria, Flor de Yarina, ca. 5°2′S, 74°30′W, 160 m, noninundated restinga forest, *Gentry et al. 38103* (MO); Iquitos, ca. 100 m, 3–11 Aug. 1929, *Killip & Smith 27442* (US); Yurimaguas, lower Río Huallaga, ca. 135 m, 23 Aug.–7 Sep. 1929, *Killip & Smith 27656* (US); Río Marañon Valley, San Lorenzo, between mouths of Río Pastaza and Río Huallaga, 150 m, 20 Aug.–9 Sep. 1929, *Killip et al. 29227* (US); Iquitos, Muena-Caño, 105 m, 9 Feb. 1932, *Mexia 6504a* (F, UC); Maynas, Río Amazonas near Tamishiyacu, 3 Sep. 1976, *Revilla 1281* (MO); Pebas on Amazon

River, 25 July 1929 (fr), *Williams 1751* (F); Pebas on Amazon, 21 July 1929 (fr), *Williams 1787* (F); La Victoria on the Amazon, 21 Aug. 1929, *Williams 2629* (F); same locality as preceding, 29 Aug. 1929, *Williams 2938* (F); alto Río Itaya (San Antonio), 145 m, Sep.–Oct. 1929 (fr), *Williams 3398* (F); Puerto Arturo, Yurimaguas, lower Río Huallaga, 155–210 m, 16 Nov. 1929 (fr), *Williams 5148* (F). PASCO: Oxapampa, Palcazu valley, Cabeza de Mono, 5–6 km W of Iscosacin, 17–20 Apr. 1983, *Smith 3787* (MO); SAN MARTÍN: Mariscal Cáceres, Tocache Nuevo, Quebrada de Cachiyacu de Huaguisha, 570 m, 16 July 1982 (fr), *Meerow et al. 1023* (FLAS); Mariscal Cáceres, Tocache Nuevo, Quebrada de Cachiyacu de Huaguisha, 570 m, 16 July 1982, *Meerow et al. 1024* (FLAS); Mariscal Cáceres, Mirama, N of Tocache Nuevo, along left bank of Río Huallaga, 500 m, *Plowman & Kennedy 5811* (GH); Mariscal Cáceres, Tocache Nuevo, Fundo La Campina, 2 km abajo de Tocache Nuevo, margen derecha del Río Huallaga, 400 m, 7 Sep. 1969, *Schunke 3396* (F, US); Mariscal Cáceres, Tocache Nuevo, Quebrada de Cachiyacu, 3 km abajo de Puerto Pizano (margen derecha del Río Huallaga), 21 Apr. 1971. UCAYALI: Coronel Portillo, Yarina Cocha, Fundo "El Pescador," cerca al Caserio Nuevo Destino, al este de Yarina Cocha, 150 m, 31 Oct. 1984, *Schunke 14153* (FLAS).

Eucharis ulei is among the more widespread Amazonian taxa of subg. *Eucharis*, extending north from its Peruvian center of distribution into Colombia and south to Bolivia (Fig. 81). The species is best recognized by its primarily narrow-elliptic leaves, chiefly five-flowered inflorescence, tube length of ca. 3–4 cm, limb spread of 4–5 cm, and reduced ovule number (generally two per locule, Fig. 89C). Both flower and ovule number have become nearly fixed throughout the range of the species. *Eucharis castelnaeana* is sympatric with *E. ulei* at times but tends to occur on seasonally inundated soils. Flower size and number, ovule number, and chromosome morphology (Meerow, 1987b) suggest close relationship to *E. cyaneosperma*, which has different tube morphology, a deeply trigonous ovary, and blue-coated seeds.

Ravenna (1982: 50) described *Urceolina moana*, citing the "absence of lobes, or teeth, in the cup." The single, poorly preserved, fragmentary flower of the holotype, however, had stamens at least shortly dentate to quadrate. As in *E. candida* and *E. formosa*, androecial toothing in *E. ulei* has little taxonomic significance. The androecial morphology of *E. moana* is well included within the range of variation for this character in *E. ulei* (Fig. 70D)—several collections of *E. ulei* have completely edentate staminal cups (e.g., *Meerow et al. 1024*, *Plowman & Kennedy 5811*, *Prance et al. 13915*). Much the same argument applies to the likewise synonymous *E. boliviensis* (Ravenna, 1988), represented by the only specimen of *E. ulei* collected in Bolivia. The only other collection assigned by Ravenna (1988) to *E. boliviensis* (*Cardenas 1553*) belongs to *E. cyaneosperma*. *Eucharis ipariensis*, inexplicably described by Ravenna (1982) as allied to *E. mastersii* (= *E.* ×*grandiflora* of subg. *Heterocharis*), is also indistinguishable from numerous collections of *E. ulei*.

Kränzlin (1913) and Macbride (1936) noted the dissimilarity of the two specimens comprising the holotype of *E. ulei* (*Ule 5737b*), one in flower, the other in fruit. I have assigned the fruiting specimen (*Ule 5737b*), with blue seeds, to *E. cyaneosperma* Meerow. When a putative isotype of *Ule 5737* was received from MG, it proved to represent *E. castelnaeana*. Ule thus collected three species under a single number, an unsurprising occurrence in areas where several *Eucharis* species are sympatric.

9. Eucharis cyaneosperma Meerow, Sida 12: 29–49. 1987. TYPE: Peru. San Martín: 20 km N of Tocache Nuevo on road to Tarapoto, Río Cañuto, 520 m, 17 July 1982, *Meerow et al. 1032* (holotype, FLAS). Figure 89A.

Bulb subglobose, 3–5 cm long, 3–3.5 cm diam., tunics light brown. Leaves 2–4; petiole (10–)15–30(–35) cm long, 5–6.5 mm thick; lamina (ovate-)elliptic, 18–25(–30) cm long, (6.5–)7–8(–13) cm wide, apically acute to shortly acuminate, attenuate at the base. Scape (3–)4–5(–6.5) dm tall, 5–7 mm diam. proximally, 3–4 mm diam. distally; bracts ovate-lanceolate, (20–)27–35 mm long. Flowers (3–)5(–7), pendent, without fragrance; pedicels (10–)15–25(–28) mm long, ca. 1.7–2 mm diam.; tube 30–40 mm long, 1.5–2 mm diam. for most of its length, dilating abruptly to 7–9 mm proximal to the throat, curved abruptly ca. 5 mm above the ovary and then ± straight; outer tepals 23–28(–32) mm long, 8–10(–13) mm wide, ovate-lanceolate, apiculate; inner tepals 21–24(–30) mm long, 10–14(–15) mm wide, ovate, acute to minutely apiculate. Staminal cup cylindrical, (8–)10–12 mm long (to tooth or lobe), 10–13(–15) mm wide, pale yellow or green proximally, quadrate or irregularly toothed between each free filament, the teeth when present < 1.5 mm long, cleft between each stamen 2–3 mm deep; each stamen 3.5–4(–5) mm wide at the base; the narrow, subulate free filament (3–)3.5–4.5(–5.5) mm long, ca. 1.5 mm wide at the base; anthers ca. 3 mm long, oblong; pollen grain ca. 47.95 μm polar diam., ca. 67.55 μm longest equatorial diam. Style 4.5–6 cm long, exserted 0.5–1 cm beyond the anthers; stigma 2–2.5 mm wide. Ovary subglobose and deeply trigonous at anthesis, 5–7 mm long, 7–10 mm wide, usually wider than long; ovules

2(–3, 5) per locule, superposed in the lower half of the cell. Capsule 10–12 mm long, 15–20 mm wide, bright orange, leathery; pedicel 25–36 mm long; seed ellipsoid, 7–9 mm long, ca. 5 mm wide, with a lustrous, cobalt blue testa. Chromosome number: $2n = 46$.

Distribution. Sporadic in the understory of premontane to lower montane rain forest of the Amazon basin and eastern Andean foothills, from Peru to Bolivia (Fig. 81), 120–800(–1,200) m elevation. Flowering at any time of the year, most commonly in August.

Additional specimens examined. BOLIVIA. EL BENÍ: vicinity of Rurrenabague, 330 m, 25 Nov. 1921, *Cardenas 1179* (AA, NY, US); Rurrenabague, 500 m, 7 Oct. 1921, *Cardenas 1553A* (NY); San Antonio, 15 Nov. 1958, flowered in cultivation 30 Apr. 1959, *Nelson 58-301* (MO); same collection as preceding, flowered in cultivation 4 Apr. 1961, *Nelson 58-301* (MO). BRAZIL. ACRE: basin of Río Purus, near mouth of Río Macauhan, 9°20′S, 69°W, 17 Aug. 1933, *Krukoff 5573* (NY); Río Branco de Obidos, Santo Antonio, 6 Aug. 1912, *Ducke 12162* (GOET, photo and fragment F). AMAZONAS: Juruá Miry, June 1901, *Ule 5737b* (B). PERU. CUZCO: Río Araza, northeast of Cuzco, 1,150 m, Jan. 1943, *Sandeman 3724* (K, OXF). LORETO: Maynas, arriba del Puerto Belen, Río Itaya, 73°25′W, 3°58′S, 120 m, 16 Nov. 1978 (fr), *Diaz et al. 621* (MO); Maynas, Yanamono, Explorama Lodge, 72°45′W, 3°25′S, 120 m, 29 May 1979 (fr), *Diaz et al. 1125* (MO); Reguena, Cocha Iricahua, Río Ucayali, 31 May 1982, *Encarnación 26186* (MO); Maynas, Yanamono, Explorama Tourist Camp, Río Amazonas halfway between Indiana and mouth of Río Napo, 72°50′W, 3°28′S, 120 m, 28 Aug. 1983, *Gentry et al. 43758* (MO); Flor de Yarina (Río Samiria), 22 Aug. 1983 (fr), *Vasquez et al. 4297* (MO); Ucayali, Canchahuayo (Isla Banos), 75°10′W, 7°5′S, 200 m, 29 Nov. 1985 (fr), *Vasquez et al. 6997* (MO); lower Río Nanay, 24 May 1929 (fr), *Williams 431* (F); La Victoria on Amazon, 21 Aug. 1929 (fr), *Williams 2619* (F); La Victoria on Amazon, 28 Aug. 1929 (fr), *Williams 2878* (F, US). JUNÍN: Puerto Yessup, ca. 400 m, 10–12 July 1929 (fr), *Killip & Smith 26394* (F, NY, US); Río Negro to Satip, 800 m, 17 Aug. 1960, *Woytkowski 5830* (MO). MADRE DE DÍOS: Tahuamanu, Iberia, 200 m, 15 Nov. 1973 (fr), *Alfaro 1684* (MO); Iberia, Miraflores, vicinity Río Tahuamanu, 1 Sep. 1945, *Seibert 2145* (US). SAN MARTÍN: (fr), *Schunke 4843* (F, US); Mariscal Cáceres, Tocache Nuevo, Quebrada de Huaguisha (margen derecha del Río Huallaga, 400–450 m, 3 July 1974 (fr), *Schunke 7146* (F). UCAYALI: middle Ucayali, Cashiboplaya, 10°S, 1923, *Tessman 3179* (G, NY, S).

Eucharis cyaneosperma is the only species of *Eucharis* with blue-coated seeds. The species appears very similar to *E. ulei* but differs by having usually shorter leaves, different tube morphology (abruptly curved at the base in *E. cyaneosperma*, sinuously curved in *E. ulei*), irregularly dentate to quadrate staminal cup (Fig. 89A), deeply trigonous ovary, and different seed color. In the southern part of its range, *E. cyaneosperma* occupies more upland sites than are usually characteristic of *E. ulei*.

10. Eucharis lehmannii Regel, Gartenfl. 38: 313–314, t. 1300, fig. 1. 1888. *Urceolina lehmannii* (Regel) Traub, Pl. Life 27: 57–59. 1971. TYPE: Colombia. Cauca: ex hort. Regel, from bulbs collected by Lehmann near Popayan, Apr. 1888, *Regel s.n.* (holotype (fragmentary), LE; photo of holotype, FLAS, K). Figure 90D–F.

Bulb subglobose, not seen. Leaves 2; petiole 45.5 cm long, 3.5 mm thick; lamina ovate-elliptic, 24–25 cm long, 16 cm wide, short acuminate, basally subcordate and attenuate to the petiole. Scape not seen; bracts lanceolate; bracteoles linear-lanceolate. Flowers 4; pedicels to 30 mm long; limb patent, spreading to ca. 4 cm; tube ca. 25 mm long, ca. 1.2 mm wide below, dilating abruptly to 8 mm at the throat; outer tepals 20–22 mm long, 8–10 mm wide, ovate-lanceolate, acute-apiculate; inner tepals 18–20 mm long, 10–12 mm wide, obtuse. Staminal cup 7–8 mm long (to apex of tooth), deeply cleft between each stamen to < 2 mm from the throat; each stamen bidentate, the teeth long-lanceolate, as long as the free filament; free filament linear, 7–8 mm long, ca. 1 mm wide; anthers sub-basifixed, versatile. Style slightly exserted beyond the anthers. Ovary globose-ellipsoid, ca. 6 mm long, ca. 4 mm wide; ovules ca. 10 per locule. Fruit and seed unknown.

Distribution. Extremely rare in the understory of moist, lower montane forest of the Cordillera Oriental in Cauca Department of Colombia (Fig. 91), 1,200 m.

Additional specimen examined. COLOMBIA. CAUCA: Aganche, Río Orejas, 1,200 m, *Lehmann 5883* (K).

Eucharis lehmannii is known only from the fragmentary type (a single flower) and a single specimen at Kew with only one flower present. An Ecuadorean specimen mislabeled as the type of *E. lehmannii*, received from Kew (*Lehmann 7775*), turned out to be *E. astrophiala* (Ravenna) Ravenna. Like *E. caucana*, to which it may be very closely related, *E. lehmannii* is a peripheral isolate of subg. *Eucharis*, with novel androecial character states. Despite the unusual staminal morphology, the plant figured in Regel's (1889) description resembles *Eucharis* subg. *Eucharis* by overall morphology and habit of the flower. In 1984, I was not able to collect this species successfully at the

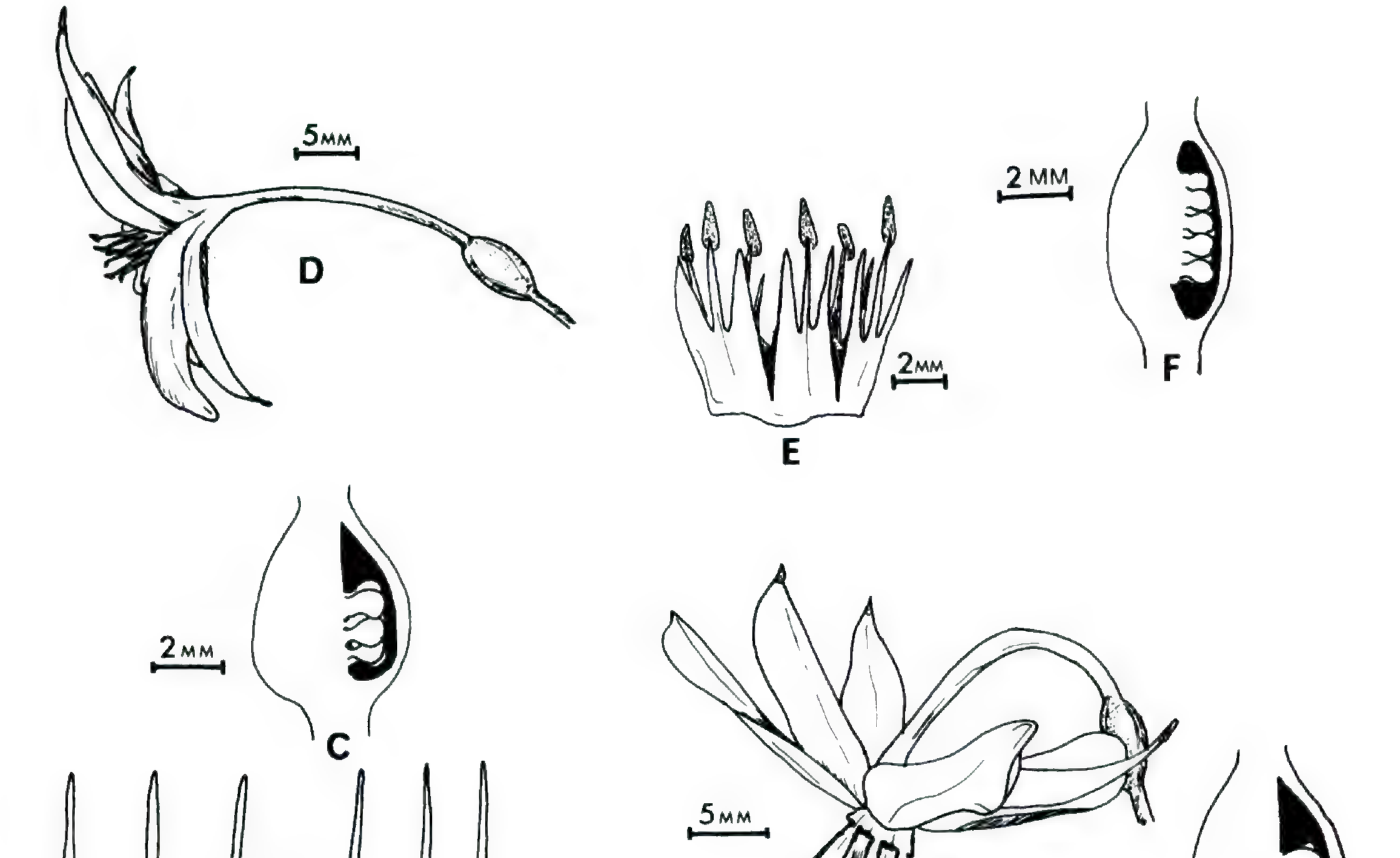


FIGURE 90. *Eucharis corynandra*, *E. lehmannii*, and *E. oxyandra*. A–C. *E. oxyandra* (isotype: *Hutchison et al. 5983*, UC).—A. Flower.—B. Androecium. Note the polymorphism.—C. Ovary, longitudinal section. D–F. *E. lehmannii* (after tab. 1300 in Regel, 1889, and a photo of the type at LE.—D. Flower.—E. Staminal cup.—F. Ovary, longitudinal section. G–I. *E. corynandra* (isotype, *Ravenna 2090*, K).—G. Flower.—H. Staminal cup.—I. Ovary, longitudinal section.

locality of *Lehmann 5883* in Colombia, an area now largely deforested.

11. Eucharis corynandra (Ravenna) Ravenna, Phytologia 57: 95–96. 1985. *Urceolina corynandra* Ravenna, Pl. Life 34: 80–81. 1978. TYPE: Peru. Cajamarca: Chinganza, between Aramango and Montenegro, 2 July 1973, *Ravenna 2090* (holotype, herb, Ravenna, not seen; isotypes, K, not seen: NY, MO). Figure 90G–I.

Bulb globose, 47 mm long, 37 mm diam.; tunics light brown. Leaves elliptic-lanceolate; petiole 25–27 cm long, 3.5–5 mm thick; lamina 20–27 cm long, 5 cm wide, apically acute. Scape 50 cm tall, slender, ca. 2 mm diam. distally; bracts lanceolate, ca. 32 mm long. Flowers 8–10; pedicels 15–23 mm long, thin; perianth tube curved, 17–18 mm long, ca. 1 mm wide for most of its length, abruptly dilated to 3–4 mm at the throat; limb spreading to 3–4 cm wide; outer tepals 27–29 mm long, 6–7 mm wide, ovate-lanceolate, acute-apiculate at the apex; inner tepals ca. 28 mm long, 8–10 mm wide; ovate, acute. Staminal cup short, funnelform, thick and waxy in texture, 3.5 mm long, 7.5 mm wide, with two obtuse teeth between each free filament, somewhat plicate; free filaments club-

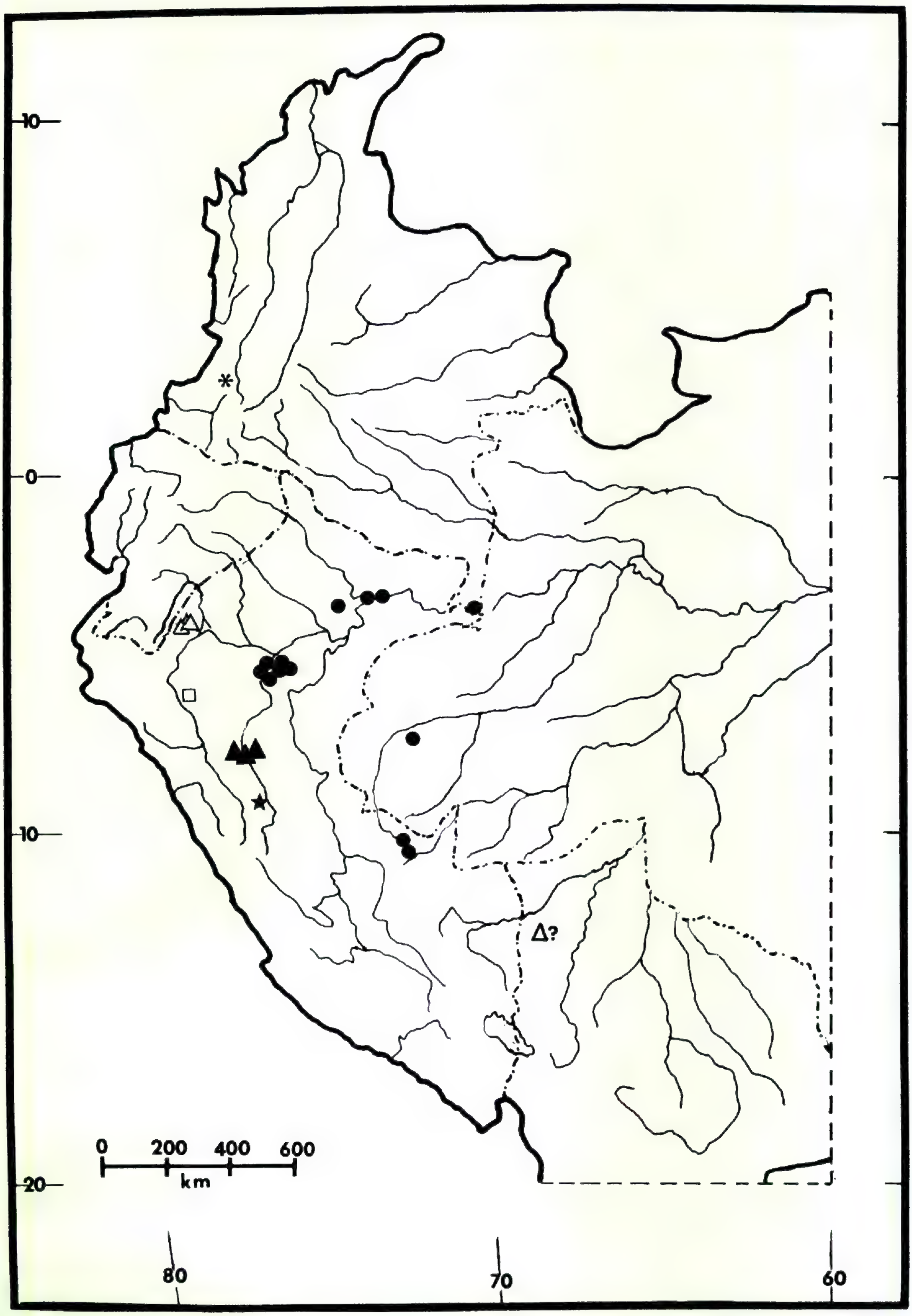


FIGURE 91. Distributions of *Eucharis castelnaeana* (circles), *E. corynandra* (squares), *E. lehmannii* (snowflake), *E. oxyandra* (stars), *E. plicata* subsp. *plicata* (closed triangles), and *E. plicata* subsp. *brevidentata* (open triangles) in northwestern-central South America.

shaped, appearing narrowly elliptic-lanceolate when dry, ca. 6.2 mm long, 1.8 mm wide, abruptly dilated to ca. 1 mm at the base, inserted adaxially between 2 of the teeth; anthers oblong-linear, ca. 3 mm long, versatile, black. Style 30–44.5 mm long, stigma trilobed. Ovary globose-ellipsoid, 6 mm long, 3 mm wide; ovules 4–6 per locule, superposed. Fruit and seed unknown.

Distribution. Known only from the type locality (Fig. 91), in tropical forest on slopes, near a small ravine with *Dieffenbachia* sp., *Heliconia* sp., *Clusia* sp., and *Xyphidium coeruleum* Aubl. Elevation not reported.

In size and number of the flowers, as well as ovule number, *Eucharis corynandra* shows affinity to *E. castelnaeana* (Baillon) Macbr. and to *E. plicata* Meerow. The short staminal cup and distinctive club-shaped free filaments (Fig. 90H) are the principal unique characters of this species. I cannot, however, confirm Ravenna's (1978) description of the anthers as densely pubescent. The collection locality suggests that it is an upland isolate from the Amazonian center of the subgenus, the plant having colonized the lower limits of the "ceja de la selva" forest formations in Cajamarca Department of Peru.

12. Eucharis oxyandra (Ravenna) Ravenna [subg. *Eucharis insertae sedis*], Phytologia 57: 95–96. 1985. *Urceolina oxyandra* Ravenna, Wrightia 7: 251–253. 1983. TYPE: Peru. Huánuco: Huánuco, Río Chinchao, below Carpish on rd. to Tingo Maria, 1,800 m, 19 July 1964, *Hutchison et al. 5983* (specimens prepared from bulbs flowered in cultivation at UC, 26 Apr. 1967) (holotype, USM, not seen; isotypes, MO, UC). Figure 90A–C.

Bulb not seen. Leaves (one seen) elliptic; petiole 17 cm long, 4–6 mm thick; lamina 25 cm long, 12 cm wide. Scape 27–28 cm tall; bracts 34–35 mm long, ovate-lanceolate. Flowers 6–7, (crateriform?), cernuous; pedicels ca. 19 mm long; tube curved, 25 mm long, 1.5 mm diam. below, dilated abruptly at the throat to 3.5 mm; tepals spreading to 27 mm wide; outer series 17–19 mm long, 6.7 mm wide, ovate-lanceolate, acute-apiculate; inner series 17–18 mm long, 8–9 mm wide, ovate, obtuse. Staminal cup very short, 0.8–1.5 mm long, 3–3.5 mm wide, edentate or with 2 obtuse teeth between the free filaments; free filaments ca. 7 mm long, ca. 1 mm wide at the base, narrowly subulate; anthers oblong, 3.3 mm long, sub-basifixed, eventually versatile; pollen grain ca. 42.36 μm polar diam., ca. 68.36 μm longest equatorial diam. Style 32.8 mm long; stigma 2–2.5 mm wide. Ovary globose-ellipsoid, 6 mm long, 4 mm wide; ovules 6–8 per locule. Fruit and seed unknown.

Distribution. *Eucharis oxyandra* is not known in the wild state. The collector's field notes (UC) indicate that three bulbs were found at the type locality (Fig. 91) "exposed on surface of ground with evidence of past cultivation, in deep shade near abandoned hut above road. The third bulb proved to be *Urceolina urceolata* (R. & P.) M. L. Green."

This unusual species has the smallest staminal cup of any Peruvian species of *Eucharis* subg. *Eucharis* (Fig. 90B). The long, almost linear, free filaments are another unusual feature of the androecium. The polymorphism of the staminal cup (both edentate and obtusely dentate forms represented in the isotypes, Fig. 90B) is puzzling and adds further credence to my suggestion that this character has been over-weighted as an indicator of species delimitation in the alpha-taxonomic literature relating to the genus. Alternatively, it is possible that the two bulbs found by the collector and representing this species were of two different origins.

In publishing *Urceolina oxyandra*, Ravenna (1983) was apparently unaware of the unusual situation in which the species was found, having examined only a duplicate at USM, which seems to have lacked the detailed field notes of the collector. He argued that the unusual morphology of the androecium (reduced staminal cup and long, narrowly subulate filaments), similar to that of *Urceolina*, supported the inclusion of *Eucharis* within *Urceolina* (Traub, 1971), a position he recently reversed (Ravenna, 1985). This type of androecial morphology is characteristic of two putative intergeneric hybrids between *Eucharis* and *Urceolina*, ×*Urceocharis edentata* Wright (1910) and ×*U. clibranii* Masters (1892).

Given that the plant was discovered as an artifact of cultivation in company with a bulb of *Urceolina*, and in a geographic area of loose sympatry for the two genera, I thought it possible that *E. oxyandra* might represent a hybrid between *Eucharis* and *Urceolina*. ×*Urceocharis edentata* was supposedly collected in the wild in Peru (Wright, 1910). Pollen of *E. oxyandra*, however, stains 100% with Alexander's (1969) stain. Both ×*U. edentata* and ×*U. clibranii* produced very little pollen (Wright, 1910), an observation confirmed when I examined specimens of both hybrids (ex hort. BM). Pollen grain size of the species is more like that of *Eu-*

charis subg. *Eucharis*, but exine sculpturing resembles that of *Urceolina* (Meerow & Dehgan, 1988). Fertile hybrids between closely related genera are not unknown in Amaryllidaceae (Traub, 1963).

Alternatively, *Eucharis oxyandra* might be a relict taxon close to the ancestor of *Urceolina*, a genus whose divergence from *Eucharis* may have been relatively recent (see previous section). Phylogenetic analysis supports this latter hypothesis. At present, it seems best to treat *E. oxyandra* as a species of *Eucharis*, even though its *known* shared characteristics with *Eucharis* are plesiomorphic, since its phylogenetic relationships are obscured by the large amount of unknown character state data. As in *E. astrophiala*, *E. caucana*, *E. corynandra*, and *E. lehmannii*, this species exhibits a pattern of morphological novelty characteristic of peripheral isolation in *Eucharis*.

13. Eucharis plicata Meerow, Brittonia 36: 18–25. 1984. TYPE: Peru. San Martín: Mariscal Cáceres, Tocache Nuevo, Quebrada de Huaguisha, right bank Río Huallaga opposite Tocache Nuevo, 8°09′S, 76°27′W, 500–600 m, 14 Dec. 1981, *Plowman et al. 11394* (holotype, FLAS; isotypes not seen, F, K, NY, USM).

Bulb subglobose, 5–6 cm long, 4 cm wide, tunics brown. Leaves 2–4 at anthesis, petiole 25–35 cm long; lamina widely elliptic to ovate, (19–)20–30 (–35) cm long, 7–12(–14) cm wide, short acuminate, very shortly attenuate to the petiole, thin, lustrous dark green adaxially, silvery-green abaxially, abaxial cuticle densely striate. Scape 40–60 cm tall; bracts 29–30 mm long, ovate-lanceolate; bracteoles successively shorter and narrower. Flowers (7–)9–10, sometimes lightly fragrant; pedicel suberect, 10–15(–25) mm long; perianth tube 25–28 mm long, 2.5–3 mm wide throughout most of its length, dilating abruptly to 6–10 mm at the throat; limb spreading to 30–40 mm; tepals ovate, recurved at the apex, subequal; outer series ca. 19–24 mm long, 9–14 mm wide, apiculate; inner series 16–23 mm long, 11–15.5 mm wide, apically acute. Staminal cup campanulate, ca. 8.5–12 mm long (to apex of teeth), 10–12(–15) mm wide, apically white, basally pale greenish yellow, plicately folded on either side of the filamental trace, bidentate; each stamen 4.5–5.5 mm wide, the anther-bearing part subulate, 2–3.5 mm long, apically obtuse; anthers oblong-linear, sub-basifixed, erect at first, then becoming versatile, grayish brown, 3.5–4 mm long; pollen grains 41.3–43.5 μm polar diam., 59.9–68.9 μm longest equatorial diam. Style 36–40 mm long; stigma ca. 2.5 mm wide. Ovary globose-ellipsoid, green, ca. 5–6 mm long, 3.4–4 mm wide; ovules 4–8 per locule. Capsule ca. 1 cm long, 2 cm wide, bright orange, leathery; seeds 1–2 per locule, ca. 1 cm long, 5 mm wide; testa shiny black. Chromosome number: $2n = 46$.

KEY TO THE SUBSPECIES OF *EUCHARIS PLICATA*

1a. Flowers not noticeably fragrant; perianth tube dilating to 6–7.5 mm at the throat; staminal cup deeply plicate, ca. 12 mm long to apex of teeth; teeth longer than subulate portion of filament, coarsely serrulate, imbricate; style reaching to half the length of the cup; ovules 7–8 per locule ..... 12a. *E. plicata* subsp. *plicata*

1b. Flowers mildly fragrant; perianth tube dilating to 7.5–10 mm at the throat; staminal cup only shallowly plicate, ca. 8–10 mm long to apex of teeth; teeth shorter than subulate portion of filament, entire, nonimbricate; style reaching to just below the teeth; ovules 4–5(–7) per locule ..... 12b. *E. plicata* subsp. *brevidentata*

12a. E. plicata subsp. **plicata.** Figure 92.

Flowers without noticeable fragrance; pedicel suberect, 10–15 mm long; perianth tube 22–24 mm long, dilating abruptly to 6–7.5 mm wide at the throat; outer tepals 18–23 mm long, 9–12 mm wide; inner tepals 16–20 mm long, 11–12 mm wide. Staminal cup ca. 12 mm long and wide, deeply plicate on either side of the filamental trace; the anther-bearing portion of each filament inserted between 2 irregular, obtuse, coarsely serrulate teeth, each 4–5 mm long, adjacent pairs somewhat imbricate and appearing as one; pollen grain ca. 43.45 μm polar diam., ca. 68.9 μm longest equatorial diam. Style reaching to ½ the length of the staminal cup. Ovules 7–8 per locule.

Distribution. Known only from the type locality, where it is locally abundant (Fig. 91). This population appears to have hybridized with *E. ulei* and contains a range of intermediate morphs in addition to true *E. plicata*. The intermediates show reduced pollen stainability, the presence of nonhomologous chromosomes, and extreme allozyme heterogeneity. It is unclear whether these represent a highly variable F_1, the F_2, or the results of introgression with *E. plicata* subsp. *plicata*. An analysis of this population is in preparation.

Additional specimens examined. PERU. SAN MARTÍN: same locality as the type, 16 July 1982, *Meerow et al. 1025* (FLAS); same locality as the type, 4 Aug. 1974, *Schunke 8046* (F). *Putative hybrids with* E. ulei: PERU.

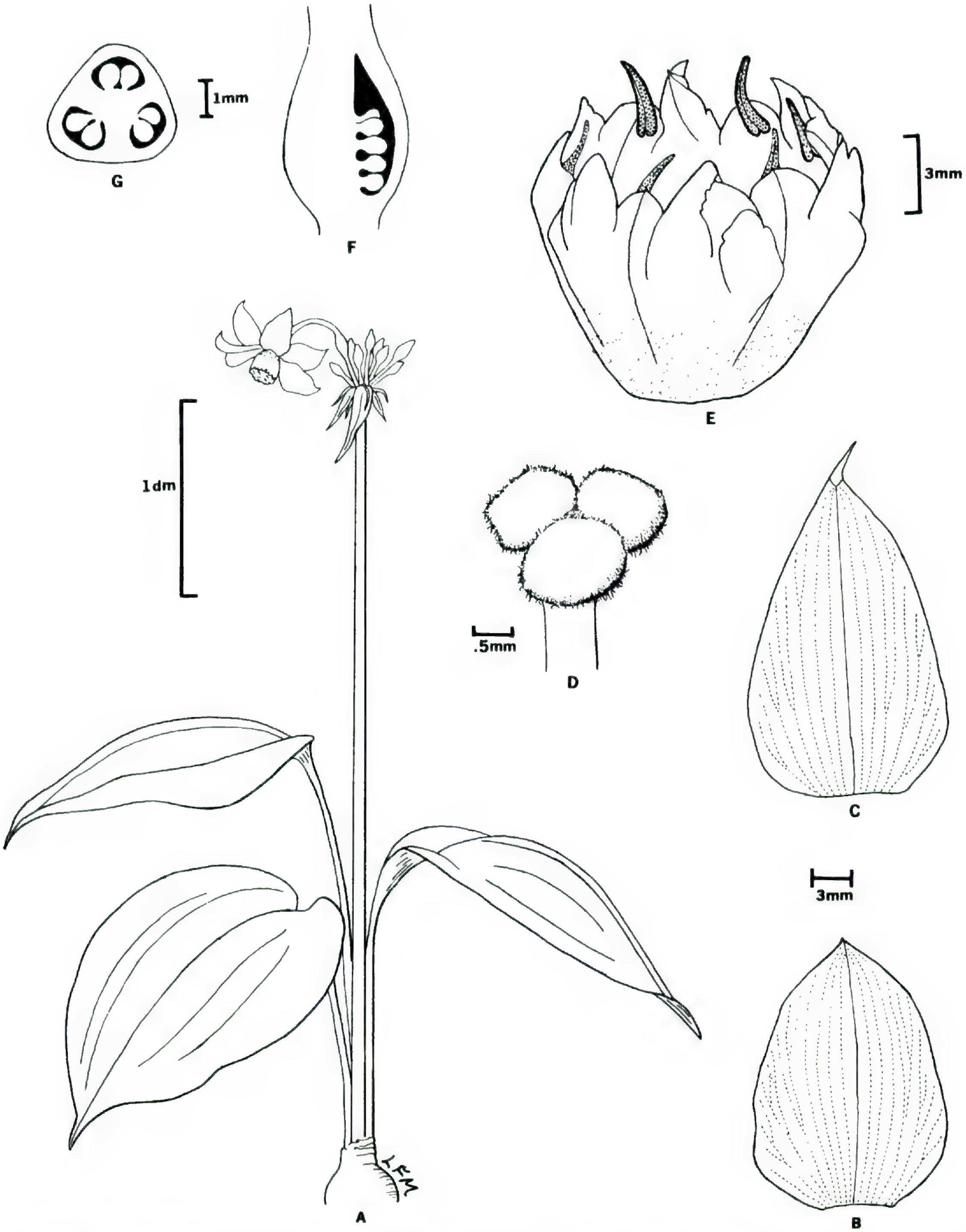


FIGURE 92. *Eucharis plicata* subsp. *plicata* (*Meerow et al. 1025*, FLAS).—A. Habit.—B. Inner tepal.—C. Outer tepal.—D. Stigma.—E. Staminal cup.—F. Ovary, longitudinal section.—G. Ovary, transverse section.

SAN MARTÍN: same locality as the type, 16 July 1982, *Meerow et al. 1030, 1031* (FLAS).

13b. E. plicata subsp. **brevidentata** Meerow, subsp. nov. TYPE: Bolivia. El Beni [?]: no collection information, ex hort. Fairchild Tropical Garden from collections by Fred Fuchs, Jr., 3 Oct. 1984, *Meerow 1143* (holotype, FLAS).

Subspecies nova differt a subspecies typica dentibus staminalibus brevioribus et non serrulatis vel imbricatis.

Flowers mildly fragrant; perianth tube 25–29 mm long, dilating abruptly to 7.5–10 mm wide at the throat; outer tepals 20–24 mm long, 9–12 mm wide; inner tepals 18.7–23 mm long, 12–15 mm wide. Staminal cup 8–11 mm long (to apex of teeth), 10.5–14 mm wide, only shallowly plicate; teeth ca. 1.5–2 mm long, reaching to about half the length of the subulate portion of the filament, obtuse, entire, nonimbricate; pollen grain ca. 41.3 μm polar diam., ca. 59.9 μm longest equatorial diam. Style reaching to just below the apex of the teeth. Ovules 4–6(–8) per locule.

The epithet of this subspecies refers to the short teeth of the staminal cup.

Distribution. Rare in the understory of premontane and lower montane rain forest of north-central Peru and Bolivia (Fig. 91), 200–420 m. Flowering August–October.

Additional specimens examined. PERU. AMAZONAS: Río Cenepa, vicinity of Huampami, ca. 5 km E of Chavez Valdivía, ca. 78°30′W, 4°30′S, 200–250 m, 11 July 1978 (fr), *Ancuash 1024* (MO); Río Cenepa, 10–12 km NW of Huampami, ca. 420 m, 2 Oct. 1972, *Berlin 148* (NY); Río Cenepa, vicinity of Huampami, ca. 5 km E of Chavez Valdivía, Quebrada Huampami, ca. 78°30′W, 4°30′S, 200–250 m, 15 Aug. 1978, *Kujikat 365* (MO).

Eucharis plicata is phenetically and cladistically closest to *E. castelnaeana*. The phenetic relationship between the two species is most evident in *E. plicata* subsp. *brevidentata*, which in characteristics of the staminal cup and ovule number is intermediate between subsp. *plicata* and *E. castelnaeana*. From the latter, *E. plicata* may be distinguished by its wider leaves and tepals, larger flowers, campanulate staminal cup which is plicate along the filamental traces (Fig. 92E), more numerous ovules, and fruit and seed morphology typical of subg. *Eucharis*.

14. Eucharis castelnaeana (Baillon) Macbride, Publ. Field Mus. Nat. Hist. Bot. Ser. 11: 47. 1931. *Caliphruria castelnaeana* Baillon, Bull. Mens. Soc. Linn. Paris 144: 1133–1136. 1894. *Urceolina castelnaeana* (Baillon) Traub, Pl. Life 27: 57–59. 1971. TYPE: Peru. Ucayali: Pampa del Sacramento, June 1847, *Castelnau s.n.* (holotype, not located; isotype, P). Figure 93.

Eucharis narcissiflora Huber, Bol. Mus. Goeldi Para 4: 543. 1906. *Urceolina narcissiflora* (Huber) Traub, Pl. Life 27: 57–59. 1971. TYPE: Peru. Ucayali: Sarayacu, Catalina, 25 June 1898, *Huber 1574* (holotype, MG; isotype (photo and fragment), F).

Bulb small, subglobose, 2.2–3(–4.5) cm long, 1.4–2.7 cm wide; neck 1–2 cm long, 1–1.5 cm wide; tunics tannish brown. Leaves 2–4; petiole (10–)13–17(–25) cm long, 3–6 cm wide; lamina narrowly ovate-elliptic, (10–)15–20 cm long, 5–7(–10) cm wide, apex shortly acuminate, lustrous dark green adaxially, lighter green abaxially, margins undulate. Scape (2.5–)3–4(–5) dm tall, 5–6 mm diam. proximally, ca. 3 mm diam. distally; bracts (2.5–)3–4 cm long, ovate-lanceolate, greenish white. Flowers (7–)8–10, pendent, small, with a faint lemon fragrance; pedicels 10–18 mm long; tube 15–25(–30) mm long, 1–1.5(–2) mm wide for most of its length, abruptly dilated near the throat to 5–6(–8) mm wide; tepals patent, spreading to (2.5–)3–4 cm, often distally recurved, sometimes strongly reflexed for their entire length; outer tepals (ovate-)lanceolate, 15–20 mm long, 5–7 mm wide, apiculate; inner tepals ovate, 11.5–18.7 mm long, 8–11 mm wide, acute. Staminal cup funnelform-cylindrical to cylindrical, usually subcylindrical proximally and abruptly dilated at ½–⅔ of its length, (5.5–)7–8(–9.5) mm long (to apex of tooth), (7–)9–11(–12) mm wide, zoned greenish yellow in the proximal ⅓–⅔, slightly incurved at the rim, waxy and slightly succulent in texture, bidentate between each free filament, conspicuously plicate between the teeth, very shallowly cleft between each tooth (< 1 mm) and as deep or more deeply cleft beteen the teeth and the free filament (> 1 mm); teeth 0.5–1 mm long, reaching to about half the length of the free filaments, obtuse, entire; free filament subulate, (1.5–)2–3(–4) mm long, ca. 1.5 mm wide at the base, obtuse or acute; anthers 3–4.5 mm long, oblong, grayish brown, sub-basifixed; pollen grain ca. 39.45 μm polar diam., ca. 55.8 μm longest equatorial diam. Style 25–35 mm long, reaching the apex of the cup or slightly inserted; stigma ca. 1.5 mm wide. Ovary globose, 3.5–5 mm diam., white to greenish white; ovules (2–)4–5(–7) per locule. Capsule subglobose, shallowly trilobed, ca. 1 cm long, 1.5 cm wide, glaucous green, thin-walled, sometimes abscising indehiscently; seeds 1–3 per locule, compressed-ellipsoid, ca. 1 cm long, 5 mm wide; testa dull black, rugose. Chromosome number: $2n = 46$.

Distribution. Understory of lowland and premontane, often seasonally inundated, primary rain forest in the Amazon basin, most commonly in Peru, rare in Colombia and Brazil (Fig. 91), 100–200 m. Flowering June–September (–December).

Vernacular names. Amangay, sacha cebolla.

Additional specimens examined. BRAZIL. AMAZONAS: Río Juruá, Río Miry, July 1901, *Ule 5737* in part (MG). COLOMBIA. AMAZONAS: vicinity Leticia, ex hort. Fairchild

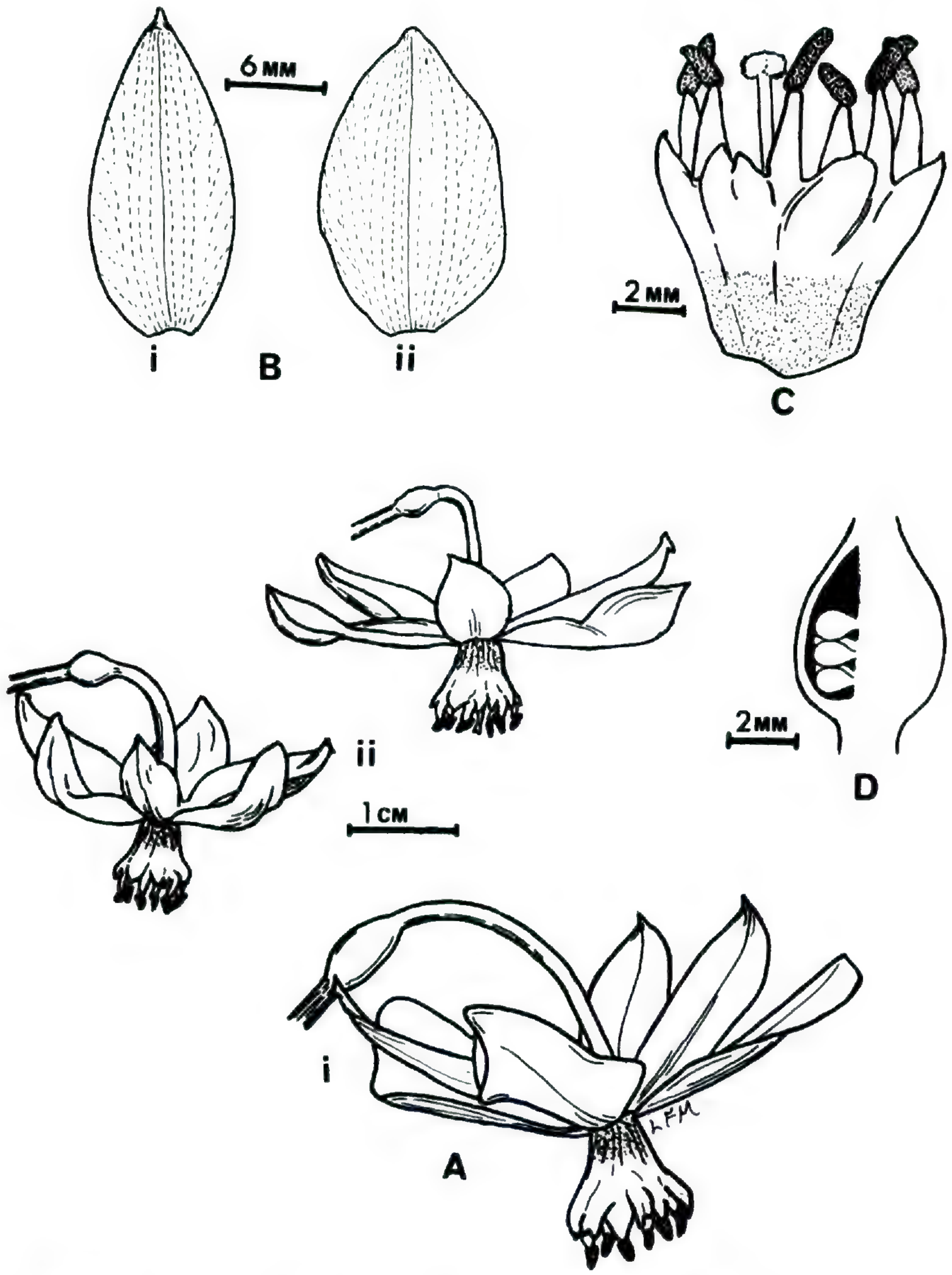


FIGURE 93. *Eucharis castelnaeana*.—A. Flowers. i, *Schunke 14154-A* (FLAS); ii, *Schunke 14156*. Note varying habit of limb.—B. Tepals (*Schunke 14156*). i, outer tepal; ii, inner tepal.—C. Staminal cup (*Schunke 14156*).—D. Ovary (*Schunke 14156*), longitudinal section.

Tropical Garden from collections made by R. Buttons, 1 Apr. 1984, *Watson 1868* (FLAS). PERU. LORETO: Isla Santa María, near Yurimaguas, Huallaga Valley, 150–200 m, 16 Sep. 1948, *Ferreyra 4984* (MO); Maynas, Quebrada Sucusari, Llachapa camp of Explorama, north side of Río Napo below Mazan, forest on somewhat sandy lateritic soil, 140 m, 6 Nov. 1979, *Gentry et al. 27569* (MO); Maynas, Yanamono, Explorama Tourist camp on Río Amazonas between Indiana and mouth of Río Napo, 72°48′W, 3°28′S, seasonally inundated tahuampa, 120 m, 28 July 1980, *Gentry et al. 29203* (MO); Puerto Arturo, lower Río Huallaga below Yurimaguas, ca. 135 m, 24–25 Aug. 1929, *Killip & Smith 27801* (NY, US); same locality, Aug. 1929, *Killip & Smith 27844* (F, NY, US); between Yurimaguas and Balsapuerto (lower Río Huallaga basin), 135–150 m, 26–31 Aug. 1929, *Killip & Smith 28249* (US); Santa Rosa, lower Río Huallaga below Yurimaguas, ca. 135 m, *Killip & Smith 28886* (F, NY, US); Maynas, Santa María de Nanay, Colonía San Fransisco de Indies Yaguas, 1.5 km del Fundo Balcón Momon, 106–110 m, 15 Nov. 1984, *Schunke 14154a* (FLAS); Alto Amazonas, Yurimaguas, camino a "Schunguyce" al sur este de Puerto Arturo, near Yurimaguas, 150–200 m, 1 Dec. 1984, *Schunke 14156* (BM, COL, F, FLAS, G, GB, GH, K, MO, NY, P, S, UC, US); Pebas on the Amazon, 30 July 1929, *Williams 1898* (F, S, US); lower Río Huallaga, Sapotoyacu, Santa Rosa, 155–210 m, 11 Nov. 1929 (fr), *Williams 4906* (F); Puerto Arturo, Yurimaguas, lower Río Huallaga, 155–210 m, 15 Nov. 1929, *Williams 5051* (F).

Eucharis castelnaeana has been collected most frequently in the vicinity of Yurimaguas in Peru

(Fig. 91) and is sometimes locally abundant in rain forest understory. It has the smallest flowers of any species in subg. *Eucharis* and is the major exception to the correlation of reduced flower size with loss of fragrance that otherwise characterizes *Eucharis*. Several living collections produce a mild lemon scent when ambient temperatures are high (as does *E. plicata* var. *brevidentata*). It is the only species of subg. *Eucharis* in which the ripe capsule is not leathery and orange. The glaucous, green, thin-walled capsule is tardily dehiscent and can abscise without opening, though the seeds within are fully ripe.

Eucharis castelnaeana is autogamous. Under greenhouse cultivation it is the only species of *Eucharis* that successfully sets fruit with self-pollen. Unmanipulated inflorescences regularly set 50–75% of their capsules.

Eucharis castelnaeana is variable in leaf and flower size (Fig. 93A) and, to a lesser extent, in androecial morphology. In his description of *E. narcissiflora*, Huber (1906) made reference to *E. castelnaeana*, described from the same location as Huber's type of *E. narcissiflora*, but differentiated his new species solely on the basis of size. The two taxa represent the extremes of size diversity of a single species and differ by no other characters. Populations represented by *Schunke 14154a* (Fig. 93Ai) have flowers almost twice as large as those of *Schunke 14156* (Fig. 93Aii) but are otherwise indistinguishable. Shape of the staminal cup in the latter collection can range from nearly cylindrical to funnelform-cylindrical.

Eucharis plicata is phenetically the closest species to *E. castelnaeana*. Baillon (1894) considered *E. castelnaeana* intermediate between *Caliphruria* and *Eucharis* in his argument for combining these two genera. Baillon probably weighed flower size heavily in his judgment, one of only two characters by which *E. castelnaeana* resembles *Caliphruria*. In Baillon's time, most other small-flowered *Eucharis* species were not yet described. Additionally, the green, thin-walled capsule of *E. castelnaeana* is like the fruit of *Caliphruria*. Baillon (1894) gave no indication whether he was familiar with the fruit of either *Eucharis* or *Caliphruria*. Nonetheless, perianth and pollen exine morphology place *E. castelnaeana* squarely in *Eucharis* despite its aberrant fruit and seed morphology.

Eucharis subg. **Heterocharis** Meerow, subg. nov.

TYPE SPECIES: *Eucharis* ×*grandiflora* Planchon & Linden, Fl. Serres Jard. Eur. Ser. 1, 9: 255. 1853.

Subgenus *Eucharis* affinis a qua imprimis differt floribus plerumque non pendulis, tubo perianthii bene infra fauce dilato, limbo plerumque minus expanso, ovario grandius et ovulis numerosis en quoque loculo.

Large bulbous perennial herbs. Leaves petiolate, persistent; lamina ovate, thin, plicate or ± smooth between the veins, undulate margined, apically acuminate, subcordate basally and shortly attenuate to the petiole, bright or dark green adaxially, light green abaxially, the abaxial epidermal cells variably striate; petiole subterete. Inflorescence scapose, umbellate, terminated by 2 green ovate-lanceolate bracts. Flowers subsessile or shortly pedicellate, 2–7, white, 7–8 cm long, strongly fragrant, declinate (rarely subpendulous), funnelform-campanulate (rarely crateriform); perianth tube cylindrical to subcylindrical below, abruptly dilated at ⅓–½ of its length, curved, tinged green below; limb of 6 ovate tepals in 2 series, imbricate for half their length, subequal, spreading somewhat above, often slightly undulate. Stamens basally connate into short or long staminal cup partially adnate to the upper portion of the tube, striped green or yellow within along the filamental traces, variously toothed or edentate; distal portion of the filaments linear or subulate, sometimes incurved; anthers linear, versatile at anthesis; pollen grain 40–60 μm (polar axis), 60–76 μm (longest equatorial axis), the exine coarsely reticulate. Style filiform, well-exserted beyond the staminal cup and slightly assurgent; stigma deeply trilobed, often green. Ovary large, ellipsoid, trigonous, appearing rostellate when dry; ovules usually 16–20 per locule, ellipsoid, biseriate. Capsule green, seeds blackish brown with a slightly rugose testa (*E. moorei*).

Three species and two natural hybrids in western Colombia, Ecuador, and rarely Peru.

KEY TO THE SPECIES AND HYBRIDS OF SUBGENUS *HETEROCHARIS*

1a. Leaves deeply plicate; staminal cup reduced to a basal connation of the filaments less than 7 mm long.
  2a. Staminal cup acutely bidentate between each filament, teeth ca. 1.5 mm long ..... 1. *E.* ×*grandiflora*
  2b. Staminal cup edentate or rarely with a single obscure tooth less than 1 mm long at the base of one or several stamens.
    3a. Perianth tube markedly curved, cylindrical for ½–⅔ of its length, then abruptly dilated distally to the throat; free filament somewhat incurved; stigmatic papillae unicellular ... 2. *E. sanderi*
    3b. Perianth tube straight or only slightly cernuous, subcylindrical proximally but distally dilating gradually towards the

throat; free filament straight; stigmatic papillae multicellular ..... 3. ×*Calicharis butcheri*

1b. Leaves shallowly plicate or relatively nonplicate; staminal cup well developed, greater than 1 cm long.

4a. Leaf length-to-width ratio usually equal to or less than 2; perianth more or less campanulate, tepals spreading only 45–60° from the throat; staminal cup acutely bidentate, strongly recurved at the margin; ovules 16–20 per locule; plants of Ecuador, very rare in Peru ..... 4. *E. moorei*

4b. Leaf length-to-width ratio usually greater than 2; perianth crateriform, tepals spreading ca. 90° from the throat; staminal cup obtusely bidentate to quadrate, not strongly recurved at the margin; ovules 9–12 per locule; plants of the Huallaga valley in Peru ..... 5. *E. amazonica*

1. Eucharis ×grandiflora Planchon & Linden, Fl. des Serres Jard. Eur. Ser. 1, 9: 255. 1853. *Urceolina grandiflora* (Planchon & Linden) Traub, Pl. Life 27: 57–59. 1971. LECTOTYPE (Meerow & Dehgan, 1984a): Fl. des Serres Jard. Eur. Ser. 1, 9: pl. 957. Figures 94–96.

Eucharis mastersii Baker, Curtis's Bot. Mag. 111: t. 6831. 1885. *Urceolina mastersii* (Baker) Traub, Pl. Life 27: 57–59. 1971. TYPE: ex hort. Sander (holotype, K; photo, F).

Eucharis lowii Baker, Gard. Chron. 13: 538–539. 1983. *Urceolina lowii* (Baker) Traub, Pl. Life 27: 57–59. 1971. TYPE: ex hort. Low (holotype, K; photo, F).

Bulb 3–5 cm diam., neck 2–4 cm long, tunics light brown. Leaves 1–3; petiole 19–36 mm long, 5–7 mm thick; lamina ovate or elliptic, 20–33 cm long, (10–)13–16 cm wide, apically acuminate, subcordate basally and shortly attenuate to the petiole, deeply plicate, adaxial surface lustrous dark or bright green, abaxial surface light green and densely striate, margins undulate. Scape 4–5 dm tall, 5–6 mm diam., subterete; bracts ovate-lanceolate, green at first, soon marcescent, 2.5–4.8 cm long, 14–17 mm wide. Flowers 2–6, funnelform-campanulate, declinate, sweetly fragrant; pedicel short, 5–7(–10) mm long, 2.5–3.4 mm diam.; tube curved, 40–55 mm long, 1.5–2 mm wide below, dilating at ½–⅓ its length to 20–25 mm at the throat, green in the proximal half, white distally; tepals ovate, imbricate for half their length, white, margins usually undulate, spreading slightly apically; outer series (30–)35–40 mm long, (18–)20–26 mm wide, acute-apiculate; inner series 25–35(–40) mm long, 23–31 mm wide, obtuse. Staminal cup short, 5–7 mm long (to apex of teeth), 23–25 mm wide, stained green or yellow where adnate to the dilated portion of the tube, with 2 acute or obtuse teeth between each stamen, teeth ca. 1.5 mm long; stamens (5–)6.7–7.5(–10) mm wide at the base from tooth to tooth; free filament 7–8.5(–10) mm long, linear or narrowly subulate, 1–1.5 mm wide at the base; anthers oblong-linear, 5.5–6.7(–7.5) mm long, slightly curved; pollen with only 10% stainability. Style filiform, (67–)74–85 mm long, green, assurgent, well exserted beyond the stamens, stigma deeply 3-lobed, 2.5–3.5(–5) mm wide, white or greenish. Ovary oblong, rostellate, 12–19 mm long, 6–8 mm wide; ovules 16–20 per locule, globose, superposed. Fruit and seed unknown, doubtfully ever formed. Chromosome number: $2n = 46$.

Distribution. Rare in the understory of primary and secondary rain forest of southern Chocó and northwestern Valle de Cauca departments of Colombia (Fig. 99), 80–600(–1,000) m elevation, but widely cultivated throughout western Colombia below 1,750 m. Rare and possibly introduced in Ecuador. The plant is functionally sterile. Most collections are from cultivation, and even seemingly native populations may be remnants of cultivation. Flowering at any time of the year.

Additional specimens examined. COLOMBIA. CHOCÓ: entre Istmina y Condoto, Río San Juan y Río Iro, 80–100 m, 5 Aug. 1944, *García-Barriga 11525* (COL, US). VALLE DE CAUCA: Río Cabrera, Tambi, Río Sumapaz, Cundinamarca, 600–1,000 m, Feb. 1883, *Lehmann 2644* (K); Cordova, Río Dagua, *Lehmann 2736* (K in part); Río Teta, Cauca Valley, 1,000 m, *Lehmann 7776* (F, GH, K, NY, US); Cauca, 1,000 m, *Lehmann s.n.* (K); cultivated 50 km SE of Buenaventura on old road to Pacific coast, Río Anchicaya, 500 m, 22 July 1984, *Meerow & Teets 1127* (FLAS). ECUADOR. CARCHI: Chical, path from Juan Maldonado to Tobar Danuso, flowered in cultivation, 23 Dec. 1982, *Madison et al. s.n.* (SEL). Guayas, Guayaquil, cultivated, Nov. 1925, *Mille 40* (QCA). Los Ríos, Hacienda Ana Maria, Canton Vinces, 60 m, *Y. Mexia 6644* (GH, US); vicinity Duran, cultivated, *Rose & Rose 23627* (US). EX HORT.: voucher of *Madison et al. s.n.*, Feb. 1983, *Meerow 1104* (FLAS).

Eucharis ×grandiflora has long been confused with *E. amazonica* Linden ex Planchon (Meerow & Dehgan, 1984a). Meerow & Dehgan (1984a) re-established *E. grandiflora* (without hybrid designation) as distinct from *E. amazonica* in *Eucharis* subg. *Heterocharis*. At the time, I considered *E. lowii* and *E. mastersii* to be distinct but closely related to *E. ×grandiflora*. In 1984, I collected material in Colombia referable to *E. lowii* Baker and received living material of *E. mastersii* collected in Ecuador. According to Baker (1893), who described these two species from cultivated material, *E. lowii* had a staminal cup half as long as

FIGURES 94–98. Natural hybrids of *Eucharis* subg. *Heterocharis*. 94–96. *E.* ×*grandiflora*.—94. Flower of *E.* "*mastersii*" form (*Madison et al. s.n.*, SEL). 95, 96. *E.* "*lowii*" form (*Meerow & Teets 1127*, FLAS).—95. Habit in Colombia.—96. Flower. 97, 98. ×*Calicharis butcheri* (*Meerow 1098*, FLAS).—97. Inflorescences.—98. Flower.

that of *E.* "*grandiflora*," probably referring to *E. amazonica* or *E. moorei* (as *E. grandiflora* var. *moorei* Baker). When I compared the staminal cup of *E. lowii* with that of the lectotype of *E.* ×*grandiflora*, the synonymy of *E. lowii* with *E.* ×*grandiflora* became evident. The two seemed identical in all respects. Baker considered *E. lowii* to be a hybrid of *E. mastersii* and *E.* "*grandiflora*" and *E. mastersii* Baker (1885) to be a hybrid between *E. sanderi* and *E.* "*grandiflora*." Baker distinguished *E. lowii* from *E. mastersii* merely by the former's slightly longer-exserted staminal cup, which does not hold up. I now believe that *E. mastersii* and *E. lowii* are elements of a slightly variable hybrid taxon, *E.* ×*grandiflora*, a putative hybrid of *E. sanderi* and *E. moorei*. Though never collected in western Colombia, *E. moorei* does occur in contiguous northwestern Ecuador. It was likely a collection of this hybrid that Planchon & Linden (1853) described as *E. grandiflora*. *Eucharis* ×*grandiflora* appears intermediate in all respects to *E. moorei* and *E. sanderi*. Virtually all collections of *E.* ×*grandiflora* are from cultivated populations in Colombia and Ecuador according to specimen labels. Pollen stainability of either Colombian or Ecuadorean collections of *E.* ×*grandiflora* is never better than 10%, and I have not succeeded in obtaining seeds in cultivation with either sibling pollen or pollen of other species. The hybrid is slightly variable in leaf morphology, num-

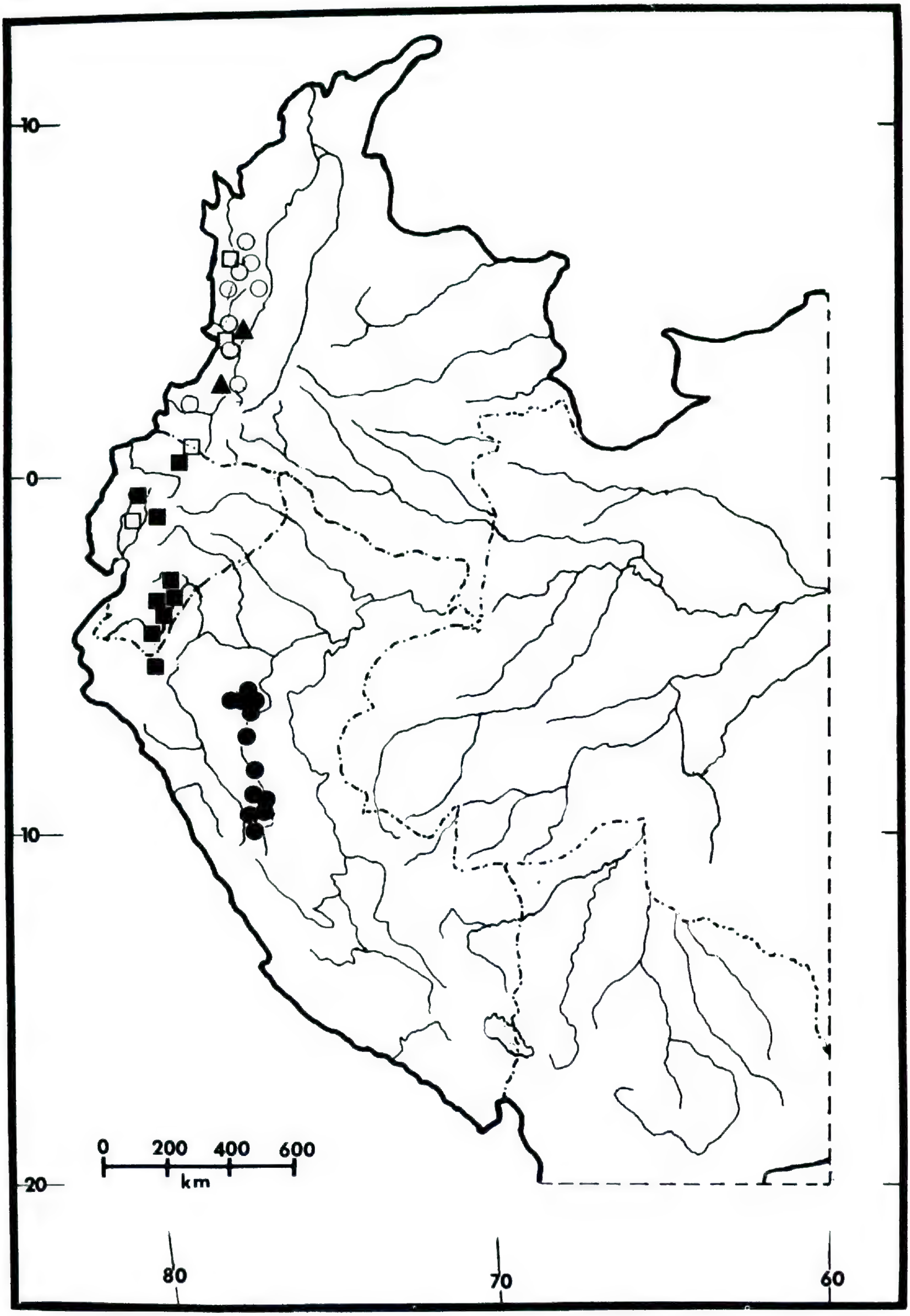


FIGURE 99. Distributions of species and hybrids of *Eucharis* subg. *Heterocharis* in northwestern-central South America. *Eucharis amazonica* (closed circles), *E. sanderi* (open circles), *E. moorei* (closed squares), *E.* ×*grandiflora* (open squares) and ×*Calicharis butcheri* (closed triangles).

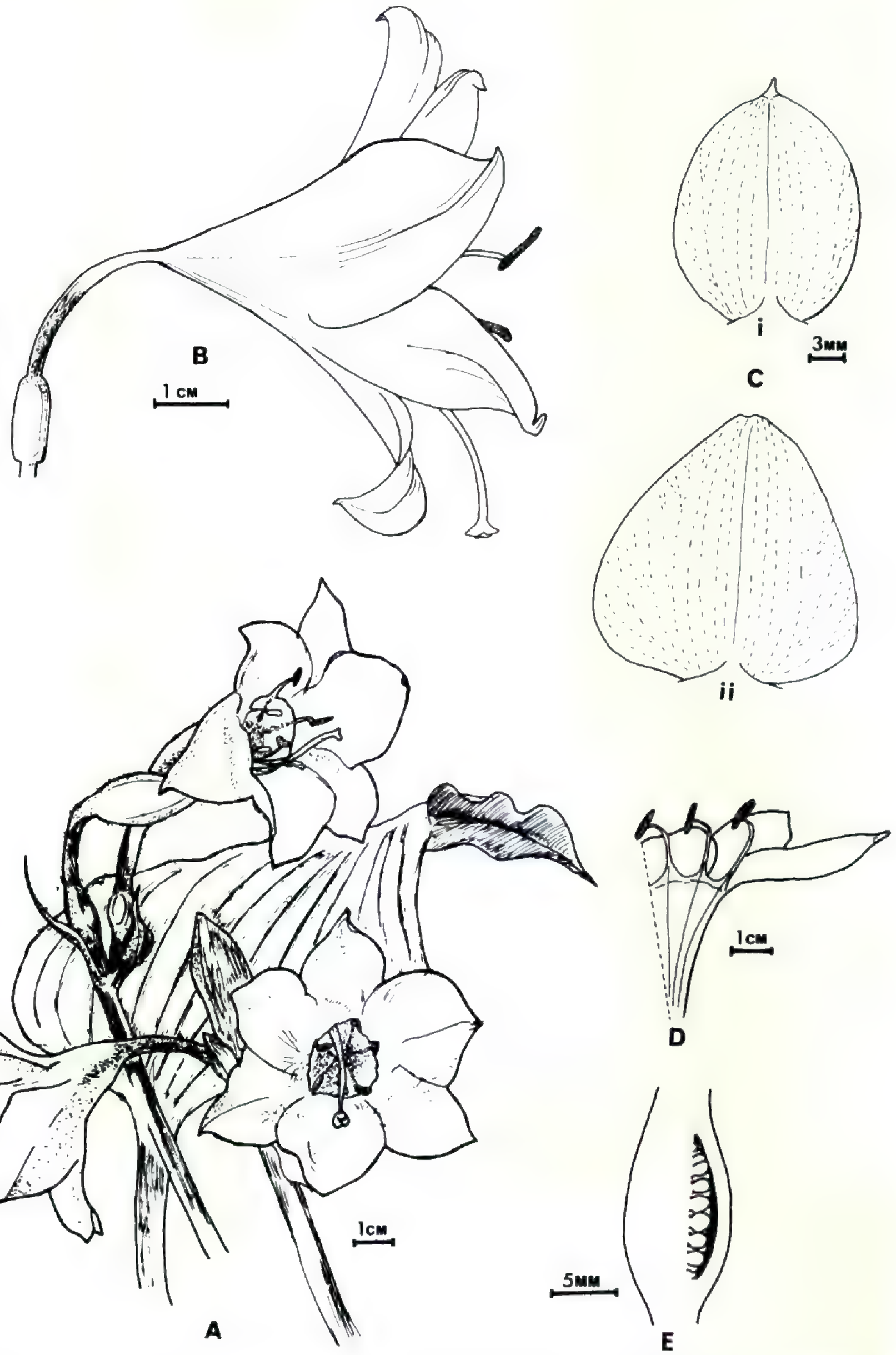


FIGURE 100. *Eucharis sanderi* (*Cuatrecasas 16380*, F). —A. Habit.—B. Flower.—C. Tepals. i, outer tepal; ii, inner tepal.—D. Detail of androecium.—E. Ovary, longitudinal section.

ber of flowers, and color of androecial pigmentation throughout its range, the extremes of which were recognized respectively as *E. mastersii* (Fig. 94) and *E. lowii* (Figs. 95, 96) by Baker (1885, 1893). The labels of all of Lehmann's collections indicate that they were prepared from material in Colombian gardens, and I encountered cultivated material referable to this hybrid in the Cauca valley and Pacific slopes of the Cordillera Occidental.

2. Eucharis sanderi Baker, Curtis's Bot. Mag. 109: t. 6676. 1883. *Urceolina sanderi* (Baker) Traub, Pl. Life 27: 57–59. 1971. TYPE: ex hort. (K). Figure 100.

Bulb 42.5–49 mm long, 32–47 mm wide; neck thick, 24–30 mm wide; tunics light brown. Leaves petiolate, persistent; petiole 31–50 cm long, 5.5–6(–8) mm thick; lamina ovate or elliptic, (23–)30–37 cm long, (10–)14–17 cm wide, thin, deeply plicate between the veins, undulate margined, apically acuminate, subcordate basally and shortly attenuate to the petiole, bright green adaxially, light green abaxially, the abaxial surface intensely striate.

Scape subterete, 45–54 cm long, 5–6 mm diam.; bracts lanceolate, 45–65(–77) mm long. Flowers 2(–3), subsessile (pedicels 5 mm or less long), strongly fragrant, declinate, funnelform-campanulate; perianth tube (45–)50–60(–70) mm long, cylindrical to subcylindrical and 2–3 mm wide below, abruptly dilated at ½ of its length to 20–27 mm wide, curved, tinged green proximally; tepals white, ovate, subequal, imbricate for half their length, spreading somewhat distally; outer series 26–32(–37) mm long, 16–20 mm wide, apiculate; inner series 24–30(–33) mm long, 20–25 mm wide. Stamens basally connate into a short staminal cup partially adnate to the upper portion of the tube, ca. 20–24 mm wide, striped green within along the filamental traces, only shortly exserted beyond the rim of the throat, edentate or rarely with one to few obscure teeth; free filaments (6–)7–9(–9.7) mm long, 1.8–2.2 mm wide at the base, linear, incurved; anthers (5.6–)6–8(–9) mm long linear, versatile, often curved; pollen grain 39.8 μm polar diam., 61.2 μm longest equatorial diam., the exine mostly coarsely reticulate. Style filiform, (66–)75–80(–90) mm long, well exserted beyond the staminal cup and slightly assurgent, white, sometimes flushed green; stigma deeply and obtusely trilobed, (2.8–)3–4 mm wide. Ovary large, ellipsoid, trigonous, appearing rostellate when dry, (10–)15–20 mm long, (5–)7–9(–11) mm wide; ovules (7–)10–20 per locule, ellipsoid, biseriate. Fruit and seed imperfectly known; capsule green; seeds several per locule.

Distribution. Endemic to western Colombia locally on sites with rich soil in the understory of wet, lowland rain forest, primarily in Chocó department (Fig. 99), frequently along watercourses; occasional in similar habitats in Valle de Cauca Dept., (5–)30–300(–1,000) m. Flowering may occur at any time of the year.

Additional specimens examined. COLOMBIA. CHOCÓ: headwaters of Río Tutunendo, E of Quibdo, 20–21 May 1931, *Archer 2197* (US); Municipio de San José del Palmar, Río Torito, 630–830 m, 5 Mar. 1980, *Forero et al. 6728* (MO); Río San Juan between Dipurdu & San Miguel, ca. 100 m, 14 Aug. 1976, *Gentry & Fallon 17687* (MO); Taparalito, Quebrada Taparal, N of Palestina, 4°15′N, 77°12′W, 30 m, 30 Mar. 1986, *Gentry et al. 53784* (FTG, MO); Corcovada region, upper Río San Juan, Yeracüi valley, 200–275 m, 24–25 Apr. 1939, *Killip 35276* (US); Andagoya, 70–100 m, Apr. 1939, *Killip 35401* (US). VALLE DE CAUCA: Río Calima, La Trojita, 5–50 m, 19 Feb.–10 Mar. 1944, *Cuatrecasas 16380* (F); Río Calima, Quebrada de La Brea, 30–50 m, 18–22 May 1946, *Cuatrecasas 21195* (F); Río Telembi, 12 Aug. 1880, *Lehmann 65* (G); Río Dagua, 0–300 m, 11 Aug. 1884, *Lehmann s.n.* (G). CAUCA: El Tambo, La Costa, 1,000 m, 3 July 1935, *von Sneidern 404* (S); El Tambo, 800 m, 7 July 1936, *von Sneidern 1129* (S). CALDAS: Riseralda [?], Tatáma, Santa Cecilia [La Celia?], 800 m, 1 Dec. 1945, *von Sneidern 5208* (S).

This species is characterized by its large, sweetly fragrant funnelform-campanulate flowers, large ovaries and capsules, and reduced staminal cups. "Natural" hybrids exist between *E. sanderi* and both *E.* "*moorei*" (*E.* ×*grandiflora*) and "*Caliphruria subedentata*" (×*Calicharis butcheri*). Despite the many putatively primitive characteristics of *E. sanderi* (e.g., large flowers, strong fragrance) in common with *E. moorei*, ovule number of *E. sanderi* is highly variable, and its leaves are deeply plicate. The reduced morphology of the androecium is the major advanced character of *E. sanderi*.

3. ×Calicharis butcheri (Traub) Meerow, Nothogen. et comb. nov. *Eucharis butcheri* Traub, Pl. Life 23: 68. 1967. *Urceolina butcheri* (Traub) Traub, Pl. Life 27: 57–59. 1971. TYPE: ex hort. Traub, purported to have been collected in Panama by J. N. Giridlian, *Traub 1051* (holotype, MO). Figures 97, 98.

Eucharis sanderi Baker var. *multiflora* Baker, Curtis's Bot. Mag. 111: t. 6831. 1885. *Eucharis sanderi* Baker subsp. *multiflora* (Baker) Traub, Pl. Life 23: 65. *Urceolina sanderi* subsp. *multiflora* (Baker) Traub, Pl. Life 27: 57–59. 1971. TYPE: Colombia. No other data, *Lehmann s.n.* (holotype, K).

Bulb 6–7 cm long, 3.8–5 cm wide, neck short and thick, tunics brown. Leaves 2–3; petiole 20–40 cm long, 5–6 mm wide; lamina elliptic, 21–26(–35) cm long, (10.5–)12–15 cm wide, shortly acuminate, subcordate-attenuate at the base, conspicuously plicate, adaxial surface bright to dark green, abaxial surface lighter green, the cuticle intensely striate. Scape 5–6 dm long, 4–5.5 mm diam.; primary bracts lanceolate, 41–57 mm long. Flowers 4–6(–7), funnelform-campanulate, fragrant; pedicels 4.5–5(–8) mm long; tube 35–42 mm long, funnelform proximally, dilating gradually from 1.5 mm wide at the base to 3.5 mm wide at median length, then abruptly dilated in the distal half to 13–16 mm wide at the throat, green for most of its length, the interior of the dilated portion stained green, most prominently along the filamental traces; tepals white, imbricate for half their length, spreading eventually to 45–55(–60) mm wide, margins nonundulate; outer series 20–28 (–35) mm long, 12–17.5 mm wide, acute-apiculate; inner series 19–27(–32) mm long, 18–25 mm wide, obtuse. Stamens shortly connate below, edentate or rarely with one obscure tooth between some of the filaments, white; free filament linear,

straight or slightly curved apically, 6.7–8.7 mm long, 0.6–1 mm wide at the base where abruptly dilated to 2.5–3 mm; anthers (4.5–)6 mm long, linear-oblong, grayish brown, mostly devoid of pollen. Style 6–7 cm long, overtopping the stamens, slightly assurgent, white distally, green proximally; stigma obtusely trilobed, (2–)2.8–3 mm wide, papillae multicellular. Ovary globose-ellipsoid, 7.7–12(–15) mm long, (5–)7–9 mm wide; ovules 7–10(–12) per locule. Fruit and seed unknown, doubtfully ever formed. Chromosome number: $2n = 46$.

Distribution. Rare in western Colombia (Fig. 99), along the Río Dagua in Valle de Cauca Department, and the lower Cauca valley.

Additional specimens examined. COLOMBIA. VALLE DE CAUCA: Río Dagua, 17 Mar. 1883, *Lehmann 2736* (BM, K); Río Dagua, 200–500 m, *Lehmann 7774* (F, K in part). CAUCA: El Tambo, La Costa, 1,000 m, 24 June 1936, *Von Sneidern 1269* (S). PROVENANCE UNKNOWN: no data, Jan. 1938, *Cuatrecasas 1620* (F). EX HORT.: Kew acc. 430.53.43001, June 1984, *Meerow 1110* (FLAS).

This putative hybrid between *E. sanderi* and *Caliphruria subedentata* was first described by Baker (1885) as *Eucharis sanderi* var. *multiflora*. It has been collected in the wild at the interface of the distributions of both parents and at intermediate elevations. The plant produces little pollen, none of it staining with Alexander's (1969) stain. Floral morphology is intermediate between both parents, although, like *C. subedentata*, the stigmatic papillae are multicellular. There is some karyological evidence of hybrid intermediacy as well (Meerow, 1987b).

4. Eucharis moorei (Baker) Meerow, Sida 13: 29–49. 1987. *Eucharis grandiflora* var. *moorei* Baker, Gard. Chron. 4: 628. 1888. TYPE: ex hort., 1888, *Glasnevin s.n.* (K). Figures 101, 102.

Bulb 6–7 cm long, 2.5–4 cm diam., tunics brown. Leaves 2–3; petiole 2–4 dm long, 5–7 mm thick, with an anomalous arc of accessory vascular bundles near the adaxial surface; lamina broadly ovate, length/width ratio ≤ 2, 17–30 cm long, 10–14 cm wide, apex shortly acuminate, base appearing cordate at the base, margins coarsely undulate, lustrous dark green adaxially, lighter green abaxially, abaxial cuticle mostly without striations. Scape 5–7 dm tall, terete, 7–10 mm diam. proximally, ca. 5 mm diam. distally; bracts ovate-lanceolate, (25–)35–45 mm long, green. Flowers usually 4, rarely up to 7, ± campanulate, declinate, sweetly fragrant; pedicels usually short, 3–10(–18) mm long; tube 40–52 mm long, cylindrical and 1.7–2 mm wide proximally, abruptly dilating at about its midpoint to (15.5–)18.5–25 mm at the throat, white except for a slight green tinge at the base; limb spreading less than 90° from the throat to ca. 70 mm wide or less; tepals ovate, the margins undulate; outer series 3.3–4 cm long; 17–22 mm wide, apiculate; inner series 2.9–3.8 cm long, 22–27 mm wide, obtuse. Staminal cup broadly cylindrical, (8–)10–15(–16.4) mm long (to apex of teeth), 20–25 mm wide, strongly recurved at the margins, white on the exterior, yellowish green on the interior, shallowly cleft between each stamen, bidentate between each free filament, teeth acute, 2.5–3 mm long; each stamen ca. 7–8 mm wide tooth to tooth; free filament subulate, (5–)6–8.5 mm long, 2 mm or less wide at the base; anthers 5.5–6.5 mm long, oblong-linear, grayish-brown; pollen grain ca. 48.6 μm polar diam., ca. 71.2 μm longest equatorial diam. Style 6–7 cm long; stigma 2.5–3.5 mm wide, white. Ovary ellipsoid-trigonous, (7–)10–13 mm long, ca. 5 mm wide; ovules 16–20, biseriate. Capsule globose, ca. 1.5 cm long, 1.3 cm wide, slightly rostellate, green, slightly glaucous; seeds 1–3 per locule, compressed globose, ca. 6 mm diam., turgid, testa blackish brown and slightly rugose. Chromosome number: $2n = 46$.

Distribution. An understory plant of primary and secondary lower montane rain forest of the Ecuadorean Andes (Fig. 99), in Morona-Santiago and Zamora-Chinchipe provinces on the east slopes, and Los Ríos, Cotopaxi, and contiguous Pichincha provinces on the western declivity, (220–)600–1,200(–1,600) m; rare in the "ceja de la selva" of Cajamarca Department, Peru. Flowering is concentrated January–March and again (June–) July–September.

Additional specimens examined. ECUADOR. COTOPAXI: km 52–53 on rd. from Quevedo to Latacunga, Río Pílalo, 800–950 m, 11 Aug. 1984, *Meerow & Meerow 1137* (FLAS); same locality, 13 Aug. 1984, *Meerow & Meerow 1141* (FLAS). GUAYAS: Guayaquil, cultivated, Nov. 1926, *Mille 40* (QCA). LOS RÍOS: km 56 Quevedo–Santo Domingo, Río Palenque Biological Station, 220 m, flowered in cultivation, *Dodson 5527* (SEL); same locality, 16 Oct. 1984, *Dodson & Dodson 15330* (MO). MORONA-SANTIAGO: 27 km SE of San Juan Bosco, 1,270 m, 27 Jan. 1981, *Gentry et al. 30913* (MO, SEL); Indanza-Limón (General Plaza), 1,300–1,600 m, 23 Mar. 1974, *Harling & Andersson 12779* (GB); 3 km N of Tucumbatza on road Gualaquiza–Indanza, 1,200 m, forest remnants, 19 Apr. 1985, *Harling & Andersson 24329* (GB); Río Yunganza, rd. Limón–Mendez (78°19′W, 2°49′S), 1,100 m, 23 Sep. 1979, *Holm-Nielsen et al. 20393 & 20407* (AAU); Río Gualaquiza and Río Bomboiza, E Andes of Sigsig, 800–1,200 m, *Lehmann 5882*

FIGURE 101. *Eucharis moorei*, after a drawing by Wendy B. Zomleffer of *Dodson 5527* (SEL).—A. Habit.—B. Flower.—C. Ovary, longitudinal section.

(K); 10–20 km from Gualaquiza on rd. to Sigsig-Cuenca, 1,300 m, 5 Aug. 1984, *Meerow & Meerow 1135* (FLAS). PICHINCHA: Nanegal, W slope Andes, 5,000 ft., *Jameson 9* (G, P). ZAMORA-CHINCHIPE: Yurupaza, 600 m, 3 June 1947, *Harling 1407* (GB); W side Río Valladolid, 2,100–2,400 m, 15 Oct. 1943, *Steyermark 54717* (F). PERU. CAJAMARCA: Jaen, Río Tabaconas valley, 900–1,000 m, May 1912, *Weberbauer 6251* (GH, US).

Herbarium material of *E. moorei*, when first received, was assigned to *E. amazonica*. In 1984, I collected the species on both sides of the Ecuadorean Andes. Morphological, anatomical, and karyological differences between these collections and the Peruvian *E. amazonica* became evident. *Eucharis moorei* is fully fertile, diploid ($2n = 46$), and of fairly wide distribution throughout Ecuador. The anomalous arc of secondary bundles that appear in petiolar transverse sections of *E. moorei*, and reduced, in *E. amazonica*, are not found in

any other species of the genus investigated. *Eucharis moorei* is putatively the most primitive species of the genus, and shares numerous plesiomorphic character states with other genera of "infrafamily" Pancratioidinae (e.g., large fragrant flower, short pedicels, and numerous ovules per locule). *Eucharis moorei* is the only species in the genus that occurs on both sides of the cordillera.

5. Eucharis amazonica Linden ex Planchon, Fl. des Serres Jard. Eur. Ser. 2, 2: 1216–1217. 1857. LECTOTYPE (Meerow & Dehgan, 1984a): Fl. des Serres Jard. Eur. Ser. 2, 2: t. 1216–1217. Figure 103.

Bulb 3.5–6 cm diam., neck 2.8–4.5 cm long, tunics brown. Leaves usually 2–4; petiole (15–)25–30(–50) cm long, 5.5–9 mm thick; lamina long-elliptic, (20–)30–40(–50) cm long, (10–)12–18 cm wide, length/width ratio usually greater than 2, acuminate, subcordate at the base and attenuate to the petiole, lustrous, dark green adaxially and shallowly or inconspicuously plicate, abaxial surface lighter green, cuticular striations obscure or largely absent, margins coarsely undulate. Scape 4.5–7(–8) dm tall, ca. 1–1.5 cm diam. proximally, ca. 5 mm diam. distally, terete; primary bracts (30–)35–58(–61) mm long, broadly ovate-lanceolate, green. Flowers (4–)5–6(–8), subpendulous, sweetly fragrant; pedicel (9–)10–15(–25) mm long; tube white throughout, curved, (41–)46–58 mm long, cylindrical below and 2–2.5 mm wide, dilating abruptly at ⅓ length to (15–)18–21(–24) mm at the throat; limb white, spreading widely to 60–90 mm wide; tepals ovate, outer series 35–45(–50) mm long, 21–30 mm wide, apiculate; inner series 30–40(–45) mm long, 25–35 mm wide, acute. Staminal cup widely cylindrical, 11.2–13.8 mm long (to apex of teeth), (22–)28–30(–34) mm wide, margins slightly recurved, the interior stained green, particularly along the filamental traces, shallowly cleft between each stamen; stamens 7–8(–9.5) mm wide at the base, each with 2 obtuse teeth, one on each side of the subulate free filament, rarely subquadrate; teeth 2–3 mm long; free filament 6.5–8(–10) mm long, 2.8–3.4 mm wide at the base; anthers oblong-linear, 6–7(–8) mm long, grayish; pollen ca. 51.6 μm polar diam., ca. 78.3 μm longest equatorial diam. Style white, 66–78(–85) mm long, exserted 1–1.5 cm from the staminal cup, slightly assurgent; stigma deeply 3-lobed, 3–3.5 mm wide when receptive. Ovary oblong-ellipsoid, (8–)10–14 mm long, (4–)5–7.5(–8) mm wide, somewhat rostellate; ovules 9–12 per locule, superposed. Fruit and seed

FIGURES 102, 103. *Eucharis moorei* and *E. amazonica*.—102. *E. moorei* (*Meerow & Meerow 1141*, FLAS).—103. *E. amazonica* (*Schunke 14179*, FLAS).

imperfectly known, capsule reported to be green and the seed ellipsoid with a black testa. Chromosome number: $2n = 68$.

Distribution. An understory herb of lower and mid-montane rain forest of northeastern Peru, most prominently in the Huallaga valley in the vicinity of Moyobamba and Tarapoto (Fig. 99), 500–1,500 m. Widely cultivated throughout the warm tropics and as a house and greenhouse plant in the temperate zone. Occasionally adventive in the West Indies and probably elsewhere. Flowering at least twice per year, (May–)July–August(–September) and December–March.

Vernacular names. Amangais blanco, amangay, flor de cebolla, azuzena, Amazon lily, Eucharist lily.

Additional specimens examined. PERU. HUÁNUCO: Huánuco, Tingo María, 20 Aug. 1940, *Asplund 13214* (S); Huánuco, Tingo María, hwy. La Oroya–Tingo María,

Mar. 1977, *Boeke 1196* (NY); Leoncio Prado, Rupa Rupa, Las Palmas, km 18.5 a la carretera Tingo María–Huánuco, 756–800 m, 22 July 1984, *Schunke 14055* (F, FLAS, MO); Leoncio Prado, Rupa Rupa, Castillo Grande, al oeste de Tingo María, 24 July 1984, *Schunke 14057* (COL, F, FLAS, GH, K, MO, NY, UC, US); Huánuco Puerte Durand north of Huánuco, Río Chinchao valley, 7 Nov. 1938, *Stork & Horton 9880* (F, US); vicinity of Afilador, 670 m, *Woytkowski 101* (F). SAN MARTÍN: Lamas, Lamas, on trail from Tabalosos to Lamas, along Río Cumbaquiri, ½ hour W of Río Mayo, ca. 1,500 ft., 13–15 Sep. 1937, *Belshaw 3416* (F); near Uchiza, Huallaga valley, 500–550 m, 6 Aug. 1948, *Ferreyra 5154* (MO); Zepaelacio near Moyobamba, 1,200–1,600 m, Mar. 1934, *Klug 3559* (F, G, GH, K, NY, S US); Pachiza, Río Huayabamba, 1 Aug. 1959, *Mathias & Taylor 3974* (F); Roque, 9 Aug. 1925, *Melin 92* (S); between Balsapuerto and Moyobamba, 3,000 ft., *Sandeman s.n.* (BM); Lamas, Lamas, Fundo San Rafael, sector Santana, near Quebrada Chupishiña, 800 m, 5 Dec. 1984, *Schunke 14171* in part (FLAS); Moyobamba, 100[?]–1,100 m, *Weberbauer 4642* (G); Lamas, near Tarapoto, 840 m, Dec. 1929, *Williams 6348* (F, US); San Roque, 1,350–1,500 m, Feb. 1930, *Williams 7802* (F).

Meerow & Dehgan (1984a) re-established *Eucharis amazonicas* distinct from *E.* ×*grandiflora*, a taxon with which it has been confused since its description by Planchon (1857). The species is indigenous only to Peru, in the upper and middle Huallaga valley, but is grown worldwide in tropical regions and may be sporadically adventive. The species has a somatic chromosome number of $2n = 68$ (Meerow, 1987b; Nagalla, 1979) and is at least partially sterile. No specimen of *E. amazonica*, in contrast to most other species, has ever been collected in fruit; pollen stainability is only 50–65%; and viable seed has never been produced in cultivation. It is therefore conceivable that all populations of *E. amazonica* constitute a single clone. Its distribution throughout its narrow range may have been promoted by transient agriculturists. I believe *E. amazonica* to be a triploid-derived ($3x-1$) Peruvian isolate of either *E. moorei* or a possibly extinct mutual ancestor. The morphological differences between these taxa are cryptic and virtually impossible to discern in most dried material without dissection of the ovary. Their close relationship is further supported by the presence of secondary vascular bundles in the petiole of both taxa, although much smaller in *E. amazonica*.

DOUBTFUL OR EXCLUDED NAMES IN *EUCHARIS*

Eucharis galanthoides hort., Linden, usually cited as *E. galanthoides* (Klotzsch) Linden (e.g., by Macbride, 1936; Traub, 1963), Ann. Cat. Hort. 17: 4. 1862. This combination is based on the erroneous assumption that Linden's *Eucharis galanthoides* was based on *Mathieua galanthoides* Klotzsch (Meerow, 1987a). The actual basionym was *Pancratium galanthoides*, a name under which Linden received material of a *Eucharis* collected by Gustav Wallis in Amazonas. *Mathieua galanthoides* was collected by Warscewicz in xeric, northwestern Peru (*Warscewicz s.n.*, B). No type has been located for Linden's plant, and the name *E. galanthoides* merely appeared as a listing in his catalog. It is likely referable to *E. castelnaeana* (Baillon) Macbride.

Eucharis himeroessa Sandwith ex Standley, Herbertia 3: 4. 1936. This name was never validly published with diagnosis or description. It was applied to a population of *E. bouchei* var. *bouchei* Woodson & Allen from San José Province in Costa Rica.

Eucharis paradoxa hort., T. Moore, Gard. Chron. 1: 242. 1876. A listed name, never described or illustrated, supposedly applied to the plant later described as *Caliphruria subedentata* Baker.

Pancratium galanthoides hort., Linden, Ann. Cat. Hort. 17: 4. 1862. See discussion under *Mathieua galanthoides*.

Caliphruria Herbert, Edwards's Bot. Reg. 30 (misc. no. 83): 87. 1844. *Urceolina* subg. *Caliphruria* (Herbert) Traub, Pl. Life 27: 57–59. 1971. TYPE SPECIES: *Caliphruria hartwegiana* Herbert.

Small bulbous perennial herbs. Leaves glabrous, petiolate, persistent or rarely hysteranthous; petiole subterete; lamina ovate, ovate-elliptic or elliptic, slightly succulent, apically acute or acuminate, basally attenuate to the petiole, margins nonundulate, dark green and smooth-surfaced adaxially, lighter green abaxially, the cuticle of the abaxial epidermis thickly striate or ridged, hypostomatic or with adaxial stomata only near and upon the midrib. Inflorescence scapose, umbellate; scape slender, terminating in 2 marcescent bracts enclosing the flowers before anthesis. Flowers pedicellate, (3–)5–10(–12) on thin pedicels, each subtended by a linear-lanceolate bracteole, declinate or subpendulous by the laxness of the pedicel, 2–4 cm long, without noticeable fragrance, white, funnelform or funnelform-tubular, protandrous; perianth tube funnelform, dilating gradually from the base, tinged green below, or subcylindrical and white throughout, straight; limb of 6 lanceolate, ovate or elliptic tepals in 2 subequal series, the segments imbricate for half their length, diverging in their distal half. Stamens connate only at the base, forming a short,

membranaceous staminal cup, variously toothed or edentate between each filament, distal portion of the filament narrowly subulate or linear, subequal; anthers oblong, erect at anthesis, eventually versatile; pollen grains medium-sized (longest equatorial axis ca. 50 μm), the exine finely reticulate. Style filiform; stigma trilobed, papillae multicellular. Ovary globose, green, with septal nectaries; ovules ellipsoid, (1–)2–7 per locule, medially superposed, placentation axile. Fruit a thin-walled, leathery, yellow-green, loculicidal capsule; seeds few per locule; globose or compressed-ellipsoid, ca. 3–5 mm long, testa black or brown. Chromosome number: $2n = 46$.

Four species, three endemic to western Colombia, one to Peru.

KEY TO THE SPECIES OF *CALIPHRURIA*

1a. Perianth more than 2 cm long; tube 9 mm or more long.
  2a. Perianth tube 9–13.5 mm long; stamens 5.8–6.8 mm long, bidentate between each stamen, length of teeth at least ½ the length of the free filament ..... 1. *C. hartwegiana*
  2b. Perianth tube 15–25 mm long; stamens 9 or more mm long, edentate or occasionally with 1–2 teeth between each stamen, teeth never more than 1/10 the length of the free filament ..... 2. *C. subedentata*
1b. Perianth equal to or less than 2 cm long; tube less than 9 mm long.
  3a. Leaves hysteranthous; perianth tube funnelform; stamens less than 5 mm long, more or less fasciculate, bidentate, teeth much exceeding the free filament in length, free filament 1–2 mm long, ovules 1–2 per locule ..... 3. *C. tenera*
  3b. Leaves persistent; perianth tube subcylindrical; stamens 7–10 mm long, divergent, edentate, free filament 7–9 mm long, ovules 4–5 per locule ..... 4. *C. korsakoffii*

1. Caliphruria hartwegiana Herbert, Edwards's Bot. Reg. 30, misc. no. 83: 87. 1844. *Eucharis hartwegiana* (Herbert) Nicholson, Illus. Dict. Gard. 1884. *Urceolina hartwegiana* (Herbert) Traub, Pl. Life 27: 57–59. 1971. The species as described by Herbert from Hartweg collections made near Guaduas, Colombia, lacks a holotype, and I have not located any specimen which could be designated as lectotype. The following neotype is herein proposed. NEOTYPE: Colombia. Huila: Río Magdalena near Paicol, 600–1,200 m, *Lehmann 6376* (neotype, K). Figure 104B.

Bulb globose with a brown tunic, ca. 32.8 mm diam., often apically articulated into a slender neck

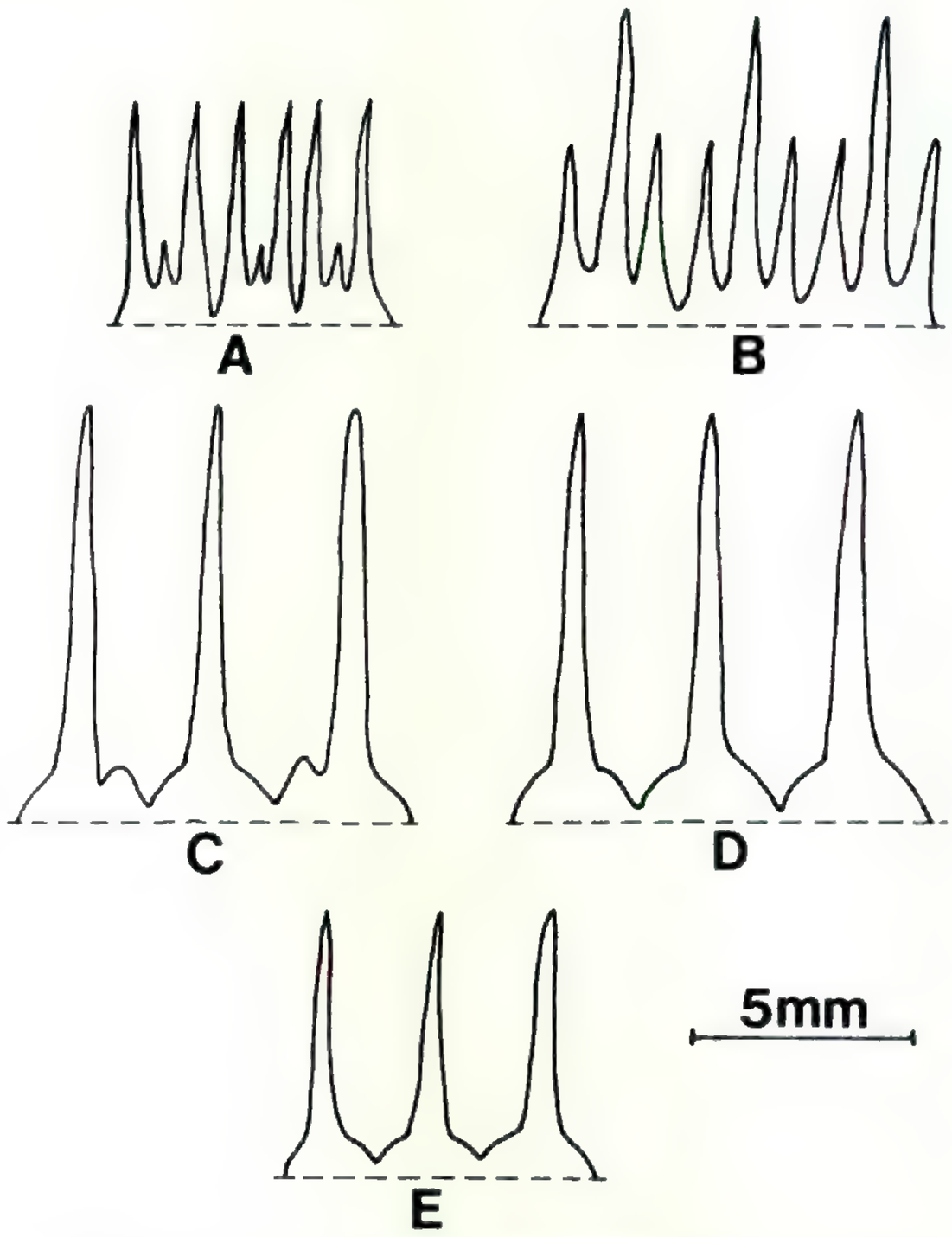


FIGURE 104. Androecial morphology of *Caliphruria* species.—A. *C. tenera* (*Triana 1289*, COL).—B. *C. hartwegiana* (neotype, *Lehmann 6376*, K). C, D. *C. subedentata*.—C. *Pittier 1009* (US).—D. Holotype, ex hort. *Beaufoy s.n.* (K).—E. *C. korsakoffii* (*Meerow 1096*, FLAS).

to 19.6 mm long. Leaves 2–4; petiole 13 cm long, 2.5–4.4 mm thick; lamina ovate to elliptic, 10–14 cm long, 3.8–6.3 cm wide, acuminate, shortly attenuate to the petiole at the base. Scape 28–31 cm tall; bracts lanceolate, 13.5–16.8 mm long and ca. 3 mm wide at the base; inner bracteoles successfully smaller and narrower. Flowers 5–7; pedicels 12.8–15.8 mm long, thin; perianth 19–26 mm long, white, except for the proximal 1/3–½ of the tube, this green; tube funnelform, dilating gradually from the base, 9–13.5 mm long, ca. 2–3 mm wide at the base, 5–6 mm wide at the throat; limb spreading to 7.5–11 mm; tepals ovate-elliptic, the outer series ca. 14.8 mm long, 3.4 mm wide, acute-apiculate, the inner series ca. 12 mm long, 5 mm wide, obtuse. Stamens 5.8–6.8 mm long, narrowly subulate for most of their length, dilated to ca. 2.5 mm basally where connate, bidentate between each free filament; teeth ca. ½ the length of the free filament; free filament ca. 1.5 mm wide at point of insertion to cup; anthers 5.2–5.4 mm long, linear, versatile. Style 25 mm long, exserted ca. 2.4 mm beyond the limb; stigma 1.8 mm wide; ovary globose, 2.8–3.1 mm diam.; ovules 2–3 per locule, axile, medially superposed. Mature fruit and seed unknown.

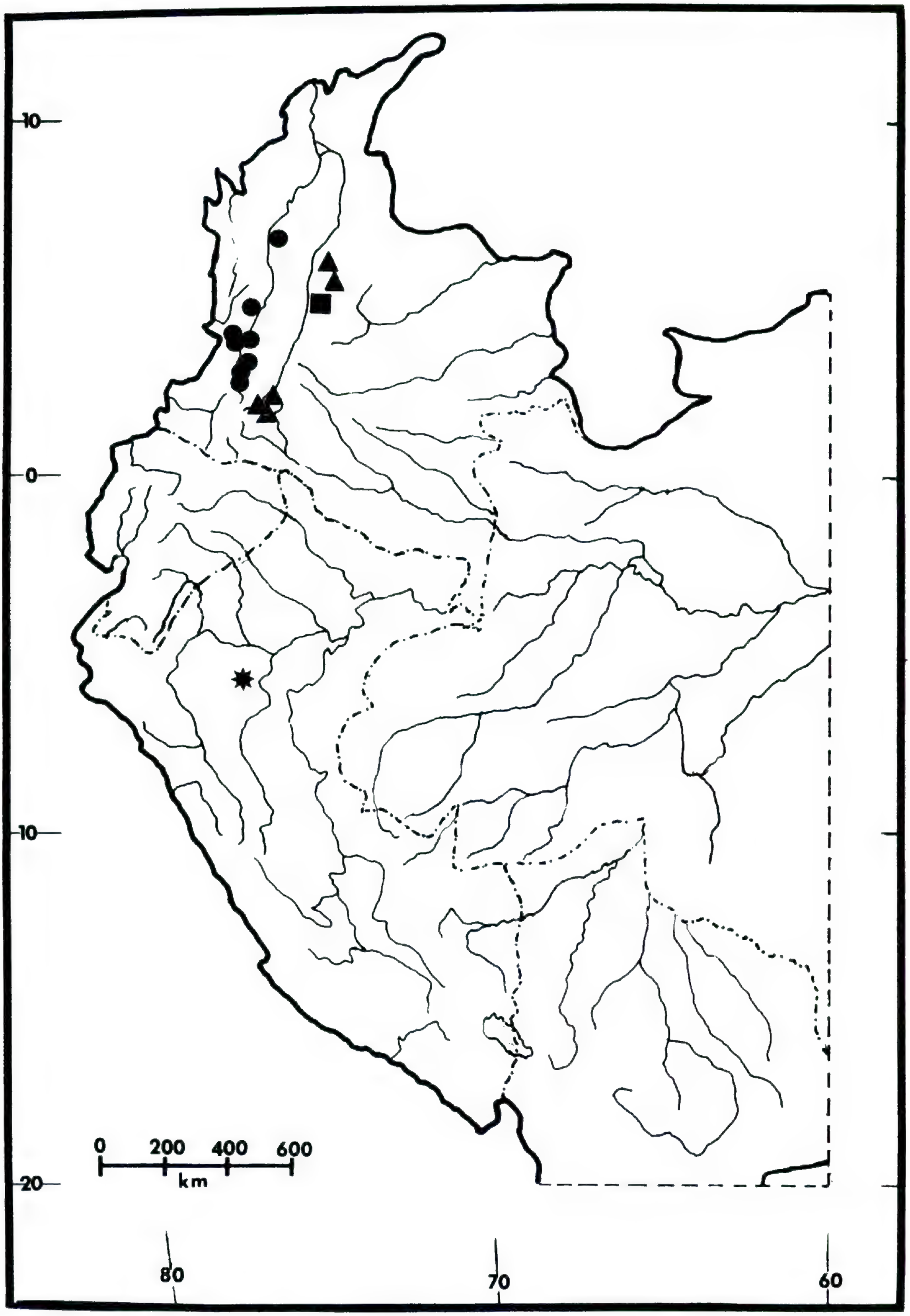


FIGURE 105. Distribution of species of *Caliphruria* in northwestern-central South America. *Caliphruria hartwegiana* (triangles), *C. korsakoffii* (star), *C. subedentata* (circles), and *C. tenera* (square).

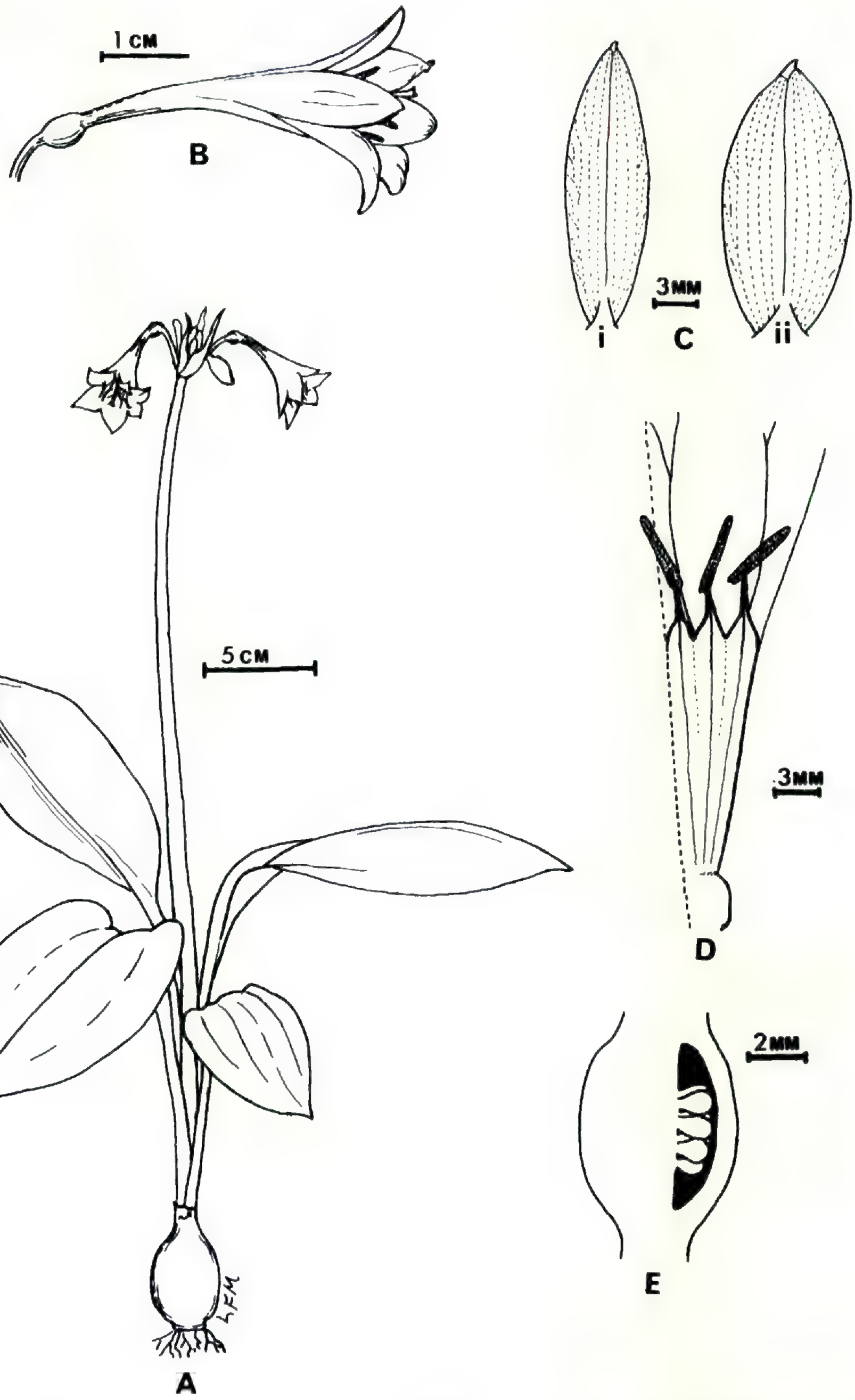


FIGURE 106. *Caliphruria subedentata* (*Meerow 1123*, FLAS).—A. Habit.—B. Flower.—C. Tepals. i, outer tepal; ii, inner tepal.—D. Longitudinal section through part of flower to show detail of androecium.—E. Ovary, longitudinal section.

Distribution. Rare in western-central Colombia, in the understory of montane forests of the Río Magdalena Valley (Fig. 105), 600–2,350 m.

Additional specimens examined. COLOMBIA. CUNDINAMARCA: Caparrapi, 1,275 m, 8–13 June 1939, *García-Barriga 7713* (COL). EX HORT.: *s.n.* (K); 1882, *s.n.* (GOET). HUILA: forest around Finca Mehrenberg, 2,350 m, 6 July 1984, *D'Arcy et al. 15634* (MO); Municipio de La Plata, Vereda Agua Bonita, Finca Merenberg, 1,200–1,300 m, 15 July 1975, *Díaz et al. 534* (COL).

This seldom-collected species is distinguished from *C. subedentata* by its smaller flowers and short stamens with long teeth interposed between the filaments (Fig. 104B).

2. Caliphruria subedentata Baker, Curtis's Bot. Mag. 103: t. 6289. 1877. *Eucharis sub-*

edentata (Baker) Bentham & Hooker, Genera Plantarum 2: 731. 1883. *Urceolina subedentata* (Baker) Traub, Pl. Life 27: 57–59. 1971. TYPE: ex hort. *Beaufoy s.n.* (holotype, K; photo of type, COL). Figure 106.

Eucharis fosteri Traub, Pl. Life 7: 36. 1951. *Urceolina fosteri* (Traub) Traub, Pl. Life 27: 57–59. 1971. TYPE: Colombia. Cauca: above Cali on road to Buenaventura, 2,000 ft., collected by M. B. Foster, 5 Dec. 1946, *Traub 17* (holotype, MO).

Bulb globose-subglobose with a brown tunic, 22–45(–63) mm long, 20–32 (–44.5) mm wide, often apically articulated into a slender neck 11.8–23.5 mm long and 10–15.7 mm wide, offsetting vigorously. Leaves 2–4; petiole 10–28(–37) cm long, 4–7 mm thick; lamina ovate, ovate-elliptic, or elliptic, 14.5–19.5(–21) cm long, (4.5–)7–10 cm wide, acuminate, shortly attenuate to the petiole. Scape 25–40 cm tall, slender, 2.5–5.5 mm diam.; bracts 13–25.5(–30.5) mm long, 3–5.2 mm wide at base; inner bracteoles 5–14 mm long. Flowers (3–)5–7(–8); pedicels (13.6–)15.2–28(–44.3) mm long, thin, ca. 1 mm diam.; perianth (24–)31.6–39(–44.8) mm long, white except for the distal ⅓–½ of the tube, this green; tube funnelform, dilating gradually from the base, 15–25 mm long, ca. 2 mm wide at the base, 5–8 mm wide at the throat; limb spreading to 12.5–21 mm wide, tepals ovate-elliptic; outer series (15–)17.5–22.5 mm long, 5–8 mm wide, acute-apiculate; inner series (13.5–)15.8–20 mm long, 7–10 mm wide, obtuse and minutely apiculate. Staminal cup less than 1 mm long, edentate, rarely with 1–2 small teeth between all or some of the filaments, white; filaments narrowly subulate-linear for most of their length, (8–)9–11.5(–14.6) mm long, dilating to 1.5–2.5 mm at their point of insertion; tooth, when present, 1 mm or less long; anthers (5–)6.2–7(–7.5) mm long, linear; pollen grain ca. 39.3 μm polar diam., ca. 50.9 μm longest equatorial diam. Style (28.9–)30–40(–45) mm long, exserted 4–6 mm beyond perianth, white; stigma 3-lobed, 1–1.5(–2.5) mm wide. Ovary globose-ellipsoid, 3–5 mm long, 2.5–5 mm wide; ovules (2–)3–5(–7) per locule, axile, superposed. Capsule ca. 1 cm diam.; seeds 1–2 per locule, compressed-ellipsoidal, 5–7 mm long, ca. 3–5 mm diam.; testa black, rugose.

Distribution. Understory of lower and middle montane forests of western Colombia in the cordilleras Occidental and Central, chiefly in the Río Cauca valley (Fig. 105), (760–)1,100–1,800 (–2,000) m. Flowering at any time of the year.

Additional specimens examined. COLOMBIA. CAUCA: Santander de Quilichao; selva densa en "Río Chiquito," 2,000 m, 6 Oct. 1954, *Fernandez 2795* (COL); Río Cauca, 1,400 m, Sep. 1881, *Lehmann 939* (BM, G); Caloto, 1,200–1,500 m, June 1883, *Lehmann 2885* (G); Quebrada Guatica, 1,800 m, *Lehmann 3269* (K); Cajamarca, *Lehmann s.n.* (K); Caloto, 1,200–1,500 m, June 1880, *Lehmann s.n.* (K); along Río La Paila above Corrinto, Central Cordillera, 1,400 m, 19 Jan. 1906, *Pittier 1009* (US); vicinity of Medellín, 23 Mar. 1927, *Toro 111* (NY). VALLE DE CAUCA: Río Dagua Valley, La Margarita, ca. 760 m, Apr. 1939, *Killip 34872* (US); "La Manuelita," Palmira, 1,090–1,100 m, May 1922, *Pennell & Smith 6182* (US). EX HORT.: 3 Apr. 1906, *Dammer s.n.* (B, GH photo); Bailey Hortorium BH 71-813, May 1982, *Meerow 1097* (FLAS); Bailey Hortorium BH 76-467, June 1984, *Meerow 1109* (FLAS); Huntington Botanical Garden HUNT 44356, June 1984, *Meerow 1123* (FLAS); Bailey Hortorium BH 60-777, July 1985, *Meerow 1153* (FLAS); ex hort. Bull, *s.n.* (K); ex hort. Linden, *s.n.* (K).

Caliphruria subedentata is the most common and variable species of *Caliphruria*, at one time found throughout the moist lower and middle montane forests of the slopes of the cordilleras Central and Occidental west of 76°W longitude (Fig. 105), and chiefly those surrounding the Cauca Valley. Much of this forest type has been destroyed in western Colombia so the species is no longer abundant. In the course of fieldwork in western Colombia in 1984, I was not able to find *C. subedentata* in its historical localities nor in the remnants of lower and middle montane forest that I explored. The species may yet persist in more inaccessible forested sites. Living material received from Mr. Thomas Fennell was said to have been collected in Ecuador, but this information is undocumented. At present, I have seen no Ecuadorean specimens of *Caliphruria*, nor encountered populations in the field.

Within the range of *C. subedentata*, variation in leaf size, flower size, dentation of the androecium (Fig. 104C, D), and number of ovules is evident, but these patterns are for the most part continuous and/or mosaic in distribution, rendering recognition of subspecific taxa inappropriate. Though Baker (1877) characterized the species by the presence of one or two small teeth between the free filaments, the flowers present on the type specimen of *C. subedentata* are completely edentate. Clonotypic material of the taxon described by Traub (1951) as *E. fosteri* is distinguishable from other living material of *C. subedentata* only by its slightly smaller leaves and flowers.

3. Caliphruria tenera Baker, Handbook of the Amaryllideae, p. 112. 1888. *Eucharis tenera* (Baker) Traub, Pl. Life 23: 65. 1967. *Urceolina tenera* (Baker) Traub, Pl. Life 27: 57–59. 1971. TYPE: Colombia. Río Magda-

FIGURE 107. *Caliphruria korsakoffii* (*Meerow 1096*, FLAS).

lena, Aug. 1844, *Goudot s.n.* (holotype: K; isotype: P).

Bulb globose or ellipsoid, ca. 25 mm diam. or 30 mm long × 17.5 mm wide, sometimes apically articulated into a short neck 10 mm long × 5 mm wide; tunic grayish brown or tan. Leaves hysteranthous, not seen. Scape terete, slender, 16–27 cm tall, 1–2 mm diam.; bracts linear-lanceolate, 17–28.3 mm long; inner bracteoles linear, the longest to 14.5 mm. Flowers 5–10; pedicels 14–23.2 mm long, thin; perianth 17–19 mm long, funnelform, white; tube 8.5–9.5 mm long, funnelform, dilating gradually from 1.3 mm wide at the base to 3–4 mm at the throat; limb spreading to 15.5 mm; tepals ovate to elliptic, the outer series 8.5–11.2 mm long, 2–2.5 mm wide, acute-apiculate; the inner series 8–10 mm long, 2.8–3.8 mm wide, obtuse. Stamens 3–5 mm long, each stamen bidentate, 1.5–2.2 mm wide, the free filament inserted between the teeth; teeth much exceeding the free filament, 3–4 mm long; free filament 0.8–1.5 mm long, linear; anthers 4–5.5 mm long, linear; pollen grain ca. 35.2 μm polar diam., 53.7 μm longest equatorial diam. Style 18–21 mm long; stigma 3-lobed, 1 mm wide. Ovary globose, 1.8–2.7 mm diam.; ovules 1–2 per locule, axile, medially superposed. Fruit and seed unknown.

Distribution. Colombia, valley of the Río Magdalena (Fig. 105), 400 m.

Additonal specimen examined. COLOMBIA. CUNDINAMARCA ?: "Prov. Bogota," Copo la Parada, 400 m, July 1853, *Triana 1289* (COL, US, photo GH).

Caliphruria tenera is the smallest-flowered Colombian representative of *Caliphruria*. It is readily distinguished by its hysteranthous leaves and the long teeth of the androecium which greatly exceed the short free filament (Fig. 104A). Unfortunately, *C. tenera* has not been re-collected since 1853. The hysteranthous leaves of this species suggest adaptation to drier habitats than usually characteristic of the genus. Pockets of xeric vegetation do occur in the vicinity of the type locality (Cuatrecasas, 1958).

4. **Caliphruria korsakoffii** (Traub) Meerow, comb. nov. *Eucharis korsakoffii* Traub, Pl. Life 23: 85–87. 1967. *Urceolina korsakoffii* (Traub) Traub, Pl. Life 27: 57–59. 1971. TYPE: Peru. San Martín: 40 km from Moyobamba, Hierra waterfalls, 1,500 m, ex hort. J. N. Giridlian from bulbs collected by Lee Moore, 16 July 1966, *Traub 1060* (holotype, MO). Figure 107.

Bulb ± globose, 31 mm long, 29.3 mm wide, without an appreciable neck, tunic brown, offsetting weakly. Leaves 2–4; petiole 4.5–10 cm long, 3–4 mm thick; lamina ovate-lanceolate to narrowly elliptic, 13–17 mm long, 3.3–4.8 mm wide, acute-acuminate, basally attenuate to the petiole, cuticle of the abaxial epidermis thickly ridged. Scape 15–25 cm tall, 3.5–3.7 mm diam.; bracts lanceolate, 19–25 mm long, 5.5 mm wide at the base; inner bracteoles 8.5–22 mm long. Flowers 10–12, 15–20 mm long, funnelform, white, declinate to slightly ascendent; pedicels 2–4 cm long; tube subcylindrical, straight, 4–6 mm long, 2 mm wide at base, 3.2 mm wide at throat; limb spreading to ca. 2

cm; outer tepals lanceolate, 10–18.5 mm long, 4–5 mm wide, acute-apiculate; inner tepals ovate, 7.5–16 mm long, (5–)7–8 mm wide, obtuse and minutely apiculate. Stamens (7–)9.5–10 mm long, 0.7 mm wide at the base, edentate, diverging distally, narrowly subulate, white; anthers 3–4 mm long, oblong, dorsifixed in lower third, versatile; pollen grain ca. 32.3 μm polar diam., 50.4 μm longest equatorial diam. Style 16–21 mm long, white, slightly longer than limb segments; stigma 3-lobed, (1.2–)2.5–2.7 mm wide. Ovary globose-ellipsoid, 3.5–5 mm long, 2–3 mm wide; ovules 4–5 per locule, medially superposed. Capsule ca. 1 cm diam., yellow-green, thin-walled; seeds 1 per locule, globose, ca. 3 mm diam., testa brown. Chromosome number: $2n = 46$.

Distribution. North-central Peru (Fig. 105) at 1,500 m. Known only from the type locality in the understory of dense lower montane rain forest in humic topsoil on steep slopes, often growing wedged in the crevices of rocks.

Additional specimens examined. EX HORT.: Clone of type collection, *s.n.* (K); clone of type collection, July 1964, *Traub s.n.* (MO); clone of type collection, May 1982, *Meerow 1096* (FLAS).

Caliphruria korsakoffii is the only species of *Caliphruria* presently known outside of Colombia. In the size of the flower this species has affinity with *C. tenera* but can be distinguished by having evergreen leaves, subcylindrical tubes, and edentate, divergent, and longer stamens (Fig. 104E), coarser pollen exine reticulation, more numerous ovules, and higher altitudinal limits. The seeds of *C. korsakoffii* have a brown testa; those of *C. subedentata* are black. The ridged cuticle of the abaxial leaf surface of *C. korsakoffii* (Fig. 12) is quite different from the narrow cuticular striations of *C. subedentata* (Fig. 11). The morphological novelties exhibited by *C. korsakoffii* suggest considerable isolation from the Colombian taxa of *Caliphruria*.

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THE SYSTEMATICS AND EVOLUTION OF *LUDWIGIA* SECT. *MICROCARPIUM* (ONAGRACEAE)[1]

Ching-I Peng[2]

ABSTRACT

Ludwigia sect. *Microcarpium*, which consists of 14 species distributed mainly in the southeastern United States, is the second-largest section in the genus, the largest being the phylogenetically central sect. *Myrtocarpus* of South America.

Plants of *Ludwigia* sect. *Microcarpium* are morphologically diverse; they form a polyploid complex of four diploids, eight tetraploids, two hexaploids, and one octoploid. They are facultatively autogamous herbaceous plants capable of reproducing both sexually and asexually (forming stolons late in the flowering season). Based on extensive crossing experiments as well as field and herbarium studies, the relationships among species of this section have been clarified. Internal genetic barriers between species are nonexistent, and natural hybridization is fairly common.

Among the diploid species, *L. linifolia* and *L. linearis* have very narrow leaves, petaliferous flowers, and elongate capsules. The two species, however, differ chromosomally by one reciprocal translocation. F_1 hybrids between them are vigorous, have ca. 50% stainable pollen, and produce moderate quantities of viable seeds. *Ludwigia stricta*, the Cuban endemic, is apparently most closely allied to *L. linifolia*, based on morphological evidence, but has not yet been studied biosystematically. *Ludwigia microcarpa*, in contrast, has spatulate-obovate leaves, small, apetalous flowers, and minute obconical capsules. Artificial hybrids between *L. microcarpa* and either *L. linearis* or *L. linifolia* form neither stainable pollen nor seeds; for the most part, the chromosomes of these hybrids do not pair in meiosis. *Ludwigia microcarpa* probably evolved relatively early from outcrossing ancestors.

Although the nine tetraploid members in sect. *Microcarpium* are sharply distinct morphologically, they can be crossed in any direction in the experimental greenhouse and form fertile F_1 offspring. Natural hybrids in plants of this group are also fairly common and in some cases blur the boundaries of the species. Somewhat surprisingly, none of the extant diploid species are considered to be direct ancestors of the tetraploids, based on cytogenetic studies.

The two hexaploid species, *L. alata* and *L. simpsonii*, are not closely related to each other. The affinity of *L. alata* is definitely with the tetraploid species group. Hybrids between *L. alata* and any other tetraploid species consistently exhibit a modal configuration of 16 II and 8 I in meiosis. Based on its morphology and the cytology of hybrids involving it, *L. alata* may have originated through hybridization between a tetraploid species, possibly *L. lanceolata*, and the diploid *L. microcarpa*, or populations ancestral to each of these species.

Ludwigia simpsonii, on the other hand, is closely related to *L. curtissii*, which is the only octoploid in sect. *Microcarpium*. The two species are unique in sect. *Microcarpium* in having loculicidal capsules and, together with the diploid *L. microcarpa*, in having spatulate-obovate cauline leaves. Cytogenetic and morphological studies suggest that the octoploid *L. curtissii* may have resulted from hybridization of *L. simpsonii* and a petaliferous diploid species, possibly *L. linifolia*, *L. linearis*, or populations like them. *Ludwigia microcarpa* is involved in the formation of the hexaploid *L. simpsonii* and therefore that of the octoploid *L. curtissii*. The other progenitors of *L. simpsonii* are not clear, but some species in sect. *Dantia* or populations ancestral to them with apetalous flowers, opposite leaves, and a prostrate habit are likely candidates.

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To summarize, recombination from somewhat differentiated populations, followed by polyploidization and the maintenance of well-adapted genetic strains by a combination of autogamy and vegetative reproduction, appears to have played a central role in the evolution of the species of *Ludwigia* sect. *Microcarpium*.

Ludwigia is a distinct genus of Onagraceae and is the only member of Jussiaeeae. Fossil records of pollen suggest that it is archaic and has existed at least 50 million years since the middle Eocene in both the Northern and Southern hemispheres (Gonzales Guzmán, 1967; Rouse, 1962; Bratseva, 1969). Except for its chromosome structure and number, which appear to be relatively specialized (Kurabayashi et al., 1962), *Ludwigia* is one of the least specialized genera as to wood anatomy (Carlquist, 1975, 1982), floral anatomy (Eyde, 1977, 1978, 1981), and leaf anatomy (Keating, 1982). Based primarily on its unusual nectary position, ovular vasculature, and independently derived epigyny, Eyde (1977, 1978, 1981) demonstrated that *Ludwigia* represents a distinct branch from the common ancestor of the family, with all other living genera on the other branch; in Hennigian terms, it is the sister group of the remainder of the family.

The genus *Ludwigia* comprises 82 species that are diverse enough, especially in fruit, seed, and flower characters, to be classified in 23 sections, 14 of which are monotypic (Raven, 1963; Ramamoorthy & Zardini, 1987). Plants of *Ludwigia* are adapted to wet habitats in the tropics and subtropics. They probably originated in South America, the most important center of diversity for *Ludwigia*, and the area where the most primitive species are found (Ramamoorthy & Zardini, 1987). The genus, however, is also well represented in temperate North America and has three endemic species in temperate Asia.

In North America, there are 23 native *Ludwigia* species, characterized by having convex or elevated nectaries, tetramerous, haplostemonous flowers, pluriseriate ovaries, free seeds with narrow raphes, and herbaceous habits. Most of these plants are confined to the Atlantic and Gulf coastal plains of the United States, although some species are more widespread, and some extend into the islands of the Caribbean; one is endemic in Cuba. Based primarily on characters of capsules, mode of perennation, and phyllotaxy, the North American plants are classified into sect. *Ludwigia* (4 species), sect. *Dantia* (DC.) Munz (5 species), and sect. *Microcarpium* Munz (14 species). Table 1 summarizes the diagnostic characters of these three sections.

Based on his study of the structure and morphology of the capsules and nectaries of *Ludwigia*, Eyde (1981) considered sections *Dantia* and *Microcarpium* to comprise a closely knit group derived from the phylogenetically central, diplostemonous *Myrtocarpus* complex, whereas sect. *Ludwigia* is different enough to have arisen independently from the *Myrtocarpus* complex.

Section *Microcarpium* was selected for the present revision because it is the second-largest section of *Ludwigia* and is very diverse, because it has not been revised in light of recent new data and evolutionary concepts, and because several species of this section are variable and taxonomically difficult, with boundaries between species often blurred by intermediates.

The purposes of this revision are to clarify species limits, to determine the degree and significance of natural hybridization, and to analyze natural affinities among species of sect. *Microcarpium*. Toward this end, more than 7,000 specimens from 44 herbaria have been consulted for morphological studies and for mapping. Furthermore, I have made three extensive field studies in the coastal plains of the southeastern United States. Searches for possible natural hybrids were made in the field whenever taxa occurred sympatrically. Seeds and/or clonal transplants of all species were propagated at the Missouri Botanical Garden for chromosome determination and morphological study.

Taxonomic History

After the establishment of the genus *Ludwigia* in 1753 by Carl Linnaeus, the first group of North American species of sect. *Microcarpium* was discovered by the British botanist Thomas Walter (1788). Four of his species are currently recognized: *L. glandulosa*, *L. linearis*, *L. pilosa* (including *L. rudis*), and *L. suffruticosa*.

Jean Baptiste A. P. M. de Lamarck (1789, 1792) published "*Jussiaea brachycarpa*" and "*Ludwigia hirsuta*," based on materials collected from South Carolina. These names are synonyms of *L. glandulosa* and *L. pilosa* respectively, as Lamarck himself suspected.

The next botanist to study North American *Ludwigia* was Andre Michaux (1803), who described nine species of *Ludwigia* in his *Flora Boreali-Americana*. Of these, *L. microcarpa* is a member of sect. *Microcarpium*.

In 1814, Jean L. M. Poiret correctly added the

TABLE 1. Comparison of the native North American sections of *Ludwigia*.

Character	Sect. *Ludwigia* (4 species)	Sect. *Dantia* (5 species)	Sect. *Microcarpium* (14 species & 1 subspecies)
Habit	Perennial. Plants erect, lacking stolons; roots tuberous	Perennial. Plants creeping, rooting at nodes; roots fibrous	Perennial. Plants erect, usually stoloniferous (rhizomatous in one species); roots fibrous
Phyllotaxy	Leaves alternate	Leaves opposite	Leaves alternate
Capsules	Capsules pedicellate, opening by a terminal pore formed after abscission of the style base	Capsules sessile or pedicellate, irregularly dehiscent	Capsules sessile or short-pedicellate, ring-, loculicidal-, or peeled-dehiscent (see text)
Seed surface	Cells in parallel columns, transversely elongate to the seed length	Cells in parallel columns, transversely elongate to the seed length	Cells ± isodiametric or in parallel columns and either longitudinally or tranversely elongate to the seed length
Petals	Petals 8–15 mm long	Petals lacking or 2–10 mm long	Petals lacking (in 3 species 3–6 mm long); vestigial petals occasionally present in some primarily apetalous species
Nectaries	4 shallow ciliate depressions on the raised summit of the ovary, alternating with the sepals and stamens	4 raised and rounded lobes, surrounding the style base and alternating with the sepals and stamens	4 raised and rounded lobes, surrounding the style base and alternating with the sepals and stamens
Chromosome numbers	$n = 8$ (4 species)	$n = 8$ (1 species) $n = 16$ (2 species) $n = 24$ (2 species)	$n = 8$ (4 species) $n = 16$ (7 species & 1 subspecies) $n = 24$ (2 species) $n = 32$ (1 species)
Pollen grains	Shed as tetrads	Shed singly or as tetrads	Shed singly or as tetrads
Genetic compatibility	Self-compatible	Self-compatible	Self-compatible

new species *L. linifolia*, collected in the southern United States; it resembles but is quite distinct from *L. linearis*.

It was not until 1821 that the species of sect. *Microcarpium* were described by American botanists. Of the four species in sect. *Microcarpium* that Steven Elliott (1816–1821) described, *Ludwigia alata*, *L. sphaerocarpa*, and *L. lanceolata* are currently recognized, whereas *L. cylindrica* represents a synonym of *L. glandulosa* Walter. Although Elliott correctly differentiated *L. alata* from *L. lanceolata*, the striking superficial resemblance of the two species, especially in dried herbarium specimens, has constantly been a source of confusion among botanists (Long & Lakela, 1976; Raven & Tai, 1979; Godfrey & Wooten, 1981; Wunderlin, 1982; Clewell, 1985). The great distinctiveness of these two species in such characters as floral morphology, pollen and seed surface features, and chromosome numbers were only appreciated recently (Peng, 1988, and this study).

In 1836, *Ludwigia polycarpa*, a distinctive member of sect. *Microcarpium* distributed mainly in the northcentral United States, was discovered in Kentucky by Charles Wilkins Short and Robert Peter.

Shortly thereafter, John Torrey and Asa Gray (1838–1840), in *A Flora of North America*, proposed two varieties in sect. *Microcarpium*, i.e., *Ludwigia cylindrica β brachycarpa* and *L. capitata β pubens*. The former is currently recognized as the small-fruited, western subspecies of *L. glandulosa* (Peng, 1986), whereas the latter represents a natural hybrid between *L. suffruticosa* and *L. pilosa* (Peng, 1988).

In 1845, George Engelmann and Asa Gray described a densely pubescent variety of *Ludwigia linearis* from Texas. Owing to the complex variation pattern and the many intermediate populations found in the range of this species, however, the variety is not recognized in the present study.

Ludwigia stricta, the only Cuban endemic in

sect. *Microcarpium*, became known when August Grisebach (1866) described *Isnardia stricta* in *Catalogus Plantarum Cubensium*. The correct combination in *Ludwigia* was made by Francisco Adolfo Sauvalle (1873) in the *Flora Cubana*.

Alvin Wentworth Chapman added *Ludwigia curtissii* (1883) and *L. simpsonii* (1892) to the genus in his study of the flora of the southern United States.

John Kunkel Small named *Ludwigia simulata* in 1903, not knowing that it represented the hybrid *L. pilosa* × *L. lanceolata*. In 1933, he grouped, for the first time, plants of *Ludwigia* sect. *Microcarpium* under "Microcarpeae," and described from the Everglades of Florida *L. spathulifolia*, which has now been merged with *L. curtissii*.

Burghard Helwig in 1928 published *Ludwigia cubensis* from Cuba, which, however, is now considered as conspecific with *L. simpsonii* from Florida.

Merritt Lyndon Fernald and Ludlow Griscom (1935) described three additional varieties for the highly polymorphic *Ludwigia sphaerocarpa*, which itself may have originated as a result of hybridization and which now intergrades with *L. pilosa* freely (Peng, 1988). These hybrids are not recognized in this paper for reasons discussed elsewhere.

Paul Munz's monograph (1944, 1965) contained the most comprehensive treatment of North American *Ludwigia* in his time. In the 1944 paper, he formally delimited sect. *Microcarpium*. His concept has since been widely accepted. James Allan Duke (1955) was the first author to indicate and to provide examples of natural hybridization among North American species of *Ludwigia*.

In the course of my biosystematic study of *Ludwigia* sect. *Microcarpium*, a number of atypical specimens initially identified as *L. pilosa* Walter were shown to be a new species, which I subsequently named *L. ravenii* (Peng, 1984). This represents the last named species of sect. *Microcarpium*, and makes the total number of species of this section 14.

Morphology

Habit

All species in *Ludwigia* sect. *Microcarpium* are erect perennial herbs ranging from about 15 to 100 cm tall. Leafy, usually unbranched stolons are produced from the base of erect stems. The stolons creep along the surface of moist ground or float on water late in the flowering/fruiting season. Some species, however, may also send out stolons in the summer while they are actively flowering or even throughout their growing season. The stolons can be long (up to 2.5 m) and stout as in *L. pilosa* or short (5–15[–20] cm) and slender as in *L. microcarpa* and *L. ravenii*. The stolons give rise to erect shoots from their tips when the growing season resumes. In *L. polycarpa* the stolons are normally up to 15 cm long, and with leaves densely congested at the apex of stolons, overlapping one another and thereby protecting the apical meristem. This is apparently an adaptation to the severe winter that plants of *L. polycarpa* have to endure in the northern States. In *L. suffruticosa* stolons are uncommon. Instead, perennation is mainly by thick, somewhat woody, branched rhizomes. New shoots arise from the nodes of the rhizomes in growing season. It may be that in drier sandy situations, the plants persist by rhizomes, whereas in wet situations, the plants send out stolons.

In *Ludwigia curtissii* and *L. simpsonii*, stolons are rarely formed; the plants simply produce new shoots, which are ascending or decumbent at first and soon become erect from the base of the previous year's stem. They may not need to overwinter with low-profile stolons, as they are distributed mainly in Florida and the Caribbean Islands where the growing season is long and the winter is not severe.

Stems

Stems are usually well branched in most species of *Ludwigia* sect. *Microcarpium*. Plants of *L. suffruticosa* are, however, often simple. When they branch, the branches are few and usually arise from upper leaf axils beneath the compact inflorescences and characteristically overtop the main flowering/fruiting stems. Unbranched flowering stems are seen also in some populations of *L. curtissii*, *L. linifolia*, *L. microcarpa*, *L. simpsonii*, and *L. stricta*. The stems of some plants of *L. microcarpa* are distinctly zigzag. The stems of most species are slightly ridged; those of *L. alata* and *L. microcarpa* are often conspicuously ridged or winged. *Ludwigia pilosa* is the only species with nearly terete stems. The lower part of the stems of all species, when entirely submerged, is swollen and spongy.

Pubescence

Many species in *Ludwigia* sect. *Microcarpium* are glabrous to subglabrous; the margins of leaf, sepal, or bracteoles, and surfaces of fruit may sometimes be minutely strigillose or minutely papillose. Only *L. ravenii* and *L. pilosa* are consis-

tently hirtellous throughout. *Ludwigia sphaerocarpa*, a species that intergrades substantially with *L. pilosa*, is variable in many aspects, especially pubescence. Populations of *L. sphaerocarpa* range from being completely glabrous to densely strigillose throughout. Similarly variable is *L. linearis*, but no interspecific hybridization has apparently played a role here. The pattern of the distribution of hairs in *L. suffruticosa* is especially interesting: some plants are completely glabrous; some plants are hirtellous either on the terminal inflorescence or on the basal stems (including stolons/rhizomes), or both, but are otherwise glabrous.

The following are the main types of pubescence:

1. *Minutely puberulent.* Hairs exceedingly short, fine, straight, erect to ascending, sparse or dense, 0.02–0.1 mm long, found occasionally in plants of *Ludwigia linearis*, *L. sphaerocarpa*, on fruits of *L. microcarpa*, and less commonly on fruits of *L. simpsonii*, *L. curtissii*, and *L. suffruticosa*.

2. *Strigillose.* Hairs coarse, translucent, unicellular, 0.1–0.6 mm long, appressed to ascending; found in some populations of *Ludwigia sphaerocarpa* and *L. linearis*.

3. *Minutely strigillose.* Similar to strigillose pubescence, but the hairs more slender and shorter, ranging from 0.02 to 0.1 mm long. Frequently seen on sepals, bracteoles, and leaves of various species; also on the wings of capsules in *Ludwigia lanceolata* and capsules of both subspecies of *L. glandulosa*, and occasionally of *L. polycarpa*.

4. *Minutely papillose.* Blunt-tipped, minute projections from the surface, ca. 0.02–0.03 mm in length. This hair type is found occasionally on the margins of leaves and sepals, on fruit walls, and on nectary discs. It may be difficult to distinguish from minutely strigillose hair when the latter is exceedingly short.

5. *Hirtellous.* Hairs coarse, stiff, straight, erect to spreading, with an attenuate apex and a slightly broadened base, 0.25–0.95 mm long, translucent or spotted with light brown pigments. Hairs of this type are typical of *Ludwigia pilosa*, *L. ravenii*, and occasionally of *L. sphaerocarpa*, as well as part of the plant body of *L. suffruticosa*.

LEAVES

The leaves are simple and alternate. *Ludwigia simpsonii* is exceptional in frequently having some opposite or subopposite leaves at the lower nodes or in the seedling stage, a feature that might be related to the derivation of one or more of its genomes from plants of the opposite-leaved sect. *Dantia* (see below). The leaves on the rhizomes of *L. suffruticosa* are small and scalelike. Those on stolons are mostly elliptic- to rhombic-obovate or suborbicular (narrowly elliptic to narrowly oblanceolate in *L. linearis* and *L. linifolia*). These are usually broader and shorter than the cauline leaves, which are usually narrowly lanceolate to lanceolate, occasionally elliptic or oblanceolate, and often gradually reduced and narrower up the stem. *Ludwigia linearis* and *L. linifolia* have sublinear leaves. In *L. curtissii*, *L. microcarpa*, and *L. simpsonii*, the leaves range from (narrowly) spatulate-oblanceolate to spatulate-obovate or spatulate.

The leaves of all species of sect. *Microcarpium* are sessile or nearly so and either narrowly cuneate or attenuate basally. *Ludwigia suffruticosa* is exceptional in having a rounded to obtuse leaf base.

As in *Ludwigia* sect. *Myrtocarpus* sensu lato (Ramamoorthy & Zardini, 1987), the leaf margin is usually subentire, with a few glandular reddish or pink teeth that have an unusual hydathodal structure (Castells et al., 1979; Keating, 1982); such teeth are especially evident in *L. microcarpa*.

The secondary veins of leaves are usually obscure adaxially and distinct abaxially in sect. *Microcarpium*. In the closely allied *Ludwigia linifolia* and *L. stricta* and in *L. simpsonii* and *L. curtissii*, the secondary veins are, however, faint on both sides of the leaves. *Ludwigia linearis*, having narrow leaves like the related *L. linifolia*, has, by contrast, on its abaxial leaf surface very evident secondary veins, which anastomose and form a pair of marginal veins along the margins.

INFLORESCENCE

The flowers are sessile or shortly pedicellate and borne singly in the (usually upper) leaf axils of the main stem and the branches. In *Ludwigia suffruticosa*, the flowers are congested in very compact terminal spikes or racemes. The leaves subtending the flowers are much reduced and bractlike. As stems of this species remain single or have only a few branches, there are only one to several such inflorescences per plant. In most other species, the stems are well branched, and the flowers are axillary and usually very abundant. In *L. alata* and *L. pilosa*, the flowers are sometimes quite congested on the upper parts of branches. In *L. polycarpa* and *L. glandulosa*, one to a few very short branches heavily laden with flowers/fruits are often seen from the very base of primary branches. This frequently gives an appearance of several flowering branches arising simultaneously from the nodes of the main stem.

PEDICELS

The flowers and fruits are nearly sessile in most species. Pedicels (measured from the base of mature fruits), when present, are usually up to 0.5 (–1) mm long. Pedicels of *Ludwigia suffruticosa* and *L. sphaerocarpa* range 0.5–1.5(–2.3) mm long. Populations of *L. linearis* from west of the Mississippi River often have distinct pedicels up to 3.5(–5) mm long.

BRACTEOLES

Bracteoles are present in pairs near the base of the ovary in all species. They are succulent and are flanked by a pair of reddish or dark purplish, glandlike stipels on their base. A small swollen emergence located immediately below the bracteole is apparently an extension of the bracteole base and is prominent in some species, especially *Ludwigia curtissii*, *L. lanceolata*, *L. microcarpa*, and *L. simpsonii*. This character is more evident in live plants than in herbarium specimens.

Despite often being variable in length, even within the same plant (in *Ludwigia linifolia*, the bracteoles range (1.5–)2.5–9(–13) mm long), a few species, including *L. glandulosa*, *L. microcarpa*, and *L. sphaerocarpa*, consistently have shorter bracteoles (less than 1.5 mm long) than those of the other species (Table 2). The bracteoles are located either at the base or higher up on the sides of the capsules. In *L. sphaerocarpa* and occasionally in *L. glandulosa*, *L. linearis*, and *L. suffruticosa*, however, the bracteoles are found on the short pedicels.

FLOWERS

Of the 15 taxa of sect. *Microcarpium*, only three diploid species are petaliferous, although vestigial petals may occasionally appear in a few flowers of polyploid species (Table 2). Flowers are consistently tetramerous, pentamerous flowers being exceptional.

SEPALS

Sepals are entire, but may be minutely strigillose along the margins in some species. Unlike plants of sect. *Myrtocarpus* sensu lato (Ramamoorthy & Zardini, 1987), the sepals persist even after the capsules mature and dehisce. Sepals are greenish in most species, but they are creamy white on the adaxial surface in *L. alata*, *L. pilosa*, and *L. suffruticosa* and are yellowish on the adaxial surface in *L. sphaerocarpa*.

PETALS

Petals are yellow, small, narrowly obovate to subrotund, and range from 2.5 to 6 mm long and from 1.2 to 5 mm wide. They fall off a few hours after anthesis, which occurs early in the morning, and are usually gone by noon. All petaliferous species are able to effect mechanical self-pollination. My field experience, however, did not allow me to judge whether these plants attract significantly more insect pollinators than other apetalous species with showy sepals.

STAMENS

Most species of *Ludwigia* are consistently either haplostemonous (stamens in one whorl) or diplostemonous (stamens in two whorls) (Ramamoorthy & Zardini, 1987). All species of sect. *Microcarpium* are haplostemonous, which is a derived condition. The stamens are antesepalous, situated between the sepal base and the nectary discs.

ANTHERS

The anthers vary from 0.1 mm long in *Ludwigia microcarpa* to 2 mm long in *L. linearis*. *Ludwigia linearis* is unique in sect. *Microcarpium* in having polysporangiate anthers partitioned horizontally by septa that include both tapetum and parenchyma (Tobe & Raven, 1986). Such specialization is shared only by *L. latifolia*, an unrelated South American species of sect. *Tectiflora*, and five other genera of Onagreae. It is worth noting, however, that these septa in the anthers disintegrate and result in a continuous sporogenous tissue before the anthers dehisce. Many conspicuous vestiges of the disintegrated septa are visible on the inner surface of the anther wall at this stage.

POLLEN

The pollen of *Ludwigia* sect. *Microcarpium* is quite uniform, being characterized by isopolar grains frequently with prominent colpal extensions and with a psilate exine (Praglowski et al., 1983). Five species of sect. *Microcarpium*—*L. alata*, *L. curtissii*, *L. microcarpa*, *L. simpsonii*, and *L. suffruticosa*—shed their pollen singly, whereas the other nine species shed their pollen in tetrads (Table 2). This character is of some taxonomic value. For example, it can be used along with seed-surface pattern to distinguish *L. alata*, which sheds its pollen singly, from *L. lanceolata*, which sheds its pollen as tetrads. These two species are similar in general aspect and in their obpyramidal, winged

TABLE 2. Diagnostic characters of species and subspecies of *Ludwigia* sect. *Microcarpium*.

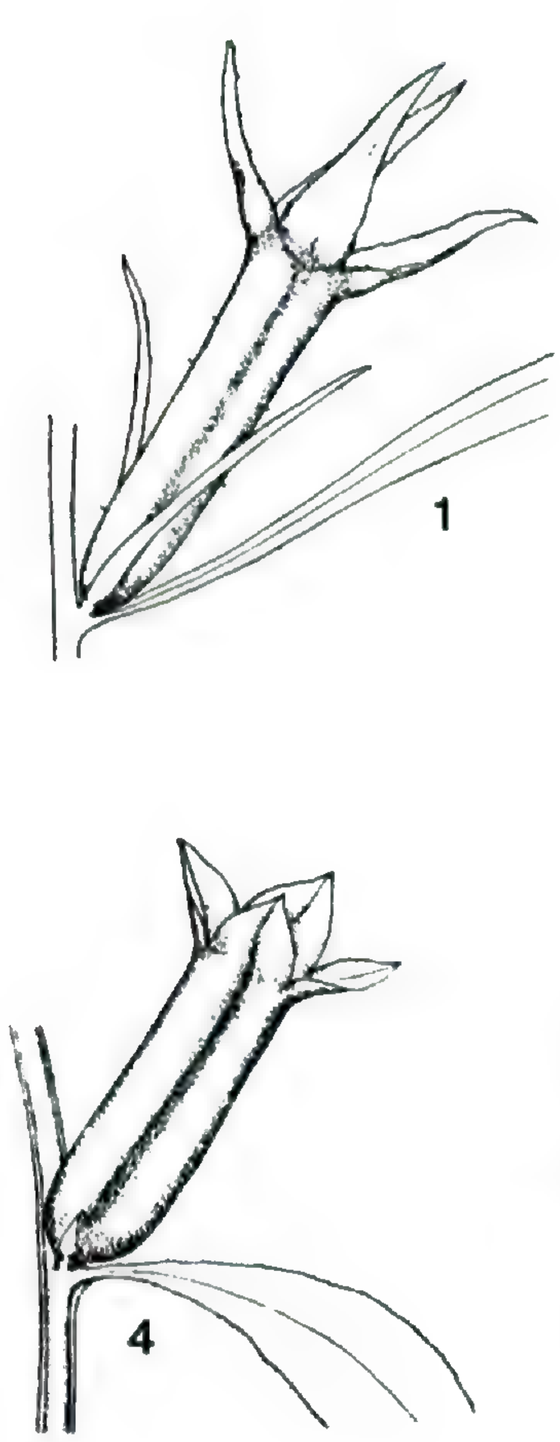
Taxon with Chromosome Number	Petals Present (+) or Absent (−)	Pollen Grains Shed Singly (S) or as Tetrads (T)	Overall Pubescence	Capsule Length (mm)	Capsule Shape	Bracteole Length (mm)	Seed Surface Cell Shape and Orientation[1]
L. linifolia, $n = 8$	+	T	Glabrous	6–12	Subcylindric	(1.5)3–10(–13)	I
L. sticta, $n = 8$	+	T	Glabrous	5–6.5	Subcylindric	1–2.5	I
L. linearis, $n = 8$	+	T	Glabrous to densely strigillose	6–10	Elongate-obpyramidal	0.5–2.5	P or T[4]
L. glandulosa subsp. *glandulosa*, $n = 16$	−	T	Glabrous but sparsely strigillose on stem and fruit	(4–)5–8	Subcylindric	0.5–1.2	P
subsp. *brachycarpa*, $n = 16$	−	T	Glabrous, but strigillose on stem and fruit	2–4	Subcylindric	0.4–0.8	T
L. polycarpa, $n = 16$	−	T	Glabrous	(4–)4.5–7	Oblong-obovoid	3.5–7.5	P
L. suffruticosa, $n = 16$	−	S	Glabrous except the inflorescence and stem base, which are sparsely hirtellous	3.5–4	Obpyramidal with rounded corners	(3–)4–5.5(–6.5)	I
L. lanceolata, $n = 16$	−	T	Glabrous	(3.5–)4–5	Obpyramidal, 4-winged	1.5–4.3	I
L. alata, $n = 24$	−	S	Glabrous	3–4	Obpyramidal, 4-winged	2.5–4.5	T
L. sphaerocarpa, $n = 16$	−	T	Glabrous to densely strigillose	2–4.5	Subglobose	0.5–1.5(–2.5)	P and T[3]
L. pilosa, $n = 16$	−	T	Hirtellous	(3–)3.5–5	Subglobose to oblong-obovoid	2.5–7.2	I
L. ravenii, $n = 16$	−	T	Hirtellous	(3–)4–5.3	Oblong-obovoid	(1.5–)2–4.3	T
L. microcarpa, $n = 8$	−	S	Glabrous	1–1.5	Obpyramidal with rounded corners	0.3–1(–1.5)	T
L. simpsonii, $n = 24$	−	S	Glabrous	1.5–2(–2.5)	Broadly turbinate	1–2.5	T
L. curtisii, $n = 32$	−[2]	S	Glabrous	(2–)2.5–4.5	Turbinate	1.5–4.5	T

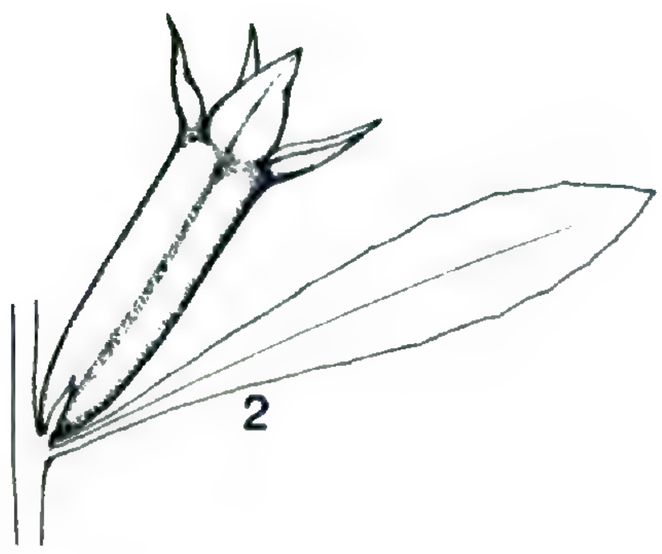
[1] Letter codes I, P, and T indicate seeds with surface cells more or less isodiametric (I), in columns elongate parallel to the seed length (P), and elongate transversely to the seed length (T).

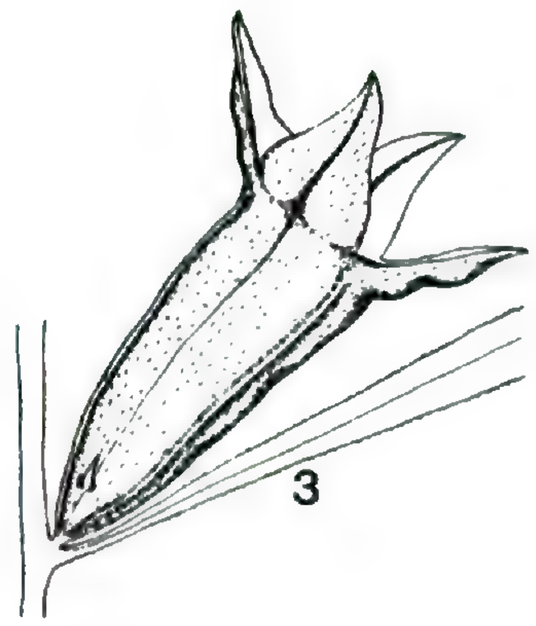
[2] Flowers with 1–3(–4) vestigial petals sometimes observed.

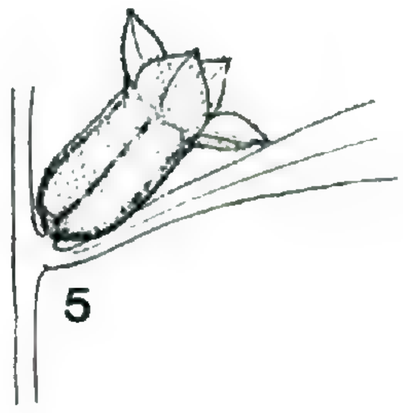
[3] Seed surface cells elongate parallel to the seed length are predominantly exhibited by more glabrous populations, whereas cells elongate transversely to the seed length are prevalent in more strigillose populations.

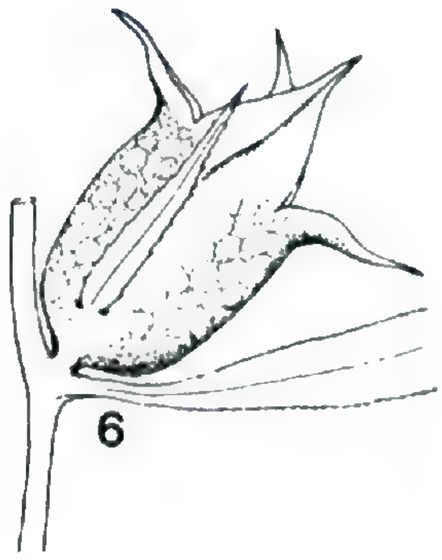
[4] Seed surface shows a mixture of cells elongate parallel or transversely to the seed length. Sometimes the orientation of these columnar cells is irregular.

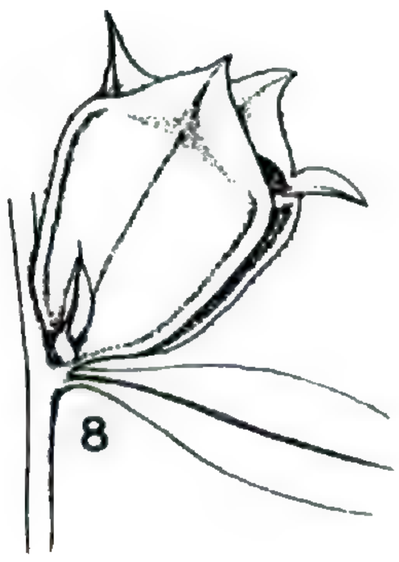


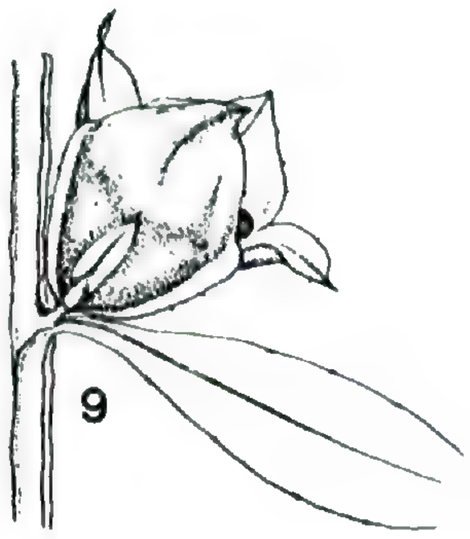


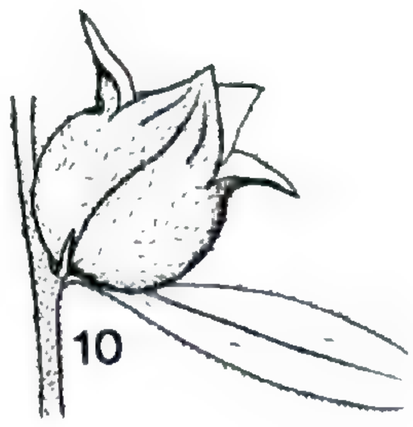


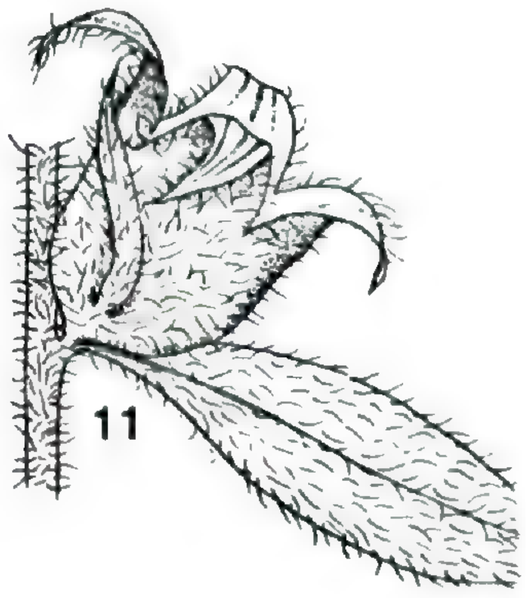


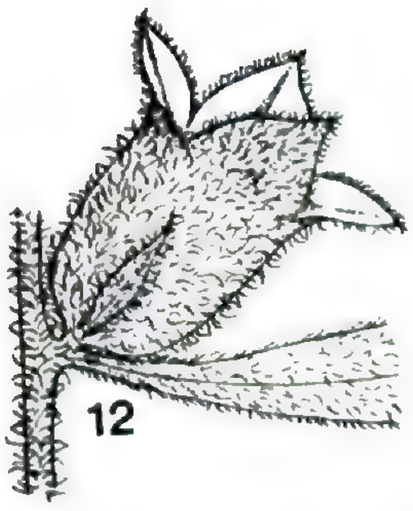


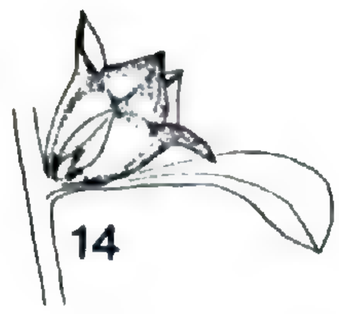


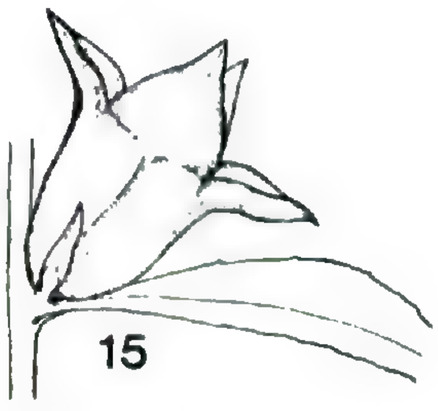






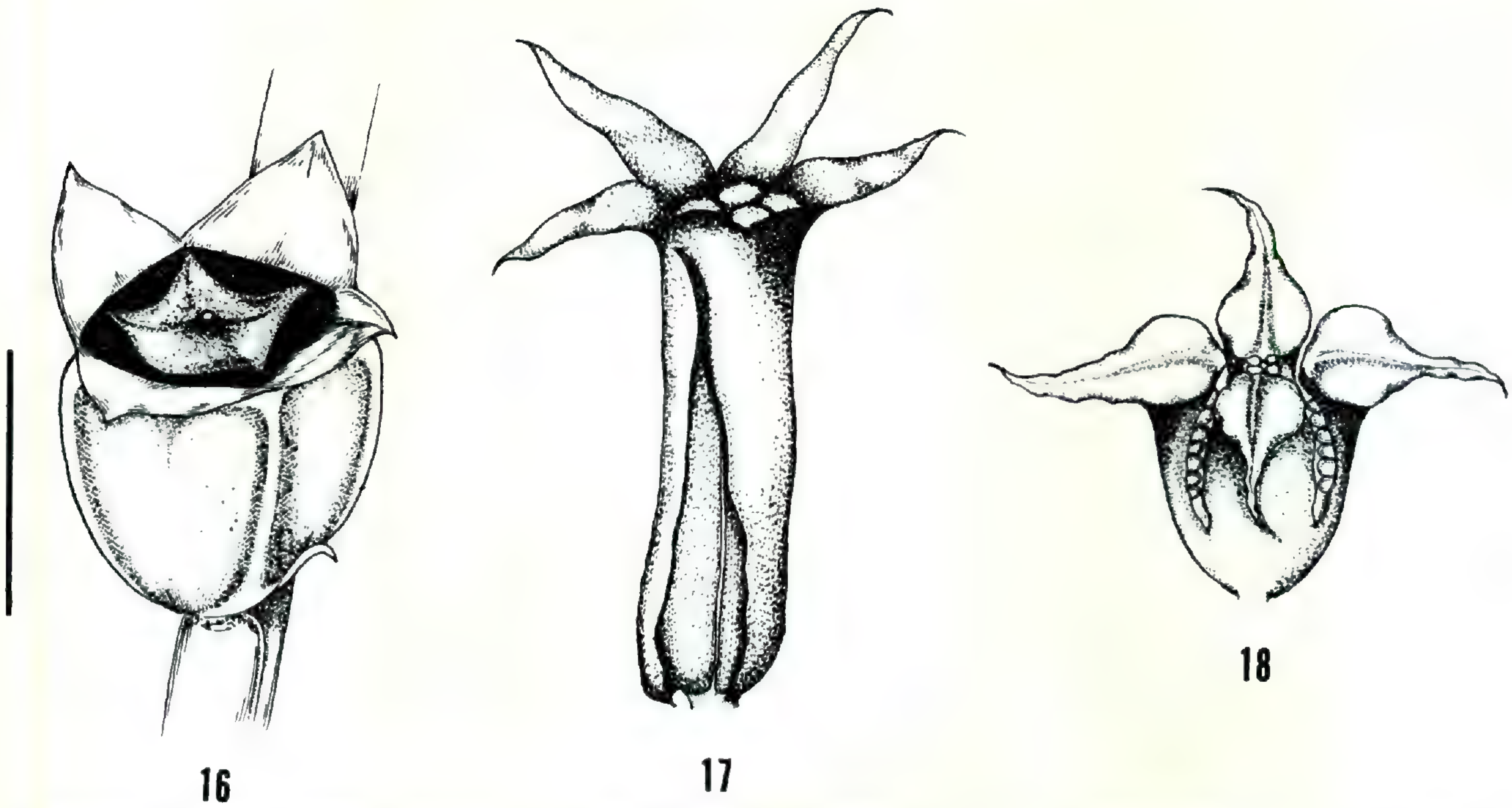






FIGURES 1–15. Mature fruits of *Ludwigia* sect. *Microcarpium*.—1. *L. linifolia*.—2. *L. stricta*.—3. *L. linearis*.—4. *L. glandulosa* subsp. *glandulosa*.—5. *L. glandulosa* subsp. *brachycarpa*.—6. *L. polycarpa*.—7. *L. suffruticosa*.—8. *L. lanceolata*.—9. *L. alata*.—10. *L. sphaerocarpa*.—11. *L. pilosa*.—12. *L. ravenii*.—13. *L. microcarpa*.—14. *L. simpsonii*.—15. *L. curtissii*. Drawn from living plants cultivated at the Missouri Botanical Garden.

fruits, and are superficially difficult to separate. The mode in which pollen is shed is useful to detect natural hybrids when their putative parents differ in this respect. Such hybrids generally exhibit both modes of pollen dispersal or pollen in very loose tetrads. Finally, the percentage of stainable pollen is useful to detect sterile hybrids or hybrids with reduced fecundity.



FIGURES 16–18. Capsular dehiscence in *Ludwigia* sect. *Microcarpium*. —16. *L. lanceolata*. —17. *L. linifolia*. —18. *L. curtissii*. Scale line equals 4 mm. Drawn from living plants cultivated at the Missouri Botanical Garden.

DISCS

One of the important characters that allows *Ludwigia* to be recognized as the sister group to all other genera of Onagraceae is that its nectary disc is situated on the summit of the ovary. By contrast, all other onagraceous plants have nectaries at the base of the floral tube; the nectaries, therefore, are androecial (Eyde, 1981).

The discs of *Ludwigia* sect. *Microcarpium* are shallowly dome-shaped, and they occur on the apex of the ovary. They are more or less distinctly four-lobed, the lobes alternating with the stamens, and are antepetalous (in petalous species). They are usually yellow or greenish at anthesis and turn dark reddish purple in fruit. In most species the discs are glabrous. *Ludwigia pilosa* is, however, usually hirtellous around the style base and between the disc lobes. Plants of *L. sphaerocarpa* are sometimes hirtellous between the disc lobes, too. In densely strigillose populations of *L. linearis*, the nectary discs tend to be strigillose throughout or between the lobes also. In *L. linifolia* and *L. stricta*, the disc lobes are minutely papillose throughout, as are their fruit and seed surfaces.

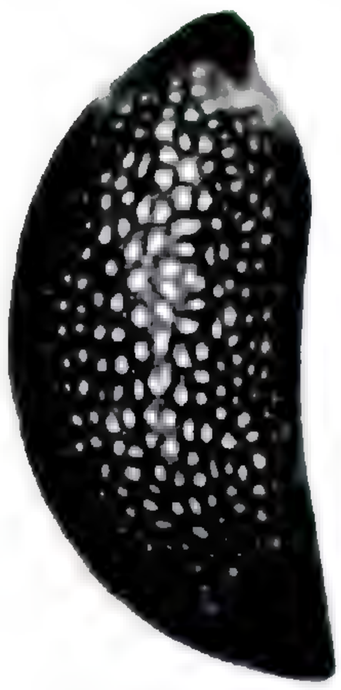
CAPSULES

Characters of the capsules have been very useful to systematic and phylogenetic studies in *Ludwigia* (Small, 1933; Munz, 1942, 1944; Raven, 1963; Eyde, 1978; Ramamoorthy & Zardini, 1987). When Small (1933) first grouped plants of *Ludwigia* sect. *Microcarpium* (as "Microcarpeae"), the mode of capsular dehiscence was one of the main criteria. Although his observations on capsular dehiscence were incomplete and not all species in this group have capsules dehiscing by the separation of flaps from the top of the nectary disc (see below), his concept was taken up by Munz (1944, 1965) who formally described and established sect. *Microcarpium*.

The shape, size, and pubescence of capsules are very diverse within sect. *Microcarpium* (Table 2, Figs. 1–15). Capsule shape ranges from obpyramidal to subcylindric, oblong-obovate, turbinate, or subglobose, and size ranges from 1 mm long in *Ludwigia microcarpa* to 12 mm long in *L. linearis* and *L. linifolia*. The surface vestiture ranges from glabrous to minutely papillose, strigillose, or hirtellous. These characters have been extremely useful for identifying species and natural hybrids.

Furthermore, in *Ludwigia* sect. *Microcarpium*, three patterns of capsular dehiscence are recognized (Peng & Tobe, 1987), each of which has a distinct anatomical basis:

Ring dehiscence. The capsule dehisces along an apical "ring" as a result of the disintegration of thin-walled cells located between the nectary disc and the sepal base (Fig. 16). This pattern is exhibited by *Ludwigia alata*, *L. lanceolata*, *L. linearis*, *L. microcarpa*, and *L. suffruticosa*. It was previously thought of as the only way capsules of *Ludwigia* sect. *Microcarpium* dehisced (Small, 1933; Munz, 1944; Raven, 1963). In these plants



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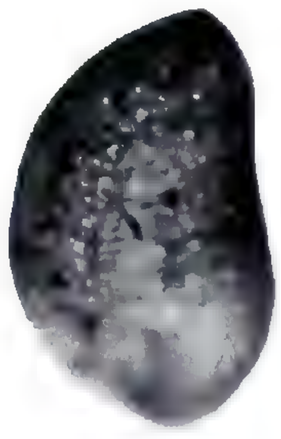

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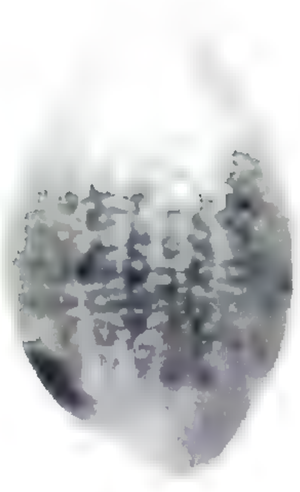

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the zonation pattern in the capsule wall is relatively simple, consisting of the outer, enlarged parenchymatous exocarp and the inner spongy endocarp.

Peeled dehiscence. The capsule dehisces by the irregular rupture of the outer capsule wall (Fig. 17). This is exhibited by *Ludwigia glandulosa*, *L. linifolia*, *L. pilosa*, *L. polycarpa*, *L. ravenii*, *L. sphaerocarpa*, and *L. stricta*. These plants have a spongy mesocarp and an endocarp with conspicuous inner hypodermis. When the seeds are dispersed, they often carry along many hypodermal cells. Whether these cells are useful for the seeds to float awaits confirmation.

Loculicidal dehiscence. The capsule dehisces by initially forming four longitudinally lenticular slits opposite each of the loculi (Fig. 18). Eventually the capsule is split into four basally united parts. This type of dehiscence is seen only in the closely related polyploids *Ludwigia curtissii* and *L. simpsonii*. In these species, the zonation pattern of the fruit wall is basically similar to that of the "ring-dehiscent" species, except that the exocarp consists only of the outer epidermis and a single-celled layer of outer hypodermis compactly aligned beneath. These hypodermal cells are remarkably enlarged and radially elongate except along the median longitudinal line facing each locule, where they are abruptly reduced or replaced by small, parenchyma cells. It is exactly along these four lines that the capsules dehisce at maturity.

To summarize, the fruit wall of all species of *Ludwigia* sect. *Microcarpium* is differentiated into a spongy zone (endocarp in ring-dehiscent and loculicidally dehiscent species, or mesocarp in peeled-dehiscent species) and a continuous zone. As Eyde (1978) suggested, such differentiation undoubtedly aids seed dispersal by reducing the effective thickness and by the differential growth rate that could result in the separation of the outer layers from the inner. The specialized hypodermis in *L. curtissii* and *L. simpsonii* appears to represent a condition that has evolved a step beyond this point.

SEEDS

In all species of sect. *Microcarpium*, seeds have a narrow raphe and are free and pluriseriate in each locule of the capsule, with a narrow raphe. The seeds are small, from 0.4 to 0.7 mm long, and are cylindric, ellipsoid, reniform, or ovoid. They are mostly yellowish, light brown, or brown in color, although three species, *Ludwigia linifolia*, *L. microcarpa*, and *L. stricta*, nearly always have dark reddish seeds.

Eyde (1978) was the first to point out that species of sect. *Microcarpium* are remarkably diverse in surface cell orientation. Like capsule morphology, or rather together with capsule morphology, seed surface pattern provides excellent diagnostic characters for identifying the species and detecting natural hybrids. The seed surface cells are either subisodiametric or are elongate parallel or elongate transversely to the seed length, with minor variation on the two ends and areas near the raphe (Figs. 19–34). Although in different populations of both *L. glandulosa* and *L. linearis* the seed surface cells are oriented in two different ways, the pattern is not random. In *L. glandulosa*, the cells are elongate parallel to the seed length in subsp. *glandulosa* (Fig. 23) and transversely elongate in the western, short-fruited subsp. *brachycarpa* (Fig. 24). Plants of *L. linearis* are extremely variable in pubescence, ranging from completely glabrous to densely strigillose. In general, seed surface pattern seems to be correlated with pubescence: subglabrous plants usually exhibit cells elongate parallel to the seed length (Fig. 21), whereas densely strigillose individuals generally have seed surface cells elongate transversely to the seed length (Fig. 22).

In *Ludwigia sphaerocarpa* the seed surface cells (Fig. 29) are not as regularly oriented as they are in the other species. They are arranged in columns both transversely elongate and parallel to the seed length, with the former alignment often dominant in the central part of the seed. Some

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FIGURES 19–34. Photographs of seeds of *Ludwigia* sect. *Microcarpium*.—19. *L. linifolia*, Florida, *Dille 408* (MO).—20. *L. stricta*, Cuba, Prov. Piñar del Río, *Britton et al. 6613* (NY).—21. *L. linearis*, North Carolina, Chatham Co., *Campbell 1077* (NCU).—22. *L. linearis*, Louisiana, St. Tammany Parish, *Dille 420* (MO).—23. *L. glandulosa* subsp. *glandulosa*, Florida, Santa Rosa Co., *Dille 412* (MO).—24. *L. glandulosa* subsp. *brachycarpa*, Louisiana, Cameron Parish, *Peng 4367* (MO).—25. *L. polycarpa*, Missouri, Lincoln Co., *Dille 443* (MO).—26. *L. suffruticosa*, Florida, Hillsborough Co., *Peng 4327* (MO).—27. *L. lanceolata*, Florida, Highlands Co., *Peng 4183* (MO).—28. *L. alata*, Florida, Wakulla Co., *Morar 11* (FSU).—29. *L. sphaerocarpa*, South Carolina, Jasper Co., *Dille 348* (MO).—30. *L. pilosa*, Georgia, Emanuel Co., *Peng 4025* (MO).—31. *L. ravenii*, North Carolina, Sampson Co., *Boufford & Wood 18898* (MO).—32. *L. microcarpa*, Florida, Collier Co., *Peng 4281* (MO).—33. *L. simpsonii*, Florida, Collier Co., *Peng 4266* (MO).—34. *L. curtissii*, Florida, Collier Co., *Peng 4357* (MO). Scale bar = 0.5 mm, except in Figure 25; there scale bar = 0.4 mm.

seeds of this species have variously oriented cells, a pattern that supports the suggestion of a hybrid origin for *L. sphaerocarpa* (see below).

Reproductive Biology

All 14 species in *Ludwigia* sect. *Microcarpium* are genetically self-compatible perennials that reproduce sexually and vegetatively. About two-thirds of them are modally autogamous—a statistic comparable to that for the whole genus (Raven, 1979). Shortly after the flowers open in the morning, the stigma becomes sticky and receptive and the stamens dehisce, exposing yellowish pollen entangled by the viscin threads. Initially the stamens are held away from the stigma and spread apart. The filaments, however, gradually arch toward the center and finally the anthers become firmly appressed to the sides of the sticky stigma in one to several hours (usually before noon), thus effecting self-pollination. This occurs in petaliferous as well as apetalous species, with the exceptions discussed in the following paragraph.

In *Ludwigia alata*, *L. pilosa*, *L. suffruticosa*, and many individuals of *L. sphaerocarpa*, the anthers also bend toward the stigma at late anthesis, but the distance between the androecium and the gynoecium is such that self-pollination is impossible without the intervention of a pollen vector. In the first three, apetalous, species the sepals are conspicuous and creamy within; in *L. pilosa* they are often tinged with pink along the main veins and the edges. Presumably these petaloid sepals serve to attract insect pollinators. In addition, these three species have yellowish discs that produce abundant nectar. *Ludwigia sphaerocarpa*, by contrast, has sepals that are yellowish within and very bright yellow discs that are more conspicuous than those of any other species, with the possible exception of *L. linifolia* (see below). Outcrossing in all four above-mentioned species is therefore not reinforced by protogyny/protandry or by male sterility, but merely by the physical separation of the stigma and the anthers. The self-incompatibility found in the more primitive members of *Ludwigia* sect. *Myrtocarpus* sensu lato is not present in sect. *Microcarpium*.

Nectary discs are present in all species in sect. *Microcarpium*, but they vary in size and in the quantity of nectar produced. *Ludwigia microcarpa*, an apetalous species with tiny flowers (the ovary is less than 1 mm long), has a nearly flat, greenish disc that produces very little nectar, and is presumably highly autogamous. Despite this, the fact that several natural hybrids—e.g., *L. microcarpa* × *L. curtissii* and *L. microcarpa* × *L. simpsonii*, and an intersectional hybrid, *L. microcarpa* × *L. palustris* ($n = 8$; sect. *Dantia*)—were collected in the field where the parental species grow sympatrically (see below) suggests that insect pollinators do occasionally visit plants with minute, inconspicuous flowers.

Living plants from two of the three petaliferous species were available for observation; *Ludwigia stricta*, endemic in Cuba, has not been studied as a living plant. Flowers of *L. linifolia* have very conspicuous nectary discs that produce copious nectar. This, along with the yellow petals, serves to make the flowers highly attractive to insects. *Ludwigia linearis* has a comparatively shallow ovary disc that secretes less nectar. This species is noteworthy in sharing with the unrelated South American *L. latifolia* (Benth.) Hara (sect. *Tectiflora*) the distinction of being the only members of the genus *Ludwigia* in which the sporogenous tissue of the anthers is divided into packets horizontally by both tapetum and parenchyma (Eyde, 1977; Tobe & Raven, 1986). This character is also shared by five other genera of Onagraceae, as mentioned previously.

Paper wasps of the genus *Polistes* have been observed to visit flowers of species of *Ludwigia* sect. *Microcarpium* grown in the netted experimental greenhouse at the Missouri Botanical Garden. In the field, more insects (usually bumblebees, honeybees, and wasps) were attracted to *L. pilosa* and, less so, to *L. sphaerocarpa*. Moths and ants have also been observed visiting *L. pilosa*. Relatively few field observations of insect pollinations on other species have been made in my trips to the southeastern United States. Circumstantial evidence from the presence of abundant natural hybrid populations suggests that insect pollination must be more common than I have observed.

In addition to sexual reproduction, nearly all species of *Ludwigia* sect. *Microcarpium* produce sprawling stolons at the base of the erect, flowering stems late in their flowering season. This vegetative reproduction enables the plants to overwinter, when the erect stems die back; in spring, they can then produce a large colony before other species can invade. Some of the sterile populations of natural hybrids also persist by this means. In *L. suffruticosa*, however, stolons are not as common as underground rhizomes. In *L. curtissii* and *L. simpsonii*, stolons are not apparent. These plants simply form new shoots from the lower nodes of the died-back stem of the previous year. These shoots are decumbent or ascending initially, but soon become erect.

Cytology

Chromosomes of *Ludwigia* are the smallest in the Onagraceae, and they may differ conspicuously in size within a single genome. The proximal ends of the chromosomes are heavily pycnotic and appear in interphase nuclei as very distinct and definite chromocenters (Kurabayashi et al., 1962). The basic chromosome number of the genus is $x = 8$, with no aneuploidy but extensive polyploidy (Raven & Tai, 1979). Through the efforts of Gregory & Klein (1960), Kurabayashi et al. (1962), Raven & Tai (1979), and Peng (1984, 1988), the chromosome numbers of all species of *Ludwigia* sect. *Microcarpium* have been established. There are four diploid species with $n = 8$ (*L. linearis*, *L. linifolia*, *L. microcarpa*, and *L. stricta*), eight tetraploid taxa with $n = 16$ (*L. glandulosa* subsp. *glandulosa*, *L. glandulosa* subsp. *brachycarpa*, *L. lanceolata*, *L. pilosa*, *L. polycarpa*, *L. ravenii*, *L. sphaerocarpa*, and *L. suffruticosa*), two hexaploid members with $n = 24$ (*L. alata* and *L. simpsonii*), and an octoploid with $n = 32$ (*L. curtissii*). For a review and discussions see Peng (1988).

Ecology and Geographical Distribution

With the exceptions of *Ludwigia stricta*, which is endemic to Cuba, and *L. polycarpa*, which is distributed mainly in the northcentral United States, *Ludwigia* sect. *Microcarpium* is confined primarily to the Coastal Plain of the southeastern United States. Several species also extend further south or east: *L. alata* to Jamaica; *L. curtissii* to the Bahamas; and *L. linifolia* disjunct to Tabasco, Mexico. *Ludwigia simpsonii* occurs in Cuba and Jamaica, and *L. microcarpa* in the Bahamas, Cuba, and Jamaica. *Ludwigia stricta* is exceptional in being endemic to Cuba. A detailed description of the ranges with maps for each species is given in the taxonomic treatment.

Like *Ludwigia* species occurring in other parts of the world, plants of *Ludwigia* sect. *Microcarpium* grow in wet habitats. They are commonly found along alluvial ground or in the shallow water of many areas, including ponds, lakes, rivers, streams, lagoons, sloughs, backwaters, swales, wet meadows or prairies, open swamp forests, drainages, and irrigation ditches. All species grow in sandy or occasionally peaty soils. A few species grow in brackish marsh or tidal flats (*L. alata*, *L. linifolia*, *L. microcarpa*, and *L. simpsonii*), in sinks in limestone prairies (*L. alata*, *L. curtissii*, *L. microcarpa*, *L. simpsonii*, *L. sphaerocarpa*, and *L. suffruticosa*), and in clay soils (both subspecies of *L. glandulosa*). None of the species in *Ludwigia* sect. *Microcarpium* exhibit the aggressiveness characteristic of weedy plants, although the following taxa have rarely been observed growing in disturbed habitats: *L. linearis*, *L. microcarpa*, *L. simpsonii*, and both subspecies of *L. glandulosa*.

Experimental Hybridization

Results from the extensive artificial hybridization among members of *Ludwigia* sect. *Microcarpium* (Peng, 1988) are summarized as follows.

1. There is generally little difficulty in obtaining hybrids between members of sect. *Microcarpium*; most F_1 plants grow to maturity, and many set abundant seeds. Hybrids between plants of the same ploidy level are generally intermediate in morphology; hybrids between plants of different ploidy levels tend to be more similar to the parent with the higher chromosome number. Character such as capsule shape and size, bracteole length, overall pubescence, presence or absence of petals, seed surface pattern, and pollen stainability are very useful in distinguishing species and identifying hybrids.
2. All diploid species can be crossed with one another and form floriferous F_1 plants. Hybrids between the petaliferous diploids with narrow leaves (*Ludwigia linearis* and *L. linifolia*) are vigorous, have ca. 50% stainable pollen, and produce a moderate amount of viable seeds. A modal meiotic configuration of a ring or chain of four plus six bivalents are frequently observed in reciprocal F_1 hybrids. Hybrids between either of the petaliferous diploids and the apetalous, diploid *L. microcarpa* are, in contrast, highly sterile as to pollen and seed set. Nearly all chromosomes remain unpaired in meiosis in these hybrids.
3. All eight tetraploid members studied are interfertile: chromosome pairing in meiosis is nearly complete, and pollen stainability and seed set are high in hybrids between any two tetraploid species, no matter how different they are from each other morphologically.
4. Although the two hexaploid ($n = 24$) species, *Ludwigia alata* and *L. simpsonii*, can be crossed and produce healthy F_1s, meiosis is irregular with abundant unpaired chromosomes. The affinity of *L. alata* is apparently with species of the tetraploid group, based on morphological characters. Hybrids between *L. alata* and any tetraploid species are easily obtained. They produce moderate seed set and have 43–71% stainable pollen. Meiosis in these F_1 individuals

typically exhibited a maximum of 16 bivalents and eight unpaired chromosomes. By contrast, the hexaploid *Ludwigia simpsonii* ($n = 24$) is clearly allied to the octoploid *L. curtissii* ($n = 32$). Hybrids between them are highly fertile, having 80–90% stainable pollen and producing good seed set. These plants consistently exhibited a meiotic configuration of 24 bivalents and eight unpaired chromosomes.

5. Seeds obtained from crossing species of any two of the following groups, (1) tetraploid species group (including the allied *Ludwigia alata*), (2) diploid species, and (3) *L. curtissii* and *L. simpsonii*, often failed to germinate. Those that germinate may either be inviable or produce flowers that set negligible or no seed and tend to have very low levels of stainable pollen. For a complete discussion of the experimental hybrids, consult Peng (1988).

Natural Hybridization

Experimental hybridization (Peng, 1988) revealed that vigorous and floriferous hybrids can readily be obtained between most members of *Ludwigia* sect. *Microcarpium*. The general lack of postzygotic barriers and the facts that all species in this section are perennial and that most of them are sympatric, have similar preference for habitats, flower in the morning during the same season, are facultatively outcrossing, and have similar kinds of indiscriminate insect pollinators, strongly suggest that natural hybrids should be fairly common in the field.

Field observations and herbarium study show that hybrid populations of *Ludwigia* sect. *Microcarpium* are indeed abundant. Except for this and the companion paper (Peng, 1988), however, very little has been reported about the natural hybrid populations of sect. *Microcarpium*. The variation patterns generated by the intergradation among some members of sect. *Microcarpium* have previously been detected by Torrey & Gray (1840) and Small (1903); such plants were given names at varietal and specific rank respectively, but no indication of their hybrid origins was mentioned. Torrey & Gray (1840) described *L. capitata β pubens* from a population of *L. suffruticosa* × *L. pilosa* from Georgia; Small (1903) applied the name *L. simulata* to a population of *L. pilosa* × *L. lanceolata* from North Carolina.

Duke (1955) was the first to point out that some *Ludwigia* species show varying degrees and patterns of intergradation in North Carolina. In his informative study, he compared the morphological characters of a mixed population consisting of plants of *L. pilosa*, *L. glandulosa*, and the intermediates, and considered the latter as possible hybrids. Upon examination of his voucher collections, it is confirmed beyond doubt that these plants represent uniform F_1 hybrids of *L. pilosa* × *L. glandulosa*. Duke (1955) further suggested that "self-pollination is the rule in this genus, and that cross-pollination is a very rare exception to the rule," and speculated that phyllophagous insect caterpillars may have brought about cross-pollination while foraging leaves. This, however, is not true, as at least four species in sect. *Microcarpium* have somewhat showy sepals and produce copious nectar and require insect vectors to pollinate their flowers to set seeds. Such insects as bumblebees, wasps, honeybees, moths, and even ants have frequently been seen obtaining nectar on the flowers of *Ludwigia* sect. *Microcarpium*.

In a biosystematic study of *Ludwigia* sect. *Dantia*, a close ally of sect. *Microcarpium* with opposite leaves and prostrate habit, Schmidt (1967) reported two intersectional hybrids, *L. repens* × *L. simpsonii* (as *L. repens* × *L. curtissii*) and *L. palustris* × *L. glandulosa* from North Carolina and Florida, respectively. His observations of the hybrid between *L. palustris* ($n = 8$; sect. *Dantia*) and *L. glandulosa* ($n = 16$; sect. *Microcarpium*) revealed very little association between chromosomes, with 0–3 weakly joined bivalents in meiosis. The other natural hybrid, involving *L. repens* ($n = 24$; sect. *Dantia*) and *L. simpsonii* ($n = 24$; sect. *Microcarpium*), yielded 48 unpaired chromosomes at mesiosis, suggesting the dissimilarity in the genomes of plants in the two North American sections.

Observation of individuals exhibiting a combination of characters intermediate between distinct taxa initially suggests natural hybridization. Members of the following species pairs, *Ludwigia alata* ($n = 24$) and *L. lanceolata* ($n = 16$), *L. pilosa* ($n = 16$) and *L. ravenii* ($n = 16$), and *L. simpsonii* ($n = 24$) and *L. curtissii* ($n = 32$), however, are usually so similar in appearance, especially in dried herbarium specimens, that their hybrids cannot be recognized readily.

Results from experimental hybridization suggest that capsule shape and size are the most important diagnostic characters for detecting hybrids in sect. *Microcarpium*. Other useful features include overall pubescence, seed surface cell shape and orientation, the presence or absence of petals, whether pollen grains are shed singly vs. in tetrads, and pollen stainability. Seed surface pattern is useful only for the determination of hybrids in the tet-

raploid group (including *Ludwigia alata*), as these nine taxa are interfertile, yield abundant seeds, and are diverse with respect to this character. Absence of developing fruits and low levels of pollen stainability, however, are characteristic of hybrids resulting from all other heteroploid crosses, with the exception of *L. curtissii* ($n = 32$) × *L. simpsonii* ($n = 24$). As a last resort, chromosome number and meiotic chromosome behavior are useful indicators of natural hybrids when the parents involved have different chromosome numbers or differentiated genomes.

The natural hybrid populations mentioned below are discussed individually following the treatment of the species in the systematic section. Full citation of these specimens of hybrids is given in the companion paper (Peng, 1988).

Field experience indicates that natural hybrid populations are fairly common wherever two or more species grow side by side. A total of 15 intrasectional hybrids and seven intersectional (among plants of sects. *Microcarpium* and *Dantia*) hybrids are recognized (Peng, 1988). Hybrids resulting from crosses among members of the tetraploid species group (including *Ludwigia alata*) are by far the most common. The following hybrid combinations are representative: *L. alata* × *L. pilosa* (four populations from Florida, one from Georgia, and one from Mississippi), *L. alata* × *L. suffruticosa* (seven populations from Florida), *L. glandulosa* subsp. *glandulosa* × *L. glandulosa* subsp. *brachycarpa* (one from Oklahoma and one from Texas), *L. glandulosa* subsp. *glandulosa* × *L. pilosa* (two from North Carolina, one from Georgia, one from Alabama, and two from Mississippi), *L. glandulosa* subsp. *glandulosa* × *L. sphaerocarpa* (one from South Carolina, one from Missouri), *L. lanceolata* × *L. pilosa* (three populations from Florida), *L. lanceolata* × *L. suffruticosa* (two from Florida), *L. pilosa* × *L. sphaerocarpa* (many populations from North Carolina, South Carolina, Georgia, Florida, Alabama, and Texas), *L. pilosa* × *L. suffruticosa* (two from North Carolina, three from Georgia, and two from Florida), and *L. polycarpa* × *L. sphaerocarpa* (two populations from Indiana). Backcrossed generations or segregates of advanced generations are found of *L. lanceolata* × *L. suffruticosa*, *L. pilosa* × *L. suffruticosa*, and most abundantly of *L. pilosa* × *L. sphaerocarpa*.

As in the case of artificial hybridization, the tetraploid hybrids are highly fertile as to seed and pollen; hybrids between the hexaploid *Ludwigia alata* and the tetraploid species have slightly lower levels of stainable pollen and seed set. It is noteworthy that in nearly all of the above hybrids at least one member of each pair of putative parents is unable to undergo mechanical self-pollination and has somewhat showy sepals. In other words, *L. alata*, *L. pilosa*, *L. sphaerocarpa*, and *L. suffruticosa* hybridize more frequently than other tetraploid species that are modally autogamous.

Sporadic occurrence of sterile triploid hybrids include *Ludwigia glandulosa* ($n = 16$) × *L. linearis* ($n = 8$) (one population from North Carolina and the other from Georgia) and *L. sphaerocarpa* ($n = 16$) × *L. linearis* (one population from Alabama). One probably diploid hybrid population of *L. linearis* × *L. linifolia* was collected from Florida in 1981. Attempts to re-collect and to study live plants of this hybrid have failed, because the habitat was destroyed (Popenoe, pers. comm.).

Hybrids between *Ludwigia curtissii* ($n = 32$) and *L. simpsonii* ($n = 24$) very probably occur in the field but would be difficult to detect. *Ludwigia curtissii* hybridizes with *L. linifolia* ($n = 8$) and with *L. microcarpa* ($n = 8$) to form sterile hybrids. At least four populations of *L. simpsonii* × *L. microcarpa* are known from Florida. It is of interest to note that among the putative parental species here concerned, only *L. linifolia* has somewhat showy petals and produces copious nectar, whereas all other species are probably modally autogamous.

Hybrids involving putative parents from sect. *Microcarpium* and sect. *Dantia* are also not uncommon. *Ludwigia repens* ($n = 24$; sect. *Dantia*) hybridizes with *L. simpsonii* ($n = 24$) and *L. curtissii* ($n = 32$) in Florida. At least eight such populations are known, all producing flowers, but the ovaries abort after mechanical self-pollination. *Ludwigia palustris* ($n = 8$; sect. *Dantia*), a widespread and apparently autogamous species, hybridizes with *L. glandulosa* subsp. *glandulosa* ($n = 16$) and forms sterile hybrid populations in Virginia (one population). It also hybridizes with the diploid, small-flowered and presumably autogamous *L. microcarpa* of sect. *Microcarpium* and forms sterile hybrids in North Carolina (one population), Georgia (one population), and Florida (three populations). In Kentucky, *L. palustris* hybridizes with *L. polycarpa* ($n = 16$) and likewise forms sterile hybrids.

The only intersectional tetraploid hybrid is known from a single population of *Ludwigia arcuata* ($n = 16$; sect. *Dantia*) × *L. pilosa* ($n = 16$) collected from Alabama. Flowers of both putative parents are showy and attract many insect pollinators. Established hybrids, however, are very rare in nature. Although some seeds were observed in mature cap-

TABLE 3. Comparison of diploid petaliferous species in *Ludwigia* sect. *Microcarpium*.

Characters	*L. linearis*	*L. linifolia*	*L. stricta*
Plant height (cm)	(22–)50–100(–145)	12–55(–62)	10–60(–85)
Cauline leaves	Very narrowly elliptic to sublinear	Oblanceolate-linear to linear	Oblanceolate or elliptic to narrowly so
Abaxial marginal veins	Distinct	Obscure	Obscure
Sepal			
Length (mm)	2.3–5(–5.6)	(3.3–)4–7	(1.8–)2–3
Width (mm)	1–3(–3.5)	1.1–1.7	0.9–1.5
Length : width	1.5–2.5	3–4	2
Anther length (mm)	1–2	0.65–1.1	0.5–0.7
Septa in anther sac	Present	Lacking	Lacking
Filament length (mm)	1.1–2(–2.2)	(1.3–)1.5–2.5(–3)	0.75–1.1
Style length (mm)	(0.4–)0.7–1.5	1.25–2.5	0.55–0.9
Stigma			
Shape	Cylindric	Depressed globose	Depressed globose
Length	(0.6–)1–1.9	0.3–0.6	0.25–0.5
Nectary disc	Shallow	Very prominent	Prominent
Capsule			
Shape	Elongate-obpyramidal	Subcylindrical	Subcylindrical
Surface	With a shallow, longitudinal groove on each side	Nearly smooth	Nearly smooth
Length (mm)	5–10(–12)	5–10(–12)	5–6(–7)
Thickness (mm)	2–5.5	1.3–2(–2.2)	1.6–1.8
Dehiscence	Ring-dehiscent from top	Peeling off from the sides	Peeling off from the sides
Bracteole length (mm)	0.4–4(–7.5)	(1.5–)2.5–9(–13)	0.7–2.5(–3)
Seed			
Color	Yellowish	Reddish brown	Reddish brown
Surface cell shape	Columnar	Subisodiametric	Subisodiametric

sules of the herbarium specimen (Mobile Co.: Audubon Bird Sanctuary, Dauphin Island, *Deramus 0643* [DS, UNA]), they are probably inviable. Such hybrids synthesized in the experimental greenhouse showed a remarkably high level of chromosome pairing (ca. 12–15 bivalents and 2–8 unpaired univalents; 1 or 2 trivalents occasionally seen) but had only 38% stainable pollen. Not a single seed was set despite many attempts at artificial self-pollination (like *L. pilosa*, this hybrid cannot undergo mechanical self-pollination).

To summarize, geographical isolation and self-pollination are the primary factors limiting natural hybridization among species of *Ludwigia* sect. *Microcarpium*. For example, *L. polycarpa* occurs in the central Midwest (Fig. 45), where it is isolated geographically from all other species of sect. *Microcarpium* except *L. sphaerocarpa*. Where the two species come into contact, hybridization occurs. *Ludwigia microcarpa*, an extreme selfer, has been hybridized successfully with most species of sect. *Microcarpium* in the greenhouse, and the resulting hybrids were vigorous. *Ludwigia microcarpa* grows sympatrically with many other species, but natural hybrids have been found only with *L. simpsonii*, *L. curtissii*, and some members of sect. *Dantia*.

In general, natural hybrids are usually frequent wherever two species occur together. This is particularly true for plants in the tetraploid group, hybrids of which were often found intermixed with putative parents. The sorts of disturbed habitats suggested by Anderson (1948) do not appear to be necessary for the establishment of natural hybrids in *Ludwigia* sect. *Microcarpium*.

As outlined above, natural hybridization is not limited to species within *Ludwigia* sect. *Microcarpium*. At least seven hybrid combinations, some of which occur commonly in nature, have been found between members of sect. *Microcarpium* and sect. *Dantia*. Most of these have also been synthesized in the experimental greenhouse. None

of the intersectional hybrids set viable seeds, although they are usually very vigorous and appear to compete well with their parents. Once established, these sterile hybrids may be able to persist in a given location due to their perennial habit. Furthermore, new colonies may be established vegetatively if entire plants or fragments are transported to suitable habitats, most likely by water.

Evolutionary Relationships

Ludwigia sect. *Microcarpium* consists of four diploids, eight tetraploids, two hexaploids, and one octoploid.

Ludwigia microcarpa is distinct among the diploid species by the more or less spatulate cauline leaves and small, inconspicuous, apetalous flowers; and it is modally self-pollinated. All three other diploid species, *L. linearis*, *L. linifolius*, and *L. stricta*, have elongate, narrow leaves and relatively showy, petaliferous flowers and are facultatively outcrossing. The divergence of *L. microcarpa* from the rest of the diploids is further demonstrated by the cytogenetic study of artificial hybrids in this group. Artificial F_1 hybrids between *L. microcarpa* and either *L. linearis* or *L. linifolia* were completely sterile; in meiosis they revealed very few chromosome associations, with 0–3 weakly joined bivalents.

Ludwigia linearis is unusual in sharing with the unrelated South American species *L. latifolia* (Benth.) Hara (sect. *Tectiflora*) the character of polysporangiate anthers in which the locules are divided by transverse septa composed of tapetum and parenchyma. Otherwise, *L. linearis* is apparently somewhat related to *L. linifolia*. The two species differ chromosomally by at least one reciprocal translocation. F_1 hybrids between them have ca. 50% stainable pollen, and they produce moderate quantities of viable seeds.

Ludwigia stricta, which is endemic to Cuba, is more closely related to *L. linifolia* than to any other species in sect. *Microcarpium*. It differs from *L. linifolia* only by the broader leaves, smaller floral parts, and shorter fruits (Table 3). The crossing relationships of *L. stricta* with other diploid species are currently being investigated.

The eight tetraploid taxa ($n = 16$) are uniformly apetalous and are otherwise remarkably diverse in overall pubescence, shape and color of sepals, shape and dehiscence of capsules, bracteole length, seed surface cell pattern, and whether pollen is shed singly or as tetrads. Correlations in these features, however, are evidently nonexistent. It is therefore of great interest to find that these eight morphologically well-delimited taxa can be crossed in any combination and produce vigorous and fertile offspring. The hybrids exhibit nearly complete chromosome pairing and high levels of stainable pollen. Natural hybridization among plants of this group is abundant, especially among those members with somewhat showy sepals. Most natural hybrids are F_1 plants that occur in more or less undisturbed habitats where the putative parents also grow. Introgressed populations or segregates of advanced generation of *Ludwigia pilosa* × *L. sphaerocarpa* hybrids, however, are also abundant and widespread. Cytogenetic studies of experimental hybrids between the tetraploid species and the diploid species suggest that no extant diploids are believed to have been involved directly in the formation of the tetraploid species group.

Ludwigia alata, a hexaploid ($n = 24$) species, resembles the tetraploids morphologically. Superficially it is most similar to *L. lanceolata* in general aspect and especially in the characters of winged capsules. Nearly all of the reciprocal hybrids between the hexaploid *L. alata* and any of the tetraploid species exhibited a modal meiotic configuration of 16 bivalents and 8 univalents, which suggests that they share two genomes in common. Judged from the morphology of the hexaploid and from the pairing of chromosomes in experimental hybrids, *L. alata* probably originated following hybridization between one of the tetraploids, perhaps *L. lanceolata*, and the diploid *L. microcarpa*, or populations ancestral to them.

The affinity of the other hexaploid, *Ludwigia simpsonii*, however, is definitely with *L. curtissii*, the only octoploid in sect. *Microcarpium*. These two species are unique in having loculicidal capsules and in having, along with the diploid *L. microcarpa*, more or less spatulate cauline leaves. *Ludwigia curtissii* and *L. simpsonii* are polymorphic and are sometimes difficult to distinguish morphologically. Cytogenetic data suggest that the hexaploid chromosome complement of *L. simpsonii* includes three different genomes, one of which is identical with that of *L. microcarpa*. Artificial hybrids between *L. simpsonii* and *L. curtissii* exhibited a meiotic configuration of 24 bivalents and eight univalents, which suggests that these two closely related species possess three genomes in common. Based on morphological characters and crossing relationships, the octoploid *L. curtissii* was probably derived following hybridization between a petaliferous, narrow-leaved diploid lineage similar to *L. linifolia* and the hexaploid *L. simpsonii*.

To summarize, following the differentiation of diploid species of *Ludwigia* sect. *Microcarpium*, some diploids have evidently become extinct. Natural hybridization among the diploid lineages fol-

lowed by polyploidy has played a major role in the evolution of this group. Postzygotic genetic barriers do not separate most of the species of this section. Rather, the major limiting factor to natural hybridization appears to be the modally autogamous breeding system of most species. Geographical isolation is important only with respect to *L. polycarpa*, which is distributed well to the north of nearly all the other taxa.

Natural hybridization is prevalent within *Ludwigia* sect. *Microcarpium*, and hybrids often grow intermixed with putative parental populations. All interploid hybrids are completely sterile except for crosses between *L. alata* ($n = 24$) and the tetraploid species ($n = 16$), and crosses between *L. curtissii* ($n = 32$) and *L. simpsonii* ($n = 24$). Even sterile hybrids, however, can persist and form large colonies, at least locally, by means of strong vegetative reproduction via stolons.

Natural hybrids are especially common among members of the tetraploid group (including *Ludwigia alata*) and are nearly always vigorous and fertile. Especially complex is the pattern of variation in the tetraploid *L. sphaerocarpa*, which is apparently comprised largely of widespread stabilized hybrid populations that exhibit a combination of characters distinguishing them from other taxa. As in the evolution of *Epilobium* in New Zealand (Raven & Raven, 1976), the recombination of genetic information from somewhat differentiated populations followed by the maintenance of well adapted genetic strains by a combination of autogamy and vegetative reproduction appears to have played a central role in the evolution of the polyploid members of *Ludwigia* sect. *Microcarpium*.

Systematic Treatment

Ludwigia sect. **Microcarpium** Munz, Bull. Torrey Bot. Club 71: 154. 1944; N. Am. Fl. ser. II, pt. 5: 42. 1965. Raven, Reinwardtia 6: 336. 1963. "*Microcarpeae*" Small, Man. S.E. Fl. 941. 1933. Type species: *Ludwigia pilosa* Walter.

Erect perennial herbs, perennating mostly by leafy, basal stolons (mainly by rhizomes in *Ludwigia suffruticosa*). Stems usually profusely branched except in *L. suffruticosa*, becoming swollen and spongy below when submerged. Leaves alternate, sessile or nearly so, subentire, usually with hydathodal glands along margins. Flowers sessile or shortly pedicellate, axillary (in very compact, short racemes or spikes in *L. suffruticosa*). Bracteoles in subopposite pairs attached from the base of the pedicel to halfway up the ovary. Flowers 4-merous, mostly apetalous (consistently with 4 petals in 3 diploid species). Sepals mostly greenish (creamy white or yellowish in 4 apetalous species). Stamens haplostemonous; anther sacs undivided except in *L. linearis*, in which the polysporangiate anthers are partitioned horizontally by tapetums and parenchyma. Pollen shed singly or as tetrads. Nectary disc 4-lobed, usually shallowly raised above ovary apex (flat in *L. microcarpa*). Capsules with ca. 10–700 seeds, obpyramidal to subcylindric, oblong-obovoid, turbinate, or subglobose, dehiscent by the separation of the disc and the ovary wall, or forming 4 longitudinally lenticular slits opposite each locule, or the irregular rupture of the outer wall. Seeds yellowish, light tan to reddish brown, free and pluriseriate in each locule, with a narrow raphe; surface cells suborbicular, elongate parallel to or perpendicular to the seed length. Self-compatible, modally autogamous in most species. Gametic chromosome number, $n = 8, 16, 24, 32$.

Distribution. Atlantic and Gulf Coastal Plain of the United States (*Ludwigia polycarpa* is exceptional by ranging into the northcentral United States), Bahamas, Cuba, Jamaica, and Tabasco, Mexico.

Key to the Species of *Ludwigia* Sect. *Microcarpium*

1a. Capsules elongate, at least twice as long as broad.
  2a. Petals absent; leaves narrowly elliptic ..... 4. *L. glandulosa*
  2b. Petals 4; leaves sublinear to linear.
    3a. Lateral and marginal veins on abaxial leaf surface distinct; capsules elongate-obpyramidal, ring-dehiscent on top; seeds yellowish; anthers 1–2 mm long, the sacs septate ..... 3. *L. linearis*
    3b. Lateral and marginal veins on abaxial leaf surface obscure; capsules subcylindric, peeled-dehiscent from the sides; seeds reddish brown; anthers 0.5–1.1 mm long, the sacs not septate.
      4a. Sepals (3.3–)4–7 mm long, ca. 3–4 times as long as wide; filaments (1.3–)1.5–3 mm long; style 1.25–2.5 mm long; bracteoles (1.5–)2.5 13 mm long; U.S. & Tabasco, Mexico ..... 1. *L. linifolia*
      4b. Sepals 1.8–3 mm long, 2 times as long as wide; filaments 0.75–1.1 mm long; style 0.55–0.9 mm long; bracteoles 0.7–2.5(–3) mm long; Cuba ..... 2. *L. stricta*
1b. Capsules various, less than twice as long as broad.
  5a. Flowers in compact racemes or spikes 1–5 cm long; stems single or with a few branches frequently overtopping the main stem; rhizomes often present ..... 6. *L. suffruticosa*

5b. Flowers axillary, in elongate, interrupted, leafy racemes or spikes 2–20 cm long; stems usually profusely branched; rhizomes absent.
6a. Plants densely pubescent throughout.
7a. Sepal apex elongate-acuminate or subcuspidate, reflexed; plants densely hirtellous; seed surface cells suborbicular ..... 10. *L. pilosa*
7b. Sepal apex acuminate, ascending; plants densely strigillose or hirtellous; seed surface cells columnar.
8a. Plants hirtellous; capsules oblong-obovoid; sepals greenish adaxially; bracteoles (1.5–)2–4.3 mm long, at or near capsule base ..... 11. *L. ravenii*
8b. Plants strigillose; capsules subglobose; sepals yellowish adaxially; bracteoles 0.5–1.5 mm long, usually on the short pedicel ..... 9. *L. sphaerocarpa*
6b. Plants subglabrous to glabrous.
9a. Capsules obpyramidal with narrowly winged corners.
10a. Stems nearly smooth or slightly ridged; sepals greenish, about ½ as long as the capsule; capsule wall flat between the wings; seed surface cells suborbicular; pollen grains shed as tetrads ..... 7. *L. lanceolata*
10b. Stems often distinctly ridged or winged; sepals creamy whitish, nearly as long as capsule; capsule wall between the wings bulging out longitudinally; seed surface cells elongate parallel to the seed length; pollen grains shed singly ..... 8. *L. alata*
9b. Capsules various, not winged.
11a. Nectary disc nearly flat on ovary apex; fruits 1–1.5 mm long, containing 10–20 seeds, often recognizable as bumps from outside; seeds reddish brown ..... 12. *L. microcarpa*
11b. Nectary disc distinctly raised on ovary apex; fruits 1.5–7 mm long, containing 40–500 seeds, not recognizable as bumps from outside; seeds light tan or yellowish.
12a. Cauline leaves lanceolate, oblong-elliptic to narrowly so; capsules dehiscing by irregular rupture of the outer walls; stolons present.
13a. Bracteoles 3.5–6.5(–8) mm long; sepals green, the apex elongate acuminate, reflexed; capsules oblong-obovoid with a constricted base ..... 5. *L. polycarpa*
13b. Bracteoles 0.5–1.5 mm long; sepals yellowish adaxially, the apex acuminate, ascending; capsules subglobose ..... 9. *L. sphaerocarpa*
12b. Cauline leaves obovate-spatulate, oblanceolate to very narrowly so; capsules dehiscing by 4 longitudinally lenticular slits on the wall opposite the loculi; stolons not common.
14a. Capsules 2.5–4.7 mm long; sepals 1.5–3 mm long; vestigial petals occasionally present; lower or seedling leaves always alternate ..... 14. *L. curtissii*
14b. Capsules 1.5–2.5 mm long; sepals 1.2–1.8 mm long; vestigial petals rare; lower or seedling leaves tending to be opposite or subopposite ..... 13. *L. simpsonii*

As in Figures 1–15 and 19–34, the sequence of the taxa in the taxonomic treatment reflects the possible phylogeny of *Ludwigia* sect. *Microcarpium*. Diploid petaliferous species that are presumably more primitively outcrossing are arranged first, followed by tetraploid members and the related hexaploid *L. alata*. *Ludwigia microcarpa*, an apetalous diploid, which definitely played a role in the formation of the distinct L. *curtissii* complex, is placed last along with the complex.

1. Ludwigia linifolia Poiret in Lam., Encycl. Suppl. 5: 513. 1817. *Isnardia linifolia* (Poiret) Kuntze, Rev. Gen. Pl. 1: 251. 1891. LECTOTYPE: "Amerique," *Poiret Herbarium* (P; lectotype here designated). Figure 35.

Plants glabrous. Stems erect or ascending, usually well branched, 12–55(–62) cm tall, aerenchyma rarely seen. Stolons slender, 4–15(–30) cm long, 0.7–1(–1.5) mm thick, seen in flowering season, the leaves narrowly obovate to narrowly oblanceolate, sometimes spatulate, 4.5–20 mm long, 1.3–6 mm wide, petioles 0.5–5 mm long. Cauline leaves linear or linear-oblanceolate, 15–40 mm long, (0.65–)0.9–4(–6) mm wide, the apex tapering into a sharp point or acute, margin entire with obscure hydathodal glands, the base very narrowly cuneate, sessile. Stipules narrowly ovate to narrowly lanceolate, 0.2–0.3 mm long, 0.1–0.2 mm wide. Flowers many, in leaf axils, their subtending leaves not reduced. Sepals green, narrowly triangular, ascending, (3.3–)4–7 mm long, 1.1–1.7 mm wide, glabrous or minutely papillose, the apex narrowly acute, the margin entire. Petals yellow, narrowly obovate-elliptic, 4–6 mm long, 2–4 mm wide, the apex obtuse or rounded, the base obtuse. Anthers 0.65–1.1 mm long; filaments yellowish, (1.3–)1.5–2.5(–3) mm long. Pollen shed as tetrads. Nectary disc bright yellow, elevated 0.3–0.7 mm on top of the ovary, 0.8–1.5 mm across, prominently 4-lobed, minutely papillose. Style yellow, 1.25–2.5 mm long, glabrous; stigma yellowish, 0.3–0.6 mm long, 0.6–0.8 mm thick, the apex

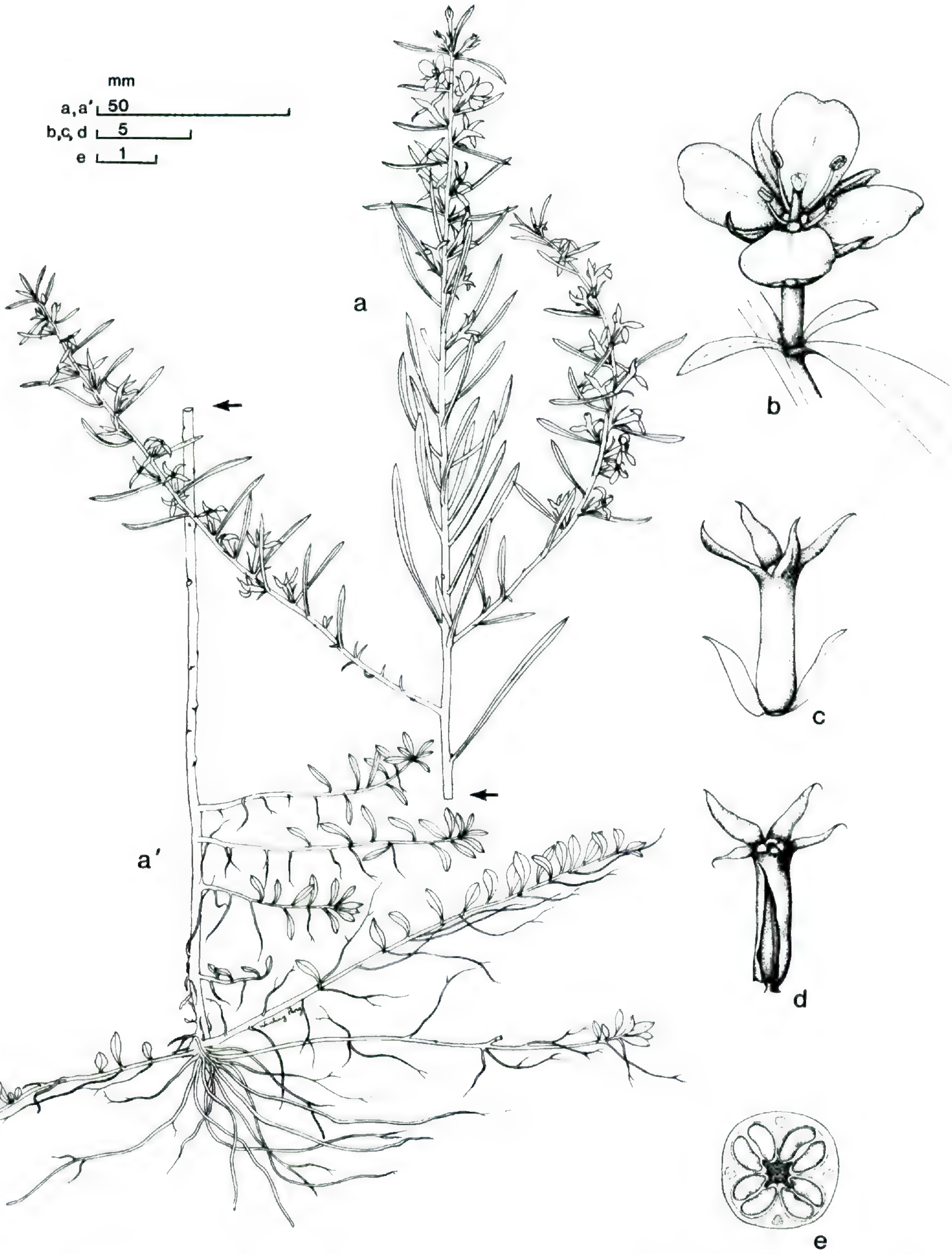

FIGURE 35. *Ludwigia linifolia*. Florida, Santa Rosa Co., *Godfrey 65936* (LL).—a. Habit, erect stem.—a′. Lower stem with basal stolons; stems continue at arrows.—b. Flower.—c. Mature capsule.—d. Dehiscent capsule.—e. Cross section of capsule.

shallowly 4-lobed. Capsules subcylindrical, slightly narrowed toward base, 5–10(–12) cm long, 1.3–2(–2.2) mm thick, densely minutely papillose, occasionally also remotely minutely scaberulous, the hairs 0.05–0.15 mm long, sessile. Bracteoles attached 0–1.5 mm above capsule base, very narrowly oblanceolate to linear, (1.5–)2.5–9(–13) mm long, 0.15–0.8 mm wide, the margin entire, ascending or spreading. Seeds reddish, oblong-elliptic with curved ends, 0.55–0.6 mm long, 0.2–0.3

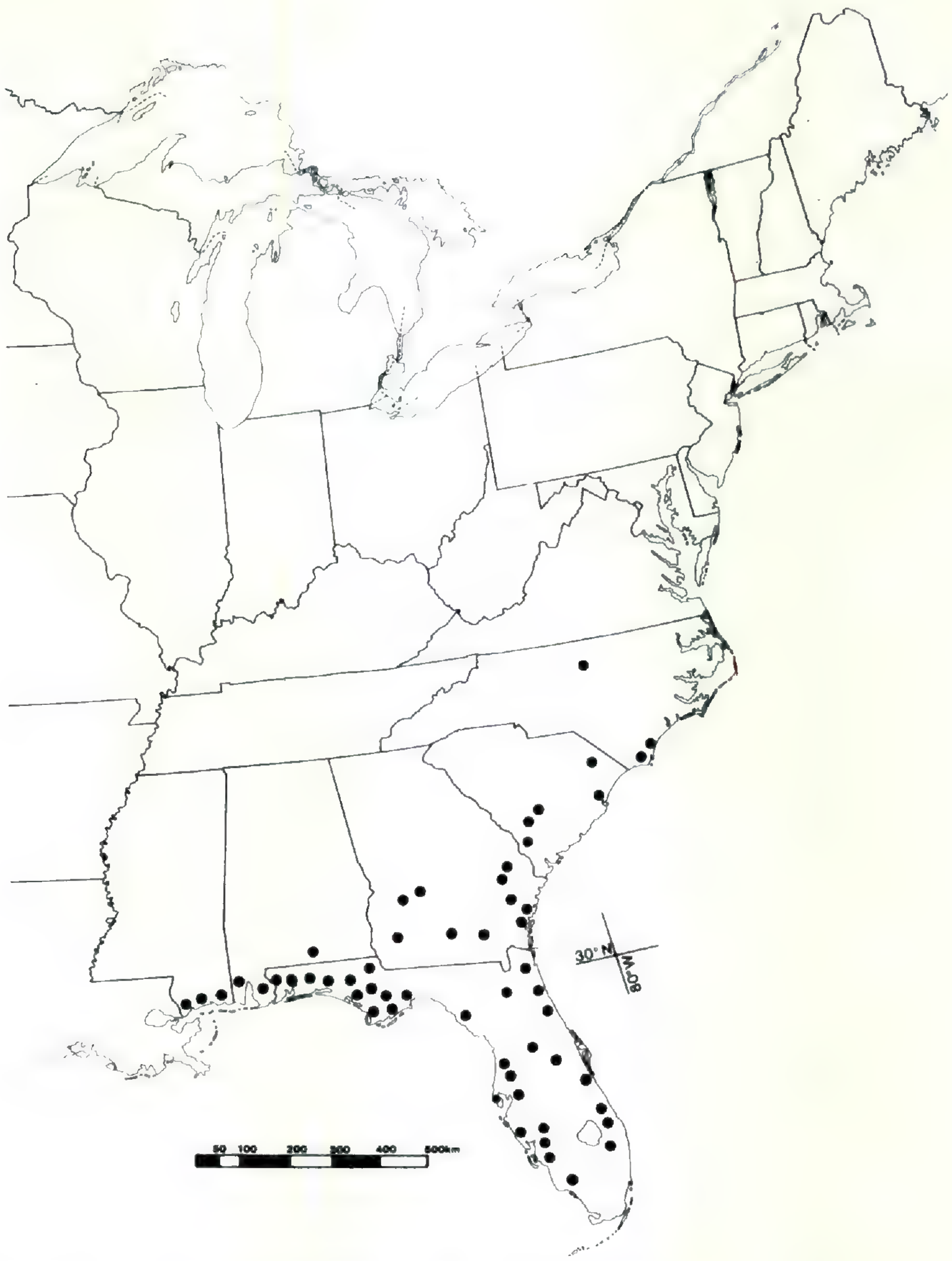

FIGURE 36. Distribution of *Ludwigia linifolia* in the United States.

mm thick, the surface cells nearly isodiametric. Self-compatible. Gametic chromosome number, $n = 8$.

Distribution. Plants of *L. linifolia* are often found in drainage ditches, along margins of creeks or swamps, on bottom meadow, on open edges of cypress swamps, in moist pineland, and along edges of brackish lakes. *Ludwigia linifolia* ranges along the Atlantic coast from extreme southeastern North Carolina and eastern South Carolina through southern Georgia and peninsular Florida. To the west, its range extends through the Florida panhandle, to extreme southern Alabama and Mississippi. A disjunct population has been collected in north-central North Carolina (Fig. 36). It is also known from a disjunct population at Huimanguillo, Tabasco, Mexico, on the Yucatán Peninsula. Flowering from late June through October; fruiting from July through November.

Representative specimens examined. U.S.A. ALABAMA: Baldwin Co., 3 mi. E of Southport, *Webster & Wilbur 3559* (FSU, GH, SMU, US). Covington Co., ca. 13.5 mi. S Opp. on US 331, *Kral 32508* (DS, GA, MO, SMU, VDB). Mobile Co., W jct. ALA 188 and county 59, *Kral 37358* (FLAS, FSU, VDB). FLORIDA: Bay Co., ca. 3.4 mi. inland from Long Beach, *Godfrey & Henderson 62969* (FLAS, FSU, TEX). Bradford Co., near US 301, *Radford 8253* (NCU). Brevard Co., Okeechobee region, *Fredholm 5937* (GH, US). Calhoun Co., ca. 1 mi. NW of Blountstown, *Thorne & Davidson 16967* (FSU). Charlotte Co., Caloosa Experimental Range, U.S. Forest & Range Station, *Adams 198* (FSU). Collier Co., S of Bonita Springs, *Atwater M-78* (FLAS). DeSoto Co., Lacy, *West 171* (FLAS). Dixie Co., 4 mi. N of Suwannee, *Godfrey 56177* (FSU, GH, NY, USF). Duval Co., near Jacksonville, *Curtiss 922* (FI, FLAS, GA, GH, M, MO, NY, RB, S, US). Escambia Co., ca. 3 mi. NW Warrington, *Kral 17580* (VDB). Flagler Co., 3 mi. W of Bunnell, *Godfrey & Reinert 61115* (FSU, SMU). Franklin Co., 38.8 mi. W of jct. of US Hwys. 98 & 319, *Peng et al. 4343* (MO). Gulf Co., 3 mi. S of Port St. Joe, *Kral & Kral 7193* (FLAS, GH, USF, VDB). Hernando Co., Sections 11 & 12, T21S, R17E, *Cooley et al. 7049* (USF).

Hillsborough Co., 7 mi. NE of USF campus, *Lakela 24117* (FLAS, GH, USF). Jackson Co., 11 mi. W of Chattahoochee, *Thorne 5956* (GH). Lake Co., vicinity of Eustis, *Nash 1240* (F, GH, MO, MSU, ND, NY, US). Lee Co., Myers, *Hitchcock 119* (E, F, GH, MO, NY, US). Liberty Co., 4 mi. E Hosford, *Kral 15601* (FSU, VDB). Martin Co., Jonathan Dickinson State Park, *Popenoe 497* (FTG, NCU). Okaloosa Co., US Hwy. 98, 11.4 mi. E of Destin Bridge, *Raven 18593* (DS, FLAS, NCU, USF). Orange Co., Bog, *Fredholm 5378* (GH, US). Palm Beach Co., Corbitt Wildlife Mgmt., *Kral 5714* (FSU, SMU, VDB). Pasco Co., 1 mi. E of Gowers Corner off US 41, *Ray et al. 9934* (USF). Pinellas Co., Gulfport, *Tracy & Lloyd 225* (CM, US). St. Johns Co., 3 mi. SE of Orangedale, along FL 16, *Godfrey 70630b* (FSU, MO, NCU). St. Lucie Co., W of Walton Beach, E of US 1, *Kral 18366* (VDB). Santa Rosa Co., near Yellow River, NW of Maxton, *Godfrey 62564* (FSU, GH, SMU, VDB). Sarasota Co., along US 41, 4 mi. S of Venice, *Henderson 63-1574* (FSU, TEX). Seminole Co., near Fern Park, *Schallert 8145* (S). Wakulla Co., near Spring Creek, *Godfrey 55882* (DUKE, GH, LL, NCU, SMU, USF, VDB). Walton Co., ca. 5 mi. NE Seagrove Beach along US 98, *Kral 19360* (VDB). Washington Co., 3.5 mi. E of Caryville, *Godfrey 5962* (DUKE, FLAS, GH, NCU, VDB). GEORGIA: Baker Co., SW corner of county, *Thorne 6972* (GA). Berrien Co., 15 mi. E of Tifton, *Sargent 6686* (Herb. unknown). Bullock Co., 3.5 mi. S of Statesboro, *Bozeman 6921* (NCU). Dooly Co., 3 mi. S-SE Pitts jct., ca. 10.5 mi. S Pinehurst, *Kral 48130* (VDB). Evans Co., 5 mi. S of Claxton, *Godfrey 72098* (FSU, NCU). Glynn Co., 1.3 mi. NW of Brunswick, *Duncan 17021* (FLAS, NCU, SMU). Long Co., 5.7 mi. SE of Ludowici on GA Rt. 99, *Boole 1140* (B, NCU, SMU). McIntosh Co., NW of graveyard on Wesley Lake Rd., *Bozeman 2227* (FLAS, GA, NCU). Sumter Co., wet pine barrens, *Harper 1109* (E, GH, MO, NY, US). Ware Co., Waycross, 1900, *s.c. 4176a* (US). MISSISSIPPI: Hancock Co., US Hwy. 90, 2.5 mi. W of jct. with State Hwy. 43, *Raven 18581* (DS). Harrison Co., Gulfport, *Lloyd & Tracy 225* (NY). Jackson Co., Hwy. 90, between Orange Grove and Pecan, *Jones 14898* (FSU, GH, NY, VDB). NORTH CAROLINA: Brunswick Co., on Co. Rt. 1335, 2 mi. NW of jct. of Co. Rt. 1340, *Leonard & Radford 2205* (C, CM, E, FLAS, MISS, NO, NY, TENN, TEX, U, UNA, USCH, VDB, WCUH). New Hanover Co., Port Fisher on the Lower Cape Fear Peninsula, *Godfrey 6195* (GH). SOUTH CAROLINA: Bamberg Co., on US 301, 0.3 mi. N of jct. with SC 64, *Bozeman et al. 11400A* (NCU). Georgetown Co., 1,750 ft. due ENE of intersection of US 17 & Belle Isle Gardens Road, *Rayner 1081* (USCH). Hampton Co., 0.2 mi. N of Luray on US Rt. 321, *Ahles & Bell 18288* (FSU, NCU, USF). Marion Co., just E of secondary road 49; 8–10 mi. N of intersection with Great Pee Dee River, *Rayner 1109* (USCH). Orangeburg Co., 2.7 mi. N of Branchville City on (just W of) US 21, *Rayner 1106* (USCH). MEXICO. TABASCO: Huimanguillo, *Cowan 2632* (MO), *2277* (NY), *3111* (MO).

Ludwigia linifolia is a relatively uniform species. Its variability chiefly affects the size of the capsules and the lengths of the bracteoles, which are attached to the sides of the capsule. Its closest affinity is definitely with *L. stricta*, a Cuban endemic, from which *L. linifolia* differs by having narrower leaves, larger floral parts (including sepals, anthers, filaments, and style), and longer fruits and bracteoles. Characters of the two species and the only other petaliferous member of the section, *L. linearis*, are listed for comparison in Table 3.

Ludwigia linifolia has somewhat showy petals and the most prominent nectary disc lobes occurring in sect. *Microcarpium*. The nectary disc is bright yellow and produces copious nectar at anthesis. Herbarium specimens often reveal empty anthers held away from the stigma (mechanical self-pollination has not occurred yet). This observation suggests that *L. linifolia* is probably modally outcrossing, which is corroborated by limited field observations.

Ludwigia linifolia occurs with *L. alata*, *L. curtissii*, *L. glandulosa*, *L. linearis*, *L. microcarpa*, and *L. pilosa* in the field. Natural hybrid populations have, however, been found only between *L. linifolia* ($n = 8$) and *L. curtissii* ($n = 32$). This is contrary to what one would expect for the outcrossing *L. linifolia*. However, experimental hybridizations (Peng, 1988) indicate that artificial hybrids between the diploid *L. linifolia* and plants of any other ploidy level in sect. *Microcarpium* are generally difficult to obtain. Repeated trials with different parental strains were successful in some cases, but the resulting hybrids were usually weak and needed special attention to reach flowering stage. Attempts to synthesize the natural hybrid *L. linifolia* × *L. curtissii* in the experimental greenhouse were unsuccessful.

2. Ludwigia stricta (Wright ex Griseb.) Wright in Wright & Sauvalle, Fl. Cubana 54. 1873. Based on *Isnardia stricta* Wright ex Griseb., Cat. Pl. Cub. 107. 1866. TYPE: eastern Cuba, 1860–1864, *C. Wright 2555* (holotype, GOET; isotypes, G, GH, MO, NY, P, US). Figure 37.

Plants glabrous throughout. Stems erect or ascending from stolons, simple or much branched, 10–60(–85) cm tall. Stolons 5–10 cm long, 1–2.5 mm thick, the leaves elliptic, 7.5–13 mm long, 3–5 mm wide, glabrous, the base attenuate into winged petioles up to 2 mm long. Cauline leaves deciduous from below in late growing season, oblanceolate to narrowly oblanceolate or narrowly elliptic, 11–22 mm long, 2.2–5.5 mm wide, glabrous, the apex acute, the margin with remote, minute hydathodal glands, the base narrowly cuneate into winged petiole 0–1.5 mm long. Stipules minute, ovate or lanceolate, succulent, dark brownish purple, 0.2–0.3 mm long, 0.1–0.2 mm wide. Flowers in upper leaf axils, their subtending leaves

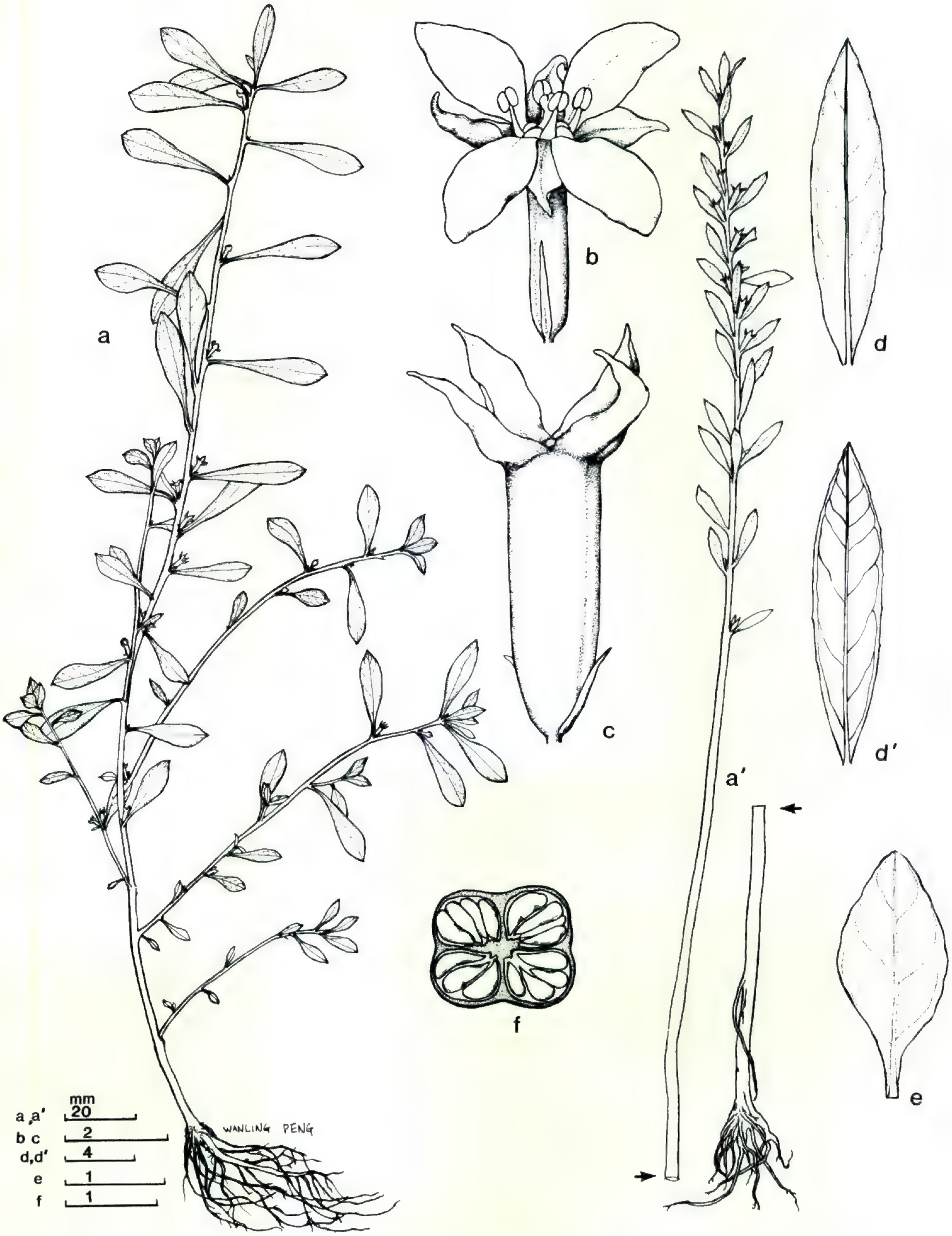

FIGURE 37. *Ludwigia stricta*. a′, c, d, d′, and f from Cuba (*Wright 2555*, US); a, b, and e from plants grown from seeds from Cuba (1982, *Leiva s.n.*, *M 3304*, MO).—a, a′. Habit, stem continues at arrows.—b. Flower.—c. Capsule.—d, d′. Adaxial and abaxial sides of leaf.—e. Petal.—f. Cross section of fruit.

not reduced. Sepals green, narrowly ovate-triangular, ascending, (1.8–)2–3 mm long, 0.9–1.5 mm wide, the apex narrowly acute or acuminate, the margin entire. Petals yellow, elliptic or narrowly obovate, 2.3–2.9 mm long, 1.2–1.3 mm wide, the apex obtuse, the base attenuate. Anthers 0.5–0.7 mm long; filaments 0.75–1.1 mm long. Pollen grains shed as tetrads. Nectary disc yellow, elevated 0.25–0.3 mm on top of the ovary, 1–1.25 mm across, 4-lobed, minutely papillose. Style 0.55–0.9 mm long, glabrous; stigma subglobose, 0.25–0.5 mm across. Capsules cylindrical, 5–6(–7) mm long, 1.6–1.8 mm thick, minutely papillose; pedicels 0–0.9 mm long. Bracteoles attached at capsule base, narrowly lanceolate, 0.7–2.5(–3) mm long, 0.2–0.4(–0.6) mm wide, the margin entire. Seeds reddish brown when mature, elliptic-oblong in outline, slightly curved on both ends, 0.5–0.6 mm long, 0.2–0.25 mm thick, the surface cells nearly isodiametric. Self-compatible. Gametic chromosome number, $n = 8$.

Distribution. *Ludwigia stricta* is a uniform species known only from Cuban lagoons and savannas (Fig. 38). Flowering and fruiting from August through November.

Representative specimens examined. CUBA. PIÑAR DEL RÍO: Herradura, *Britton et al. 6613* (NY); Piñar del Río, *Britton et al. 7233* (NY); 3 km S of Herradura, *Ekman 17742* (S). ISLA DE JUVENTUD (ISLA DE PINOS): between Los Indios and La Siguanea, *Ekman 12179* (S); Hotel Colony, *Rostánski 2028* (MO); 1982, *Leiva s.n.* (cultivated, MO).

Ludwigia stricta has a close affinity with *L. linifolia*, which is distributed in the southeastern United States and occurs on the Yucatán Peninsula in Tabasco, Mexico. Both are diploids; they are similar in stature, have four petals, shed their pollen as tight tetrads, have subcylindric capsules that dehisce irregularly from the sides, and have reddish brown seeds with subisodiametric surface cells. A comparison of these two species and the other petaliferous diploid species, *L. linearis*, is presented in Table 3.

Viable seeds of *L. stricta* have become available only recently. Plants have been grown and crossed with all three other diploid species of sect. *Microcarpium* in order to assess their genetic relationships.

3. Ludwigia linearis Walter, Fl. Carol. 89. 1788. *Isnardia linearis* (Walter) DC., Prodr. 3: 60. 1828. TYPE: U.S.A. "the Carolinas": *T. Walter 665* (holotype, BM, Walter Herbarium, p. 66; photograph, MO). Figure 39.

Ludwigia angustifolia Michaux, Fl. Bor.-Am. 1: 88. 1803. LECTOTYPE: U.S.A. South Carolina: near wet ditches, fl. Aug.-Sept., 1785–1796, *A. Michaux s.n.* (P; photographs, GH, MO; isolectotypes, MO, P—2 sheets; lectotype here designated, based on best collection of authentic material at P).

Ludwigia linearis Walter var. *puberula* Engelm. & A. Gray, Boston J. Nat. Hist. 5: 217. 1845. TYPE: U.S.A. Texas: Harris Co., Houston, July 1843, *F. J. Lindheimer 58* (holotype, GH; isotypes, BM, GOET, MO, P, PH, US).

Plants glabrous to densely minutely strigillose or sometimes puberulent, the hairs 0.05–0.15 mm long. Stems erect, often well branched, (22–)50–100(–145) cm tall, often with distinct aerenchyma in lower part. Stolons up to 30 cm long, 0.8–0.25 mm thick, seen in late fruiting season only, the leaves purplish, narrowly elliptic to very narrowly elliptic, 12–23 mm long, 2.8–8.5 mm wide, glabrous to sparingly minutely strigillose, the base attenuate into petioles up to 5 mm long. Cauline leaves green, linear to elliptic linear, 16–60(–85) mm long, 0.9–3.7(–5.6) mm wide, glabrous to densely minutely strigillose or puberulent, the apex very narrowly acute, the margin entire, the hydathodal glands obscure, the base very narrowly acute or cuneate, subsessile. Stipules narrowly ovate or lanceolate, 0.15–0.3 mm long, 0.05–0.15 mm wide. Flowers many, in leaf axils, their flower-subtending leaves not reduced. Sepals green, triangularly ovate to narrowly triangular, the apex acuminate or elongate acuminate to cuspidate, ascending, 2.3–5(–5.6) mm long, 1–3(–3.5) mm wide, glabrous, densely minutely scaly strigillose, strigillose, or puberulent without, glabrous within. Petals yellow, obovate to subrotund, 3–6 mm long, (2–)2.5–5 mm wide, the apex obtuse, the base attenuate. Anthers lanceolate oblong, 1–2 mm long, sporogenous tissue 4–8 packeted; filaments 1.1–2(–2.2) mm long. Packets in the sporogenous tissue opening and shedding tetrad pollen almost simultaneously. Nectary disc yellow, elevated (0.25–)0.35–0.55(–0.7) mm on top of the ovary, 1.3–2.5 mm across, 4-lobed, glabrous to minutely strigillose or strigillose, especially around lobe margins. Style yellowish green, (0.4–)0.7–1.5 mm long, glabrous throughout to densely strigillose, especially in the lower part. Stigma yellowish green, elongated, shallowly 4-lobed on apex, (0.6–)1–1.9 mm long. Capsules elongate obpyramidal, often with a shallow, central, longitudinal groove on each side, 5–10 (–12) mm long, 2–5.5 mm thick, glabrous, densely scaly strigillose, strigillose, or puberulent, subsessile or with distinct pedicels up to 3.5(–5) mm long. Bracteoles subequal, attached near capsule base to 4.5 mm above base or on the pedicel, linear, 0.4–

FIGURE 38. Distributions of *Ludwigia alata* (circles) and *L. stricta* (triangles).

4(–7.5) mm long, 0.1–0.3 mm wide, deciduous. Seeds light brown, oblong-elliptic with slightly curved ends, 0.45–0.65 mm long, 0.15–0.25 mm wide, the surface cells oblong, elongate either parallel or transversely to the seed length. Self-compatible. Gametic chromosome number, $n = 8$.

Distribution. *Ludwigia linearis* is common in drainage ditches, along river or stream banks, swales, edges of pocosins, sandy soil in wet meadows, brackish marshes, and occasionally on disturbed ground. It is distributed along the Atlantic coast from southern New Jersey through Delaware, the eastern halves of North and South Carolina, southern Georgia, to its southern limit in central Florida. Westwards, this species extends through the panhandle of Florida and across Alabama, southern Mississippi, and Louisiana, to the central Gulf coast of Texas. To the north, *L. linearis* ranges through eastern Texas and across southern Arkansas, and there is a northward range extension from northern Alabama into Tennessee (Fig. 40).

FIGURE 39. *Ludwigia linearis*. All but a′ from South Carolina (Jasper Co., *Boufford et al. 21633*, MO); a′ from Virginia (Nansemond Co., *Fernald et al. 15322*, GH).—a. Habit, erect stem.—a′. Lower stem with basal stolons.—b. Leaves.—c. Flower bud.—d. Flower.—e. Petal.—f, f′. Adaxial and abaxial views of stamen.—g, g′. Immature and mature capsules.—h. Cross section of capsule.

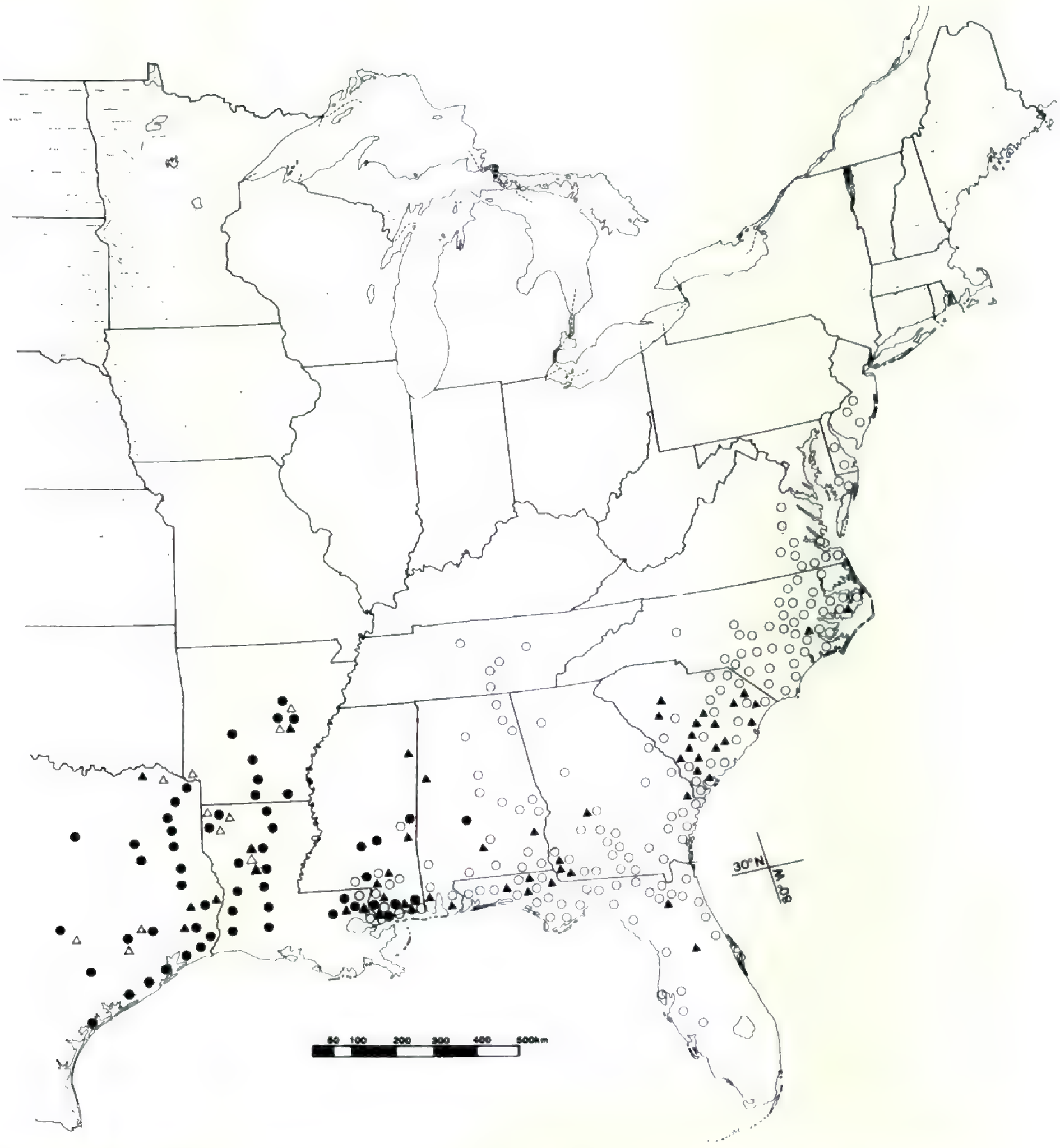

FIGURE 40. Distribution of *Ludwigia linearis*. ○ = subglabrous morph; ● = densely strigillose morph; △ = glabrous morph; ▲ = intermediate morph.

Incorrectly reported from Japan (see discussion). Flowering from late June through September; fruiting from late July through mid December.

Representative specimens examined. (1: subglabrous morph; 2: densely strigillose morph; 3: glabrous morph; 4: intermediate morph—see following discussion.) U.S.A. ALABAMA: Baldwin Co., 1.5 mi. N of Gulf Shores, *Kral 38264* (4, VDB); 13.5 mi. W of Foley on US Hwy. 98, *Raven 18590* (1, DS). Barbour Co., ca. 5 mi. S Eufaula by Lake Eufaula, *Kral 33241* (4, SMU, VDB). Butler Co., ca. 11 mi. N of Georgiana, by US Hwy. 65, *Kral 40891* (1, VDB; mixed with 2). Cherokee Co., by Little River, Canyon Mouth Park, *Kral 43824* (1, VDB). Chilton Co., near Clanton, 1874, *Smith s.n.* (1, UNA). Covington Co., ca. 6 mi. N of Florala on US Hwy. 331, *Davenport 788* (1, UNA). Cullman Co., 1897, *Eggert s.n.* (1, MO). Dale Co., by Choctawhatchee River just N of Newton by AL Hwy. 123, *Kral 54450* (1, VDB). Dallas Co., *Mohr s.n.* (2, F). De Kalb Co., near Mentone, *Ruth 415* (1, NY, US). Elmore Co., 5 mi. N of Wetumpka, by AL Hwy. 9, *Kral 36595* (1, VDB). Escambia Co., 4.6 mi. E of Boykin, just W of Conecuh River by US Hwy. 29, *Kral 44811* (1, VDB). Geneva Co., 3.2 mi. S of Hartford on AL Hwy. 167, *Kral 36723* (1, GA, VDB). Houston Co., E of jct. S of Spring Hill Church, *Clark 7342* (1, NCU). Jackson Co., N of Flat Rock, *Kral 36531* (1, FSU, VDB). Lee Co., near Auburn, 1897, *Earle & Baker s.n.* (1, F, MO, MSC, NY). Macon Co., near Society Hill, 1857, *s.c.* (1, NY). Mobile Co., 2 mi. NE of Theodore on US Hwy. 90, *Kral 29673* (1, FSU, NCU, SMU, VDB); Dauphin Island, near Bienville Blvd., *Deramus D707* (4, NCU, UNA). Pickens Co., S side of Aliceville, *Kral 51383* (4, VDB). Russell Co., 1.3 mi. NW of Phenix City, by US Hwy. 280, *Kral 44243* (1, VDB). Shelby Co., 4 mi. N of jct. AL Hwy 25 & Calera turnoff by US Hwy. 65, *Kral 33584* (1, SMU, VDB). Washington Co., 3.1 mi. S of St. Stevens, *Kral 37216* (1, FLAS, VDB). ARKANSAS: Ashley Co., Lone Pine Prairie, *Demaree 21603* (2, MO, NO, NY SMU, TENN, TEX). Calhoun Co., 10 mi. S of Hampton, *Kral 24536* (2, VDB). Dallas Co., near Fordyce, *Demaree 67870* (1, MO). Garland Co., near Carlisle, *Demaree 38024* (2, SMU). Little River Co., near Ben Lomond, *Demaree 63154* (3, MO). Lonoke Co., near Carlisle, *Demaree*

37980 (2, SMU, VDB; 3, SMU). Prairie Co., near Hazen, *Demaree 37904* (3, SMU, VDB); along Hwy. 70, E of Carlisle, 1956, *Buker s.n.* (4, CM, mixed with 3). Union Co., near El Dorado, *Hoiberg 591* (2, SMU). White Co., 1.2 mi. S of McCrae, by US Hwys. 67, 167, & 64, *Thomas & Smith 15187* (2, DS, SMU, TENN). DELAWARE: Kent Co., near Hamington, 1872, *Canby s.n.* (1, F). Sussex Co., 3 mi. S of Laurel, *Hotchkiss 7919* (1, US). FLORIDA: Alachua Co., E of Gainesville, 1940, *Murrill s.n.* (1, US). Baker Co., near McClenny, *Curtiss 6007* (1, DS, FLAS, GA, GH, MO, NCU, NY, SMU, US). Bay Co., near Lynn Haven, *Godfrey 59120* (1, FSU, SMU). Bradford Co., near Sampson City, *Dennison & Arnold 171* (1, FLAS); W of Lawtey, *Raven 18694* (4, DS). Calhoun Co., 5 mi. W of Blountstown, *Godfrey & Kral 55035* (1, FSU, GA, GH, NY, S, SMU, TENN, UNA, USF). Citrus Co., near Chassahowitzka, *Genelle & Fleming 1562* (1, GA, TENN, USF). Clay Co., near Doctors Inlet, 1939, *Murrill s.n.* (1, DUKE, MO). Columbia Co., near Lake City, 1893, *Rolfs s.n.* (1, F, FLAS, MO). DeSoto Co., near Lacy, 1938, *Arnold s.n.* (1, FLAS). Dixie Co., 4 mi. N of Suwannee, *Godfrey 56179* (1, FSU, GH, NY, USF). Duval Co., ca. 8 mi. from jct. with FL Hwy. 17 on Starrett Rd., *Youree 663* (1, FLAS). Escambia Co., S of Playground Music Center, *Burkhalter 4781* (1, FLAS). Flagler Co., 3 mi. E of Bunnell, 1937, *West et al. s.n.* (1, FLAS). Franklin Co., 41.7 mi. W of jct. US hwys. 98 & 319, *Peng et al. 4351* (1, MO). Gulf Co., between Weewahitchka & Port St. Joe, *Godfrey & Kral 54167* (1, DUKE, FSU, GH, NY). Hamilton Co., 11 mi. E of Suwannee River by FL Hwy. 6, *Godfrey 75386* (1, FSU). Hillsborough Co., 1.5–1.7 mi. S of Hwy. 674, on E side of Taylor Grill Dr., *Peng 4325* (1, MO). Holmes Co., near Westville, *s.c. 4175c* (1, JE; 4, GH, US). Jackson Co., N of Sneads, Lake Seminole, *Godfrey & Houk 61398* (4, TEX); S of Marianna, along Hwy. 71, *Hood 2642* (1, TEX). Jefferson Co., ca. 15 mi. SSW of Monticello, *Kral 5825* (1, FSU, GH, SMU, USF). Lake Co., near Eustis, *Nash 1490* (4, NY). Leon Co., N of Woodville, *Perdue & Godfrey 1858* (1, C, GH, LL, NCU, SMU, TEX, US, USF). Liberty Co., 1 mi. E of Telogia, *Morar 8* (1, DUKE, FSU, MSU). Madison Co., 8 mi. W of Greenville, *Kral 3742* (1, FSU, GH, NCU, SMU). Manatee Co., NE of jct. hwys. 62 & 39, *Shuey 1710* (1, USF). Okaloosa Co., E of Oak Grove by FL Hwy. 2, Yellow River, *Godfrey 75428* (1, FSU). Pinellas Co., Brooker Creek, *Poppleton 698* (1, USF). St. Johns Co., near Crescent Beach, 1941, *West & Arnold s.n.* (1, FLAS). Santa Rosa Co., NW of Maxton, Yellow River, *Godfrey & Houk 62565* (1, FSU). Taylor Co., 18 mi. WSW of Madison, *Kral 3771* (1, FSU, GH, NCU). Union Co., 1 mi. S of Railford, 1940, *Murrill s.n.* (1, FLAS). Volusia Co., S of Seville, 1943, *West & Arnold s.n.* (1, FLAS). Wakulla Co., near St. Marks Refuge, *Morar 17* (1, FSU, NCU, SMU, US, VDB). Walton Co., at Mossy Head, *Godfrey 55244* (1, FLAS, FSU, GA, GH, NY, S, SMU, TENN, UNA, USF); 4 mi. S of Freeport, along Laird Drive, *Davis & Davis 15485* (4, FLAS). Washington Co., 3.5 mi. E of Caryville, *Kral & Godfrey 5960* (1, FSU, USF); S of Chipley along Hwy. 77, *Hood 2836* (4, FLAS). GEORGIA: Bartow Co., ca. 4.5 mi. SE of Adairsville on Cassville Mountain, *Greear 64349* (1, GA, NCU). Berrien Co., ca. 3 mi. W of Alapaha, *Duncan 23488* (1, GA, VDB). Charlton Co., along GA Hwy. 94 between Moniac & St. George, *Jones et al. 23045* (1, GA). Chatham Co., along Dutchtown Road, 1959, *Mellinger s.n.* (1, GH); 4 mi. N of Richmond Hill, *Kral 18947* (4, VDB). Coffee Co., near Douglas, 1900, *Harper s.n.* (1, NY, US). Cook Co., 7.6 mi. SE of Adel, Jim Reeves Pond, *Faircloth 2928* (1, GA, NCU). Decatur Co., 1.5 mi. E of Climax, *Godfrey 75563* (4, FSU). Dooly Co., 0.75 mi. S of Georgia Pacific Plant, S of Vienna by US Hwy. 41, *Godfrey 76005* (4, FSU); 2.7 mi. S-SE of Unadilla, *Harper et al. 16817* (1, GA). Early Co., 2 mi. S of Hilton, *Thorne 6021* (1, US). Echols Co., 2.6 mi. E of Statenville, *Kral 51639* (1, VDB). Emanuel Co., 0.8 mi. S of Interstate 16 on US Hwy. 1, *Peng 4023* (1, MO). Glynn Co., 2 mi. W of Brunswick, *Pyron & McVaugh 279* (GA). Grady Co., 3.5 mi. NW of Calvary, *Faircloth & Faircloth 1509* (1, MO, NCU). Irwin Co., 7.3 mi. SW of Irwinville, at Tift–Irwin Co. line, *Faircloth 5410* (1, GA, NCU). Lanier Co., 1 mi. E of Lakeland, *Faircloth 3605* (1, GA, NCU). Lee Co., 1.5 mi. SW of Smithville, *Pyron & McVaugh 1948* (1, GA). Liberty Co., Camp Stewart near Hinesville, 1943, *Guimm s.n.* (1, CM). Long Co., 4.2 mi. SW of jct. of US hwys. 301 & 25 and GA Hwy. 99, on US hwys. 301 & 25, *Peng 4120* (4, MO); 5.5 mi. W of US Hwy. 301 on GA Hwy. 261, *Bozeman & Radford 1917* (1, NCU). Lowndes Co., 13 mi. E of Valdosta in Grand Bay, *Faircloth 2080* (1, GA, NCU). McIntosh Co., NE section of Sapelo Island, *Duncan 20554* (1, CAS, DUKE, F, GA, GH, MISS, NCU, SMU, TEX, USF). Miller Co., 1.5 mi. W of Colquitt, *Thorne 6716* (1, GH; 4, GA). Pike Co., 0.5 mi. N of Meansville, *Harper 2244* (1, GH, MO, NY). Richmond Co., 1903, *Cuthbert s.n.* (1, FLAS). Screven Co., E of Sylvania, *Eyles 7637* (1, DUKE, GA). Seminole Co., 1.5 mi. E of Donaldsonville, *Godfrey & Clewell 63210* (4, FSU). Thomas Co., near Thomasville, 1903, *Taylor s.n.* (1, TEX). Tift Co., 2.5 mi. W of Alapaha River jct. with Tift & Berrien counties, *Plummer & Pullen 897* (1, GA). Turner Co., 4 mi. WNW of Ashburn on US Hwy. 41, *Ernest 134* (1, NCU). Ware Co., near Waycross, *Eggleston 5078* (1, NY). Wayne Co., near Jesup, *Curtiss 921* (1, CM, F, GA, GH, M, MO, ND, NY, US). LOUISIANA: Acadia Parish, 1.5 mi. W of Midland on US Hwy. 90, *Raven 22095* (2, DS, NCU). Beauregard Parish, 14 mi. W of DeRidder, *Kral 20743* (2, VDB). Bossier Parish, 10 mi. S of Plain Dealing, *Shinners 24488* (3, NO; 4, SMU). Caddo Parish, ca. 2.5 mi. N of Oil City, *Thieret 24467* (3, DS); along LA Hwy. 1, S of jct. LA Hwy. 2, Vivian, *Thomas & Overby 36294* (2, NCU). Calcasieu Parish, ca. 2.5 mi. W of Sulphur, near Stegall, *Thieret 20580* (2, DS, DUKE, FSU, GA, LL, SMU). Evangeline Parish, 6.2 mi. SE of jct. of LA hwys. 106 & 107, *Sullivan 1633* (2, USF). Grant Parish, 4.5 mi. N of Dry Prong, *Shinners 24945* (4, SMU); 1.5 mi. E of US Hwy. 165 opposite LA Hwy. 123, Barrett Quail Farm, *Thomas et al. 2995* (2, NCU, SMU, VDB). Livingston Parish, 5 mi. S of Montpelier, *Thieret 24850* (2, DS). Natchitoches Parish, ca. 4 mi. E of Bellwood, *Kral 16192* (2, VDB). Ouachita Parish, 2 mi. E of Fairbanks, *Thomas et al. 30860* (2, FLAS, GH, SMU, TENN). Rapides Parish, 8 mi. N of Woodworth, *Kral 15828* (2, VDB). St. Tammany Parish, 2.5 mi. N of Talisheek, *Raven 22104* (1, DS, NCU); Hwy. I-59 at Pearl River exit, *Darwin & Sundell 578* (2, NO); 3.7 mi. E of Slidell, along hwy., *Raven 18579* (4, NCU). Tangipahoa Parish, ca. 1.2 mi. E of Arcola, Tangipahoa River, *Thieret 27823* (2, DUKE, FSU, GA); Ponchatoula, *Cocks s.n.* (4, NO). Union Parish, 4 mi. NE of Haile, *Thieret 23691* (2, DS, SMU). Vernon Parish, 2 mi. E of LaCamp, *Kral 15805* (2, VDB). Washington Parish, near Franklinton, *Demaree 46898* (1, DS, SMU, VDB). Webster Parish, ca. 2 mi. W of Springhill, *Allen 8474 &*

Vincent 1798 (3, FLAS, VDB). Winn Parish, 3 mi. N of Winnfield by LA Hwy. 1231-2 at jct. with US Hwy. 165, *Thomas & Cicala 31931* (4, NCU, NY). MARYLAND: Wicomico Co., 6 mi. E of Salisbury, 1872, *Canby s.n.* (1, NY). Worcester Co., near Ocean City, 1909, *Carter s.n.* (1, NY). MISSISSIPPI: Clarke Co., 2.4 mi. NNE of Pachuta, *Jones 10750* (4, MISS). Forrest Co., ca. 3.5 mi. N of Stone Co. line, W of Hwy. 49, *Rogers 4664* (1, MO, NCU); near Ragland Hills, *Rogers 3807* (4, MISS, NCU, VDB). George Co., near Agricola, *Demaree 32789* (1, SMU, VDB). Hancock Co., Kiln Post Office, *Demaree 36311* (1, GH, SMU); Waveland & Hwy. 90, *Jones & Jones 9435* (2, MISS, NCU); on MS Hwy. 43, ca. 5 mi. NE of MS Hwy. 603, *Peng et al. 4363* (4, MO). Harrison Co., near Biloxi, 1900, *Tracy & Lloyd s.n.* (1, F, GH, MSC, US; 4, NY); 2 mi. N of Gulfport, *Jones 10343* (2, GA, MISS). Jackson Co., Ocean Springs, *Seymour 82* (1, CAS, DUKE, F, FSU, GH, MO, MSC, NCU, SMU, TENN, TEX, USF), *Demaree 28232* (2, SMU, TEX, VDB); on MS Hwy. 57, 2.8 mi. N of US Hwy. 90, *Peng et al. 4355* (4, MO). Lamar Co., 5 mi. SW of Hattiesburg, *Ray 5957* (MISS; 1, GA, GH, NCU, NY, USF; 4, NY). Lauderdale Co., S of Lauderdale, *Jones 14990* (1, GA, MISS); E of Chunky, US Hwy. 80 crossing of Chunky River, *Kral 22036* (2, VDB). Marion Co., S of Hwy. 48/35 jct., ca. 3 mi. N of MS–LA border, *Musselman 1238* (2, NCU). Monroe Co., near Amory, 1916, *Bailey s.n.* (4, MISS). Pearl River Co., 5.8 mi. S of Carriere, N of Picayune, *Jones & Hudson 9748* (1, MISS); 1 mi. E of Picayune, *Sargent 9879* (2, MO); 8 mi. NW of Picayune, *Sargent 8376* (4, CAS). Perry Co., 5 mi. E of Runnelstown, *Jones 9587* (1, MISS). Simpson Co., 5.8 mi. S of Puckett and N of Mendenhall, MS Hwy. 13, *Jones 19257* (2, GA, MISS). Smith Co., near Taylorville, *Tracy 8715* (2, F, GH, MO, MSU, NCU, NY, TAES, US). Walthall Co., along MS Hwy. 21, just over LA border, *Kral 19393* (1, VDB). NEW JERSEY: Atlantic Co., near Egg Harbor City, *Mackenzie 5582* (1, DUKE, GH, MO, NY, SMU). Burlington Co., near Atsion, 1879, *Martindale s.n.* (1, F, NY, US). Camden Co., near Atco, 1872, *Commons s.n.* (1, NY). NORTH CAROLINA: Beaufort Co., along NC Hwy. 33, 3 mi. S of jct. of Cox Road, *Duke 54-228* (1, NCU). Bertie Co., 10 mi. E of Windsor, on NC Hwy. 17, *Blomquist 16226* (1, DUKE). Bladen Co., 5.2 mi. W of Dublin, *Duke 5499* (1, NCU). Brunswick Co., 0.2 mi. W of Longwood on NC Hwy. 904, *Peng et al. 3885* (1, MO). Carteret Co., ca. 14 mi. NE of Beaufort on Rt. 70, *Wilbur 9336* (1, DUKE). Chatham Co., 3.1 mi. S of Wilsonville, on Co. Rd. 1008, *Campbell 1077* (1, NCU). Columbus Co., 2.1 mi. NW of Old Dock on NC Hwy. 130, *Leonard & Radford 2192* (1, CM, FLAS, FSU, GA, NCU, NY, SMU, USF, VDB). Craven Co., 0.8 mi. N of US Hwy. 17 on Co. Rd. 1224, *Peng et al. 3737* (1, MO); jct. of US Hwy. 70 & Street Ferry Rd., *Duke 5468* (4, NCU). Cumberland Co., 8 mi. N of Fayetteville, on Hwy. 15A, *Duke 54152* (1, NCU). Dare Co., along US Hwy. 64 N of Manteo, *Duke 54-236* (1, NCU). Duplin Co., 2.5 mi. SSE of Rose Hill on US Hwy. 117, *Ahles 35773* (1, NCU). Edgecombe Co., between Whitakers & Enfield, *Godfrey & Fox 49642* (1, NCSC). Gates Co., 1 mi. NE of Chowan on US Hwy. 158, *Beal 2121* (1, NCSC). Greene Co., 0.7 mi. ESE of Jason, *Radford 40379* (1, NCU). Halifax Co., near Weldon, 1900, *Williamson s.n.* (1, NY). Harnett Co., near Dunn, *Godfrey 6149* (1, DUKE, GH, US). Hoke Co., 4 mi. SSW of Ashley Heights, *Ahles 36379* (1, NCU). Hyde Co., 8.5 mi. SW of Fairfield, *Duke 54-233* (1, NCU); 1.2 mi. NW of Sladesville, *Radford 39039* (4, CTES). Iredell Co., near Statesville, s.d., *Hyanis s.n.* (1, DS). Johnston Co., 4 mi. SE of Benson on NC Hwy. 50, *Lloyd 1121* (1, MO). Jones Co., 0.4 mi. W of Co. Rd. 1105, on Forest Service Rd. 172, *Peng et al. 3798* (1, MO). Lee Co., ca. 1.5 mi. NW of jct. of Deep & Haw rivers, *Beard 745* (1, NCU). Lenoir Co., near Savannah, 2 mi. W of Deep Run, *Radford 31671* (1, NCU). Martin Co., 2 mi. W of Hamilton on NC Hwy. 125, *Duke 54182* (1, NCU). Nash Co., 0.8 mi. S of Taylors Cross Roads and 1.3 mi. E of paved road, *Ahles & Bell 16714* (1, CM, NCU). New Hanover Co., 7 mi. N of Sea Breeze, *Bell 16055* (1, NCU). Northhampton Co., 4 mi. NNE of Jackson, Taylor's Mill Pond, *Beal 2758* (1, NCSC). Onslow Co., 5.5 mi. S of Hwy. 41, on Co. Rd. 1003, S of Comfort, *Peng et al. 3790* (1, MO). Pamlico Co., 4 mi. W of Grantsboro, *Duke 54-225* (1, NCU). Pender Co., 5 mi. NE of Burgaw on NC Hwy. 53, *Radford 5045* (1, GA, NCU). Pitt Co., 3 mi. E of Grimesland, near US Hwy. 264, *Fox 3182* (1, FSU, GH, MO, NCSC). Richmond Co., 3.5 mi. NE of Hoffman at Camp Mackall, *Radford 14440* (1, FLAS, NCU). Robeson Co., 3 mi. N of Lumberton, on NC Hwy. 72, *Duke 54157* (1, NCU). Sampson Co., 1.5 mi. S of Co. Rd. 1003 on US Hwy. 421, *Boufford & Wood 18899* (1, CM, MO). Scotland Co., 4.5 mi. S of Wagram, *Kral 19087* (1, VDB). Tyrell Co., 1.5 mi. NW of Columbia, *Radford 42484* (1, NCU). Washington Co., 4.2 mi. ESE of Skinnersville, *Radford 38893* (1, NCU). Wayne Co., Neuse State Park, *Gillespie CP70* (1, NCSC). Wilson Co., 1.5 mi. WSW of Buckhorn crossroads near NC Hwy. 42, *Radford 44401* (1, WCUH). SOUTH CAROLINA: Aiken Co., near Aiken, 1869, *HWR s.n.* (1, US). Allendale Co., 0.4 mi. E of Barton on Co. Rd. 20, *Ahles & Bell 18420* (4, NCU, U). Bamberg Co., 4 mi. SW of Denmark on Co. Rd. 26, *Ahles 37605* (4, NCU). Beaufort Co., Bluffton, 1873, *Mellichaeux s.n.* (1, NY); 2 mi. SSE of jct. of Co. Rd. 43 & US Hwy. 17 on Co. Rd. 43, *Ahles & Bell 18018* (4, NCU). Berkeley Co., 10 mi. NW of Bonneau, *Godfrey & Tryon 1628* (1, GH, NY); 0.7 mi. E of Interstate 26 and US Hwy. 17-A, *Peng 4390* (4, MO). Calhoun Co., 0.5 mi. NE of jct. of Co. rds. 26 & 27 on 26, *Ahles 35400* (4, NCU). Charleston Co., 4.8 mi. E of SC Hwy. 174 on Hwy. 17, E of Osborn, *Peng et al. 3901* (1, MO); 24.5 mi. N of SC Hwy. 41, on US Hwy. 17, *Peng et al. 3903* (4, MO). Chesterfield Co., Montrose near Hwy. 52, *Radford 15762* (1, TENN). Clarendon Co., 3.5 mi. NE of Turbeville, *Radford 28107* (4, NCU). Colleton Co., 1.2 mi. W of Dorchester Co. line, on SC Hwy. 61, *Raven 20462* (4, DS); 1.2 mi. S of Orangeburg-Colleton Co. line by US Hwy. 21, *Bell 4542* (1, C, NCU). Darlington Co., near Boggy Gully Bay, *Sawyer 2569* (1, USCH). Dillon Co., 1.7 mi. NE of Bingham on SC Hwy. 34, *Ahles 37126* (1, NCU). Dorchester Co., 0.3 mi. S of jct. of hwys. 15 & 178 on 15, *Ahles & Haesloop 37816* (4, NCU). Florence Co., NW of Florence Radio Tower, *Bell 10690* (4, NCU). Georgetown Co., Savannah, *Radford 28679* (4, NCU). Hampton Co., 0.8 mi. NNW of Shirley on Co. Rd. 20, *Ahles & Bell 18255* (1, NCU). Horry Co., Myrtle Beach, *Godfrey & Tryon 1161* (1, DUKE, F, GH, MO, NY, TENN, US); along Waccamaw River at the crossing of SC Hwy. 9, *Raven 18721* (4, DS, NCU). Jasper Co., 0.2 mi. N of Co. Rd. S 27-101 on US Hwy. 17, just S of Ridgeland, *Peng et al. 3935* (1, MO). Lee Co., 3 mi. NE of Woodrow near SC Hwy. 441, *Radford 29422* (1, NCU). Lexington Co., 4.5 mi. W of Edmund, Congaree Creek, *Radford 29890* (1, NCU). Marion Co., ca. 15

mi. S of Britton Neck on Co. Rd. 49, *Bell 11005* (1, NCU); 5 mi. S of Britton's Neck, *Kral 19177* (4, VDB). Marlboro Co., 3.5 mi. E of Wallace, *Radford 19085* (1, NCU). Newberry Co., Billy Dreher Island, *Buff 80* (4, USCH). Orangeburg Co., near Eutawville, *Eggleston 5013* (1, GH, NY); Orangeburg, 1900, *s.c., s.n.* (4, US). Saluda Co., 1 mi. E of Ward, Hwy. 23, *Massey & Massey 3005* (1, NCU); 1 mi. WSW of Ward, *Radford 30358* (4, NCU). Sumter Co., 4 mi. S of Scottsville, near US Hwy. 378, *Radford 29575* (1, NCU). Williamsburg Co., 2.3 mi. NW of Greeleyville, near US Hwy. 521, *Radford 28280* (1, GH, NY, VDB). TENNESSEE: Coffee Co., near Tullahoma, *s.c. 4175* (1, GH, NY, US). Cumberland Co., NE of Crossville, Finger Lake, *Norris & Sharp 16183* (1, TENN). Davidson Co., near Nashville, Cumberland River, s.d., *Gattinger s.n.* (1, DS). Franklin Co., ca. 4.5 mi. SE of jct. of TN hwys. 41A & 4420, Highland Rim Forest Experiment Station, *Wofford et al. 50923* (1, TENN). Warren Co., ca. 1.5 mi. N of Morrison, by TENN Hwy. 55 & power station, *Kral 53781* (1, VDB). TEXAS: Anderson Co., floodplain, *Barkley 13576* (2, F, MO, NY, TEX, US). Angelina Co., 0.5 mi. N of Bouton Lake campgrounds, *Mitchell 4003* (2, LL). Aransas Co., Aransas Wildlife Refuge, *Fleetwood 9344* (2, LL). Bastrop Co., Bastrop, *Tharp 1942* (3, TEX, US). Bowie Co., near Buchanan, 1898, *Eggert s.n.* (2, CM, DS, F, MO, NY). Brazoria Co., near Columbia, *Bush 1542* (2, GH, MO, NCU, NY, US). Brazos Co., 8.5 mi. E of College Station on TX Hwy. 6, *Massey 311* (2, NCU, TEX). Chambers Co., 1932, *Tharp s.n.* (2, TEX). Galveston Co., E side of Hwy. 45, Dickinson, *Waller 3030* (2, GH, TAES). Gregg Co., 1939, *York s.n.* (2, TEX). Hardin Co., near Fletcher, *Palmer 10673* (2, DS, MO); NW of Saratoga, *Kral 21084* (4, VDB). Harris Co., near Sheldon, *Reverchon 3837* (2, MO, NY). Henderson Co., ca. 4 mi. S of Athens, along TX Hwy. 175, *Correll & Correll 33944* (2, LL). Jasper Co., 1.5 mi. N of Kirbyville, *Correll 26762* (2, GH, LL). Jefferson Co., W edge of China, between Rt. 90 & R.R., *Correll 36478* (2, LL). Johnson Co., near Buchanan, 1898, *Eggert s.n.* (2, MO). Lamar Co., E of Manchester on Farm Rd. 195, *Correll & Correll 35909* (4, LL). Lavaca Co., Borcher Ranch, ca. 18 mi. SE of Yokum, *Tharp et al. 49176* (2, TEX). Matagorda Co., ca. 5 mi. SW of Wadsworth, *Sharik S73-1585* (4, MO). Montgomery Co., 17 mi. W of Cleveland, *Kral 21039* (2, VDB); Conroe, 1929, *Tharp s.n.* (3, TEX). Morris Co., ca. 1 mi. W of Naples, *Correll 37471* (2, LL). Nacogdoches Co., *Waller 258* (2, DS, TAES, TEX). Newton Co., along Rt. 87 N of jct. with Rt. 253, *Correll 18719* (2, MO, NY, TEX); 1939, *Tharp s.n.* (4, MO). Orange Co., ca. 1 mi. E of Bridge City, *Correll 34257* (2, LL). Red River Co., N of Clarksville, *Lundell 14011* (3, NY, TEX). Rusk Co., 1879, *s.c., s.n.* (2, F, MO). Travis Co., near Austin, 1929, *Whitehouse s.n.* (2, CAS). Tyler Co., ca. 1.5 mi. S of Warren, E of Rt. 69, *Correll 34015* (4, LL). Upshur Co., 3 mi. S of New Diana, *Shinners 18977* (2, SMU). Waller Co., near Hempstead, *Hall 221* (2, NY; 3, F, mixed with 2, GH, MO, NY, mixed with 2, US, mixed with 2). VIRGINIA: Caroline Co., SE of Guinea, *Fernald & Long 9108* (1, GH). Dinwiddie Co., 12 mi. E of McKenny, *Kral 11336* (1, NCU). Henrico Co., 0.25 mi. W of Elko, *Grimes 4187* (1, GH). Nansemond Co., 3 mi. ENE of Suffolk, *Kral 9508* (1, FSU, NCU). Norfolk Co., 0.5 mi. W of Bowers Hill, *Hubricht B2567* (1, MO). Prince George Co., ca. 3 mi. SE of Petersburg, at head of Poo Run, *Fernald & Long 6652* (1, GH, NY). Princess Anne Co., near Cape Henry, *Fernald & Long 4961* (1, GH, NY, US). Southampton Co., SW of Corinth, Whitefield's Millpond, *Fernald et al. 15320* (1, GH, NY, US). Sussex Co., 3 mi. W of Stony Creek, *Howell 20491* (1, NCU). Warwick Co., near Newport News, 1907, *Long & Long s.n.* (1, US).

The variation pattern of *Ludwigia linearis* is highly complicated as a result of a great deal of intergradation among slightly differentiated geographical races. I have classified the varied populations into four categories: 1) the subglabrous morph, 2) the densely strigillose morph, 3) the completely glabrous morph, and 4) the intermediate morph, which is discussed below.

1. *Subglabrous morph.* Stems sparingly minutely strigillose. Cauline leaves glabrous except for the minutely strigillose margin. Sepals 2.3–4 (–4.5) mm long, 1.3–2.4(–3) mm wide, the apex acuminate, minutely scaly strigillose abaxially. Anthers 1.1–1.6 mm long, the filaments 1.3–1.8 (–2.1) mm long. Nectary disc minutely scaly strigillose around margins of the lobes. Style (0.4–)0.7–0.9(–1.2) mm long, glabrous. Stigma (0.6–)1–1.5 mm long. Capsules densely minutely scaly strigillose, 5–8.5(–10) mm long, 2–4(–5) mm thick, sessile or with a constricted, pedicel-like base. Bracteoles 0.4–1.6(–2.5) mm long. Seed surface cells columnar, elongate parallel to the seed length.

The type of *Ludwigia linearis* Walter belongs to this morph. Plants of this sort are distributed along the Atlantic coast from southern New Jersey through Delaware, eastern Maryland, eastern Virginia, eastern halves of North Carolina and South Carolina, and Georgia, to their southern limit in the central Florida peninsula. They extend westward through the panhandle of Florida and across Alabama and southern Mississippi, reaching eastern Louisiana (Washington and St. Tammany parishes only). Northward, they occur throughout the eastern half of Alabama and extend to central Tennessee.

2. *Densely strigillose morph.* Stems and leaves densely minutely strigillose to puberulent in some cases. Sepals 3–5 mm long, 1.5–2.5(–3.5) mm wide, the apex cuspidate or elongate-acuminate, minutely strigillose or puberulent abaxially. Anthers (1.1–)1.3–2 mm long, the filaments (1.2–)1.5–2(–2.2) mm long. Nectary disc minutely scaly strigillose throughout or only surrounding margins of the lobes. Style (0.6–)0.9–1.5 mm long, glabrous to densely strigillose, especially on the lower part. Stigma (1–)1.3–1.9 mm long. Capsules densely minutely strigillose or puberulent, 5–10 (–12) mm long, 3–5.5 mm thick, the base sessile

or with distinct pedicels up to 5 mm long. Bracteoles 0.5–4(–7.5) mm long. Seed surface cells columnar, elongate transversely to the seed length.

Plants of this morph were recognized at varietal rank, *Ludwigia linearis* var. *puberula*, by Engelmann & Gray (1845). They occur most frequently in central and southern Arkansas, western Louisiana, and the eastern half of Texas. Scattered populations, however, occur east of the Mississippi River in eastern Louisiana and southern Mississippi. A single population was found in Dallas County in southcentral Alabama.

In addition to being much more pubescent than plants of the subglabrous morph, plants of the densely strigillose morph are slightly larger in the size of most floral parts. Furthermore, their seed surface cell pattern is different from that of the subglabrous morph. The cells are elongate parallel to the seed length in the subglabrous morph but are elongate transversely to the seed length in the densely strigillose morph.

3. *Completely glabrous morph.* Characters of this morph are exactly the same as those of the densely strigillose morph, except that the former is glabrous throughout. Indeed, many plants of the completely glabrous morph were collected along with those of the densely strigillose morph. Examples are as follows:

U.S.A. ARKANSAS: Prairie Co., low moist areas in rice paddies, P. O. Hazen, *Demaree 37904* (completely glabrous morph: TEX, VDB-22422, VDB-47595; mixed collection of both the completely glabrous morph and the densely strigillose morph: VDB-33725). Lonoke Co., moist low ground, prairie in rice belt, P. O. Carlisle, *Demaree 22327* (mixed collection of completely glabrous morph and the densely strigillose morph: CAS). LOUISIANA: Bossier Parish, 10 mi. S of Plain Dealing, fire lane in young pine–hardwood stand, sandy loam, *Shinners 24488* (completely glabrous morph: NO; densely strigillose morph: SMU). TEXAS: Waller Co., ditches, Hempstead, *Hall 221* (completely glabrous morph: GH, MO; densely strigillose morph: NY; mixed collection: F, NY—2 sheets, US).

In these cases floral and vegetative characters and even the seed surface pattern are exactly the same in the completely glabrous and the densely strigillose individuals. Plants of these two morphs may well differ only by a single allele that controls the expression of pubescence in plants. It is also worth noting that plants of the completely glabrous morph are only found scattered in Arkansas, Louisiana, and Texas, the main distribution range of the densely strigillose populations. Plants of the completely glabrous morph were previously included by Munz (1944, 1965) as a part of the population of the subglabrous morph (as *Ludwigia linearis* var. *linearis*), which is certainly not appropriate, as discussed above.

Similarly, completely glabrous individuals that are apparently single-allele mutants in populations consisting mainly of densely pubescent plants but are otherwise similar morphologically occur in *Ludwigia hirtella* Raf. (sect. *Ludwigia*; Peng, unpublished).

4. *Intermediate morph.* Any plant that is more pubescent than those of the subglabrous morph and less pubescent than the densely strigillose morph is considered "intermediate" here. The pubescence ranges from scattered minutely strigillose on abaxial midvein and/or submarginal veins to sparingly strigillose on both surfaces of the leaves. The capsule wall is minutely strigillose and not scaly strigillose. Floral characters generally fall in the intermediate range of the subglabrous and the densely strigillose morphs. The seed surface cells, mostly elongate transversely to the seed length, are similar to those of the densely strigillose morph. In some cases, however, the seed surface does not have well-defined cells and is difficult to study. At other times, it is clearly intermediate between that of the subglabrous and the densely strigillose morphs.

Plants of the intermediate morph are widely scattered throughout the range of both the subglabrous morph and the densely strigillose/completely glabrous morphs. They are found in two counties in coastal North Carolina, very well represented in the Coastal Plain of South Carolina, scattered in a few counties in Georgia, Florida, and Alabama, and abundant in Mississippi, where the subglabrous and densely strigillose morphs meet. West of the Mississippi River, they are also found as scattered populations in Arkansas, Louisiana, and Texas, the main distribution range of the densely strigillose morph.

Plants designated as "intermediate morph" here represent an artificial assemblage of plants of *Ludwigia linearis* that may have originated from various combinations of somewhat differentiated populations. For example, the intermediate plants east of the Mississippi River often co-occur with subglabrous plants and may represent hybrids and their derivatives between plants of the subglabrous and of the densely strigillose morphs. On the other hand, intermediate plants that grow west of the Mississippi River may represent hybrids and their derivatives between the completely glabrous morph and the densely strigillose morph, as suggested by the following mixed collections:

U.S.A. ARKANSAS: Prairie Co., along 70, E of Carlisle, *Buker in 1956* (mixed collection of one glabrous plant

TABLE 4. Comparison of subglabrous and densely strigillose populations in *Ludwigia linearis*.

Characters	Subglabrous Populations	Densely Strigillose Populations
Leaves	Completely glabrous on both sides but with minutely strigillose margins	Densely minutely strigillose or puberulent on both surfaces
Bracteole length (mm)	0.4–1.6(–2.5)	0.5–4(–7.5)
Sepal		
Apex	Acuminate	Elongate-acuminate or cuspidate
Length (mm)	2.3–4	3–5(–5.6)
Vestiture	Densely minutely scaly-papillose, the hairs 0.02–0.05 mm long, appressed	Densely minutely strigillose, the hairs 0.06–1 mm long, appressed to ascending
Stigma length (mm)	(0.6–)1–1.5	(1–)1.3–1.9
Style	Glabrous	Glabrous to densely minutely strigillose
Seed surface cells	Elongate parallel to the seed length	Elongate transversely to the seed length
Pedicel length (mm)	0–0.4	0–3.5(–5)

and two intermediate plants). LOUISIANA: Winn Parish, infrequent in open area in dry pine forest ca. 3 mi. NW of Atlanta, in sec. 21 T10N R4W, *Allen 7172* (completely glabrous morph: USF; intermediate morph: NCU).

Plants of the subglabrous populations are somewhat distinguishable from the densely strigillose plants (Table 4) and are separable geographically (the boundary is roughly along the Mississippi River). Engelmann & Gray (1845) formally recognized the distinctiveness of the two morphs. However, with the abundant intergradation between the two races of *L. linearis*, as already noted by Engelmann & Gray (1845), ". . . these characters (of *L. linearis* var. *puberula*) gradually shading away into the ordinary *L. linearis*, . . . ," as well as the occurrence of the completely glabrous populations that have further complicated the character combinations of *L. linearis*, I think a discussion of the variation pattern within this species is more useful than recognizing infraspecific taxa.

Ludwigia linearis was reported as naturalized in marshy areas of Japan (Asai, 1970), and this report was taken up by Osada (1976) in his illustrations of the naturalized plants of Japan. However, an examination of Asai's voucher specimen at TI (Japan: Honshu, Mie Pref., Suzuka-shi, Asahigaoka-machi (Shirako-machi), October 9, 1966, *H. Ohta s.n.*) revealed that it actually represents *L. perennis* L. (sect. *Caryophylloidea*), which is widely distributed in the tropics and subtropics of the Old World and ranges north to Taiwan and southeastern China (Raven, 1963).

Ludwigia linearis can readily be recognized by its sublinear leaves, four yellow petals, and elongate-obpyramidal capsules with a shallow, central, longitudinal groove on each side. The only other species in sect. *Microcarpium* with which *L. linearis* might be confused is *L. linifolia*, which also occurs in the Coastal Plain and the Florida peninsula, but much less commonly. These two species are similar in having very narrow leaves, petaliferous flowers, and elongate capsules. My biosystematic study (Peng, 1988) has shown that they differ by at least a reciprocal translocation. A comparison of morphological characteristics in these two related species and *L. stricta*, which is endemic to Cuba, is petaliferous, and has elongate capsules, is summarized in Table 3.

Ludwigia linearis and the unrelated Latin American congener *L. latifolia* are unique in the genus in having conspicuous, transverse parenchymatous septa in the anthers, which divide the sporogenous tissue into packets (Eyde, 1977; Tobe & Raven, 1986). Before the dehiscence of the anther, however, all of these packets fuse and form one continuous area of sporogenous tissue as a result of disintegration of the septa, leaving the conspicuous vestiges of the distintegrated septa on the inner surface of the anther wall (Tobe & Raven, 1986).

Ludwigia linearis is facultatively outcrossing, having four stamens held away from the stigma at early anthesis and arched over, tightly appressed against the unique, elongate stigma a few hours after anthesis.

Ludwigia linearis is usually very floriferous and has the highest seed set per capsule in sect. *Microcarpium*, about 600 seeds per mature capsule.

Ludwigia linearis co-occurs with *L. glandulosa*, *L. lanceolata*, *L. linifolia*, *L. microcarpa*, *L. pilosa*, *L. sphaerocarpa*, and *L. suffruticosa* in the field. Confirmed natural hybrids include *L. linearis* × *L. glandulosa* (two collections) and *L. linearis* × *L. sphaerocarpa* (one collection). In both cases, hybrids are triploid, fertility as to seed and pollen is nearly zero. Ovaries turn yellowish

or pink after anthesis and then abort. One to four petals are often present in most flowers.

4. Ludwigia glandulosa Walter, Fl. Carol. 88. 1788. TYPE: U.S.A. "the Carolinas": s.d., *T. Walter 612* (holotype, BM, Walter Herbarium, p. 66; photograph, MO).

Plants subglabrous. Stems erect, usually well branched, 10–80(–100) cm tall, glabrous to sparingly minutely strigillose on the ridges formed by the decurrent leaf bases, the hairs ca. 0.05–0.1 mm long. Stolons up to 20 cm long, the leaves purplish, narrowly elliptic, 15–35(–55) mm long, 5–12.5(–20) mm wide, attenuate into petioles 3–10 mm long. Cauline leaves narrowly elliptic to sublinear, sometimes elliptic, those on the main stem 30–120 mm long, 3–25 mm wide, those on the branches usually reduced, 8–45 mm long, 2–10 mm wide; leaves glabrous to sparingly minutely strigillose on abaxial veins, the hairs ca. 0.025–0.05 mm long, apex acute to very narrowly acute, margin entire in outline, densely fringed with microscopic, papillose-strigillose hairs, hydathodal glands often visible, base attenuate, sessile or with petioles up to 15 mm long. Stipules reddish purple, ovate-triangular, succulent, ca. 0.15–0.35 mm long, 0.05–0.25 mm wide. Flowers often numerous, congested in leaf axils. Sepals ovate-deltoid, ascending, 1.1–2.3 mm long, 1–1.75 mm wide, glabrous, apex short acuminate or acute, margin entire, fringed with minute strigillose hairs. Petals 0. Anthers 0.3–0.5 mm long; filaments nearly translucent, 0.55–1 mm long. Pollen grains shed as tetrads. Nectary disc greenish, raised ca. 0.25–0.4 mm on top of ovary, 0.6–1.8 mm across, 4-lobed, glabrous. Style pale green, 0.3–0.75 mm long, glabrous. Stigma greenish, subglobose, 0.25–0.5 mm across. Capsules subcylindrical with 4 shallow grooves, each below the midvein of the sepal, 2–7(–9) mm long, 1.3–2(–3) mm thick, glabrous to minutely papillose-strigillose, the hairs 0.02–0.05 mm long, sessile or with pedicels up to 0.35 (–0.5) mm long, well spaced on main stems and primary branches, often congested on short secondary or tertiary branches. Bracteoles flanking capsule base or attached up to 2.1 mm above capsule base, rarely on the short pedicel, lance-linear or linear, 0.35–1 mm long, 0.1–0.35 mm wide. Seeds light brown, kidney-shaped, the ends slightly pointed, ca. 0.5–0.75 mm long, 0.25–0.4 mm thick, surface cells columnar, elongate either parallel or transversely to the seed length. Self-compatible. Gametic chromosome number, $n = 16$.

KEY TO THE SUBSPECIES OF *LUDWIGIA GLANDULOSA*

Capsules (4–)5–8(–9) mm long; seed surface cells elongate parallel to seed length ..... a. subsp. *glandulosa*

Capsules 2–4 mm long; seed surface cells elongate transversely to seed length ..... b. subsp. *brachycarpa*

The two entities here regarded as subspecies of *Ludwigia glandulosa* were first recognized as distinct by Torrey & Gray (1838–1840). *Ludwigia glandulosa* subsp. *brachycarpa* differs from subsp. *glandulosa* in its smaller stature, narrower leaves, and smaller flowers and capsules. Furthermore, the seed surface pattern of these two entities—a feature that is often diagnostic in *Ludwigia* sect. *Microcarpium*—is sharply distinct, as given in the key.

Ludwigia glandulosa subsp. *glandulosa* is very common and widespread throughout the Atlantic and Gulf coastal plains and the Mississippi Embayment, westward to eastern Texas and southeastern Oklahoma. Subspecies *brachycarpa* ranges just on the western edge of that of the subsp. *glandulosa* in northern Texas and Oklahoma. It grows in the same area as subsp. *glandulosa* throughout much of its range but extends farther south and west. The general distinctiveness of these two subspecies, without doubt, is maintained by their modal autogamy; vegetative reproduction by means of stolons may likewise play a role in preserving favored genotypes.

4a. Ludwigia glandulosa Walter subsp. **glandulosa.** Figure 41.

Jussiaea brachycarpa Lam., Encycl. 3: 331. 1789. TYPE: U.S.A. South Carolina: s.d., *J. Fraser s.n.* (holotype, P, photograph, MO).

Ludwigia heterophylla Poiret in Lam., Encycl. Suppl. 3: 512. 1814. TYPE: U.S.A. "the Carolinas": 1798–1800, *L. A. G. Bosc s.n.* (holotype, P).

Ludwigia cylindrica Elliott, Sketch Bot. S.C. & Ga. 1: 213. 1817. TYPE: U.S.A. South Carolina: Beaufort Co., Burton's Hill, near Beaufort, Aug.–Sept., s.d., *W. Baldwin s.n.* (holotype, CHARL; isotypes, GH, MO, NY; possible isotype, PH).

Stems often reddish, (20–)40–80(–100) cm tall. Cauline leaves elliptic to very narrowly elliptic, those on main stem 32–120 mm long, 4–21 mm wide, those on the branches much smaller, 10–45 mm long, 3–10 mm wide, petioles 1–15 mm long. Sepals ovate-deltoid, the apex acuminate, 1.25–2.3 mm long, 1.15–1.7 mm wide. Petals 0. Anthers 0.3–0.5 mm long; filaments 0.55–1 mm long. Pollen grains shed as tetrads. Nectary disc glabrous. Style 0.3–0.5 mm long; stigma 0.35–0.5 mm across. Capsules (4–)5–8(–9) mm long, 1.6–2(–3) mm thick, sessile or with pedicels up to

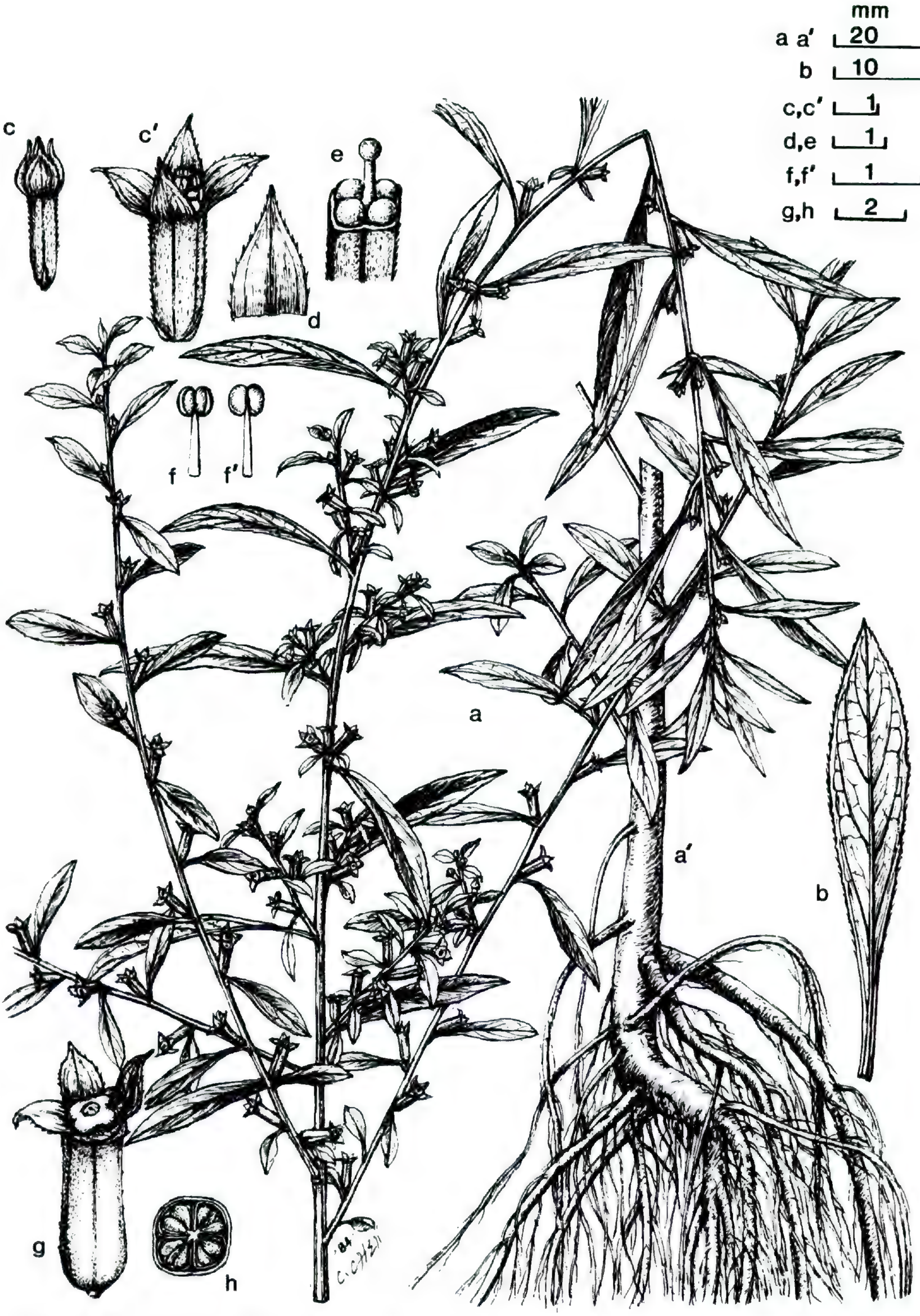

FIGURE 41. *Ludwigia glandulosa* subsp. *glandulosa* (Virginia: Southampton Co., *Fernald & Long 9109*, GH).—a. Habit, upper stem.—a′. Lower stem.—b. Leaf.—c. Flower bud.—c′. Flower.—d. Sepal.—e. Partly dissected flower.—f, f′. Adaxial and abaxial views of stamen.—g. Capsule.—h. Cross section of capsule.

0.35(–0.5) mm long. Bracteoles flanking capsule base or attached up to 2.1 mm above capsule base, rarely on the short pedicel, 0.5–1 mm long, 0.15–0.35 mm wide. Seeds 0.5–0.7 mm long, 0.25–0.35 mm thick, the surface cells oblong, elongate parallel to the seed length. Self-compatible. Gametic chromosome number, $n = 16$.

Distribution. Plants of *L. glandulosa* subsp. *glandulosa* are commonly found in roadside ditches, marshes, pond borders, wet meadows, swales, alluvial floodplains, peaty bogs, moist pinelands, swampy woodlands, and occasionally on waste ground. *Ludwigia glandulosa* subsp. *glandulosa* occurs throughout the Coastal Plain from extreme southeastern Virginia southward through eastern North Carolina, South Carolina, south and central Georgia to the panhandle of Florida and westward across southern Alabama, Mississippi, and Louisiana, reaching its western limit in eastern Texas. To the north, this subspecies extends through extreme southeastern Oklahoma, south and central Arkansas, and up the lower Mississippi basin to southeastern Missouri, central and eastern Tennessee, extreme western Kentucky, southernmost Illinois, and southwestern Indiana. Disjunct populations of *L. glandulosa* subsp. *glandulosa* are found in northcentral Missouri (Fig. 43). Flowering from June to September; fruiting from June to October.

Representative specimens examined. U.S.A. ALABAMA: Autauga Co., near Pratville, 1880, *Mohr s.n.* (US). Baldwin Co., 5.2 mi. N of Spanish Fort, by AL Hwy. 225, *Kral 37447* (VDB). Barbour Co., ca. 5 mi. N of Eufaula, on AL Hwy. 165, *Kral 33190* (C, FSU, VDB). Colbert Co., near Littleville, along US Hwy. 43, *Kral 44012* (VDB). Dale Co., near Clayhatchee, *Kral 22078* (VDB). Dallas Co., at mi. 161 of Alabama River, in Miller's Ferry Reservoir, *Wiersema 401* (UNA). Escambia Co., W of Conecuh River by US Hwy. 29, 4.6 mi. E of Boykin, *Kral 44816* (VDB). Geneva Co., NE side of Geneva by Choctawatchee River, *Kral 31911* (FSU, VDB). Greene Co., ca. 1 mi. E of Gainesville, *Harper 4524* (GA, GH, MO, NCU, UNA, WCUH). Houston Co., ca. 6 mi. S of Cottonwood, Spring Creek, *Kral 40043* (VDB). Lee Co., Uchee Creek Pond, 20 mi. S of Auburn on AL Hwy. 37, 1959, *Johnson s.n.* (NCU). Lowndes Co., ca. 1 mi. S of Ft. Deposit, *Kral 40910* (VDB). Macon Co., 19 mi. W of Tuskegee, near US Hwy. 80, *Raven 18562* (DS). Marengo Co., ca. 11 mi. S of Linden along Beaver Creek, *Haynes 6750* (UNA). Mobile Co., *Curtiss 6503* (DS, MO, NY, US). Monroe Co., 3 mi. E of Chrysler on AL Hwy. 59, Shome Creek, *Kral 40948* (VDB). Montgomery Co., 2 mi. N of Montgomery near Tyler-Goodwin Bridge on Alabama River, *Justice & Isely 137* (US). Morgan Co., E of Decatur on AL Hwy. 67, *Kral 36436* (VDB). Perry Co., W of Sprott on Hwy. 183, Cahaba River, *Davenport 779* (UNA). Russell Co., ca. 1 mi. S of Rutherford, *Clark 16208* (NCU). Tuscaloosa Co., 1878, *Vasey s.n.* (F, NY). Wilcox Co., 0.5 mi. E of Camden, 1958, *Williams s.n.* (FSU). ARKANSAS: Ashley Co., near Wilmot, *Demaree 70209* (MO). Calhoun Co., near Thornton, *Demaree 36618* (DS). Clark Co., near Arkadelphia, *Palmer 8069* (CAS, MO, NY). Clay Co., near Corning, *Palmer 6082* (DS, POM, US). Cleveland Co., near Kingsland, *Demaree 23304* (MO, SMU). Columbia Co., near Magnolia, *Demaree 39191* (FSU, GH, NCU, SMU). Conway Co., near Petit Jean Mountain, *Moore 811* (SMU, TENN). Craighead Co., near Lake City, St. Francis River, *Demaree 7076* (F, GH, ND, SMU, TEX, US). Desha Co., near Dumas, *Demaree 48844* (DS, NO, SMU). Drew Co., near Wilmar, *Demaree 66828* (MO). Garland Co., on Big Island in Lake Hamilton, *Demaree 39457* (CAS, SMU, VDB). Grant Co., near Sheridan, *Demaree 19467* (MO, NY, POM, SMU). Greene Co., near Paragould, 1893, *Eggert s.n.* (CM, F, MO, NY, TEX, US). Hempstead Co., near Chidestar, *Demaree 46023* (DS, NCU, SMU). Hot Spring Co., 1896, *Eggert s.n.* (MO). Lee Co., SE of Haynes, S of Clay Hill, *McDaniel 837* (GA). Lonoke Co., near Carlisle, *Demaree 56843* (DS, SMU). Monroe Co., near Holly Grove, *Demaree 37423* (GH, NCU, SMU). Ouachita Co., near Chidester, *Demaree 69674* (MO). Perry Co., near Plainview, *Demaree 46649* (DS, NCU, SMU). Pike Co., near Diamond Mine, *Demaree 51410* (DS). Prairie Co., near Hazen, *Demaree 15457* (DS, MO, NY, SMU). Pulaski Co., near Little Rock, 1885, *Hasse s.n.* (CM, NY). St. Francis Co., 2.5 mi. NE of Madison, upper end of Keithley Lake, *McDaniel 9730* (FSU, MO). Sebastian Co., Massard Prairie, *Armstrong 193* (TEX). Yell Co., near Plainview, *Demaree 46645* (DS, NCU, VDB). FLORIDA: Escambia Co., near Hwy. 4 on Escambia River, *Redfearn & Kral 2777* (FSU, GH). Gadsden Co., River Junction, *Nash 2390* (F, GH, MO, MSC, NCU, ND, NY, US). Gulf Co., near Iola, 1896, *s.c., s.n.* (US). Hamilton Co., ca. 2 mi. S of Genoa, 1946, *Arnold & West s.n.* (US). Holmes Co., 0.5 mi. E of Westville, *Kral & Redfearn 2836* (FSU, GH, NCU). Jackson Co., N of Sneads, Lake Seminole, *Godfrey & Houk 61400* (FSU, SMU, US). Jefferson Co., 3.9 mi. S of Lloyd on FL Hwy. 59, *Raven 18617* (DS). Leon Co., 2 mi. E of Tallahassee, *Godfrey 55604* (FSU, GA, GH, NY, USF). Liberty Co., W side of Ochlockonee River, *Morar 7* (SMU, TEX, VDB). Madison Co., 6.8 mi. W of Greenville on US Hwy. 90, *Raven 18628* (DS). Okaloosa Co., Yellow River by FL Hwy. 2, E of Oak Grove, *Godfrey 75429* (FSU). Santa Rosa Co., 1 mi. E of Milton on US Hwy. 90, *Dille & Dille 412* (MO). Taylor Co., N of Shady Grove, *Godfrey & Kral 54954* (FSU, GH, NY, USF). Wakulla Co., 5 mi. N of Crawfordsville, *Kral 3006* (FSU, GH). Walton Co., at Mossy Head, *Godfrey 55243* (FLAS, GA, GH, NY, SMU, TENN, UNA, USF). GEORGIA: Bibb Co., Ocmulgee River, SE of Macon, 1965, *Welch s.n.* (GA). Bryan Co., on US Hwy. 17, 0.5 mi. SW of GA Hwy. I-95, *Dille & Dille 351* (MO). Camden Co., 2 mi. S of Woodbine, on GA Hwy. I-95, *Dille & Dille 355* (MO). Chatham Co., 12.5 mi. W25°S of Savannah City Hall, *Duncan 21152* (NCU, SMU, US). Decatur Co., Lake Seminole, *Adams 260A* (FSU, NCU, SMU). Dougherty Co., 8 mi. W of Albany, Miller Slough, *Thorne 6758* (GH). Emanuel Co., 0.8 mi. S of Interstate Hwy. 16, on US Hwy. 1, *Peng 4013* (MO). Evans Co., 1 mi. S of jct. of GA Hwy. 169 & US hwys. 25 & 301, on US hwys. 25 & 301, *Peng 4103* (MO). Grady Co., 9.5 mi. SE of Cairo, *Kral 15174* (VDB). Jeff Davis Co., NW of Appling Co. line along Co. Rd., Bullard Creek, *Bozeman 9550* (NCU). Long Co., 4.2 mi. SW of jct. of US hwys. 301 & 25 & GA Hwy. 99, on US hwys. 301 & 25, *Peng*

4119 (MO). Lowndes Co., E side of Nevins Hall, Valdosta State College, *Faircloth 4723* (NCU). McDuffie Co., Bowden's Pond, 11.75 mi. S31°E of Thomson, 1.5 mi. SSE of Arrington Mill, *Duncan 11522* (GA, MO, SMU). McIntosh Co., 3.2 mi. NW of jct. of Cox Rd. & Hwy. 251, on Cox Rd., *Peng 4139* (MO). Screven Co., near Murray Hill, 1907, *Cuthbert s.n.* (FLAS). Seminole Co., paved Co. rd. between Desser & Reynoldsville, *Jones et al. 23645* (GA). Sumter Co., Muckalee Creek, Americus, 1897, *Harper s.n.* (GH, NY). Tattnall Co., Altamaha River, 2 mi. NE of Lane's Bridge, GA Hwy. 169, *Bozeman 5912* (NCU). Thomas Co., Tall Timbers Research, *Godfrey 77177* (FSU). Twiggs Co., Ocumulgee River along GA Hwy. 96, *Bozeman 7539* (NCU). Walton Co., Mossy Head, *Godfrey 55243* (S). Wilkes Co., 7.9 mi. N58°W of Tignal, *Fitzgerald 358* (GA). Worth Co., 5 mi. W of Sylvester, *Thorne 6331* (GA). ILLINOIS: Massac Co., Mermet Lake, SW of Mermet, *Evers 85808* (DS, MO). Pulaski Co., along Cache River, W of Pulaski, *Bailey & Swayne 2710* (NCU). INDIANA: Posey Co., SW corner of Sect. 32 of Point Tp., ca. 10 mi. SW of Mt. Vernon, *Deam 37699* (GH, NY, US). KENTUCKY: Calloway Co., near Backusburg, on W fork of Clarks River, *Athey 2471* (NCU, NY, VDB). Fulton Co., near Hickman, along KY Hwy. 1282, 0.7 mi. E of jct. of KY Hwy. 94, *Athey 2060* (NCU, NY). Graves Co., along KY Hwy. 339, Obion Creek bottoms, *Browne et al. 73E7.8* (NCU, NY). Marshall Co., along KY Hwy. 1523, 0.5 mi. from jct. with US Hwy. 62, *Athey 1132* (NCU, NY). McCracken Co., Pool Road, *Athey 1117* (NCU, NY). LOUISIANA: Acadia Parish, 5 mi. S of Eunice, *Kral 17195* (VDB). Allen Parish, 7.2 mi. W of Kinder, *Shinners 21504* (SMU). Beauregard Parish, 1–1.5 mi. S of Bayou Amacoco, *Ewan 20106* (DS, NO). Bienville Parish, along US Hwy. 20 at Leaterman Creek, W of Gibsland, Sect. 10, T18N, R7E, *Thomas et al. 5209* (SMU, TENN). Bossier Parish, along Clear Lake, S of Eastgate Road, *Balogh 552* (NCU). Calcasieu Parish, 2.5 mi. SW of Starks, *Shinners 25084* (SMU). Caldwell Parish, 3 mi. SW of Grayson, *Shinners 21917* (SMU). Catahoula Parish, 3 mi. W of Harrisonburg, International Paper Co. forest, *Thomas et al. 3979* (DS). DeSoto Parish, 11 mi. W-SW of Mansfield, *Shinners 20349* (SMU). East Feliciana Parish, MacManus RR station, E of Jackson, *Ewan 18772* (NO). Franklin Parish, Winnsboro, Civitan Park, *Thieret 30050* (A, B, FLAS, GA, NCU, SMU, TEX, VDB). Iberia Parish, old air base, New Iberia, *Thieret 31371* (DUKE, FSU, GA, SMU, TEX). Iberville Parish, in woods, 1881, *Langlois s.n.* (NY). Jefferson Parish, 5 mi. S of Marrero, LaFitte Road, *Ewan 17757* (DS, GH, NO, NY). Lafayette Parish, 1 mi. N of Lafayette, *Correll & Correll 9436* (DUKE, GH, NY). Lincoln Parish, 4.5 mi. E of Ruston, *Kral 15736* (VDB). Livingston Parish, Denham Springs, 0.5 mi. N of Range Ave. & US Hwy. 12, *Montz 2253* (NO). Morehouse Parish, ca. 4 mi. NE of Beekman, Sect. 26, T23N, R6E, *Vincent 456* (DUKE, USF). Natchitoches Parish, ca. 1 mi. W of Clarence, along Red River, *Thieret 30247* (DS, DUKE, FLAS). Orleans Parish, near New Orleans, 1836, *Arnott s.n.* (P). Quachita Parish, 3 mi. SW of West Monroe, *Kral 8094* (FSU). Rapides Parish, vicinity of Alexandria, *Ball 640* (F, GH, MO, NY, US). Richland Parish, ca. 1 mi. S of Mangham along LA Hwy. 15, *Vincent 499* (FSU, USF). Sabine Parish, near bridge across Sabine River to TX Hwy. 21, *Demaree 48220* (DS, NO, SMU, VDB). St. Charles Parish, Bonnet Carre Spillway near river road at westguide levee, *Montz 2929* (NO). St. Landry Parish, ca. 4 mi. NW of Grand Coteau, *Thieret 16454* (DS, DUKE, FSU, GA, SMU, VDB). St. Tammany Parish, edge of Pearle River under Interstate Hwy., N of Pearle River, *Raven 18576* (DS, NCU). Tangipahoe Parish, W limits of Hammond, *Raven 22100* (DS). Tensas Parish, ca. 3.5 mi. W of Newellton, along Hwy. to Newlight, *Thieret 23962* (DS, SMU). Terrebonne Parish, near Houma, 1913, *Wurzlow s.n.* (NY). Union Parish, ca. 2.5 mi. S of Lillie off US Hwy. 167, *Vincent 397* (GA). Vermillion Parish, ca. 2 mi. SW of Abbeville, along Vermillion River, *Thieret & Bernard 17863* (DUKE, FSU, SMU, TEX, USF). Vernon Parish, S limits of Leesville on Hwy. 171, *Raven 22088* (DS, NCU). Washington Parish, Mitchell Rd., ca. 3 mi. S of Bogalusa, *Darwin et al. 763* (MO, NO). Webster Parish, 3.5 mi. E of Minden exit on US Hwy. 20, *Kral 27284* (MSU, VDB). West Carroll Parish, 1903, *Moseley s.n.* (US). West Feliciana Parish, 1 mi. NW of Wakefield, *Thieret 24068* (DS). Winn Parish, ca. 2.5 mi. N of Verda, S27, T9N, R3W, *Vincent 166* (DUKE, FLAS, USF). MARYLAND: Somerset Co., Crisfield, 1890, *Holmes s.n.* (MSC, mixed with *L. palustris*). MISSISSIPPI: Adams Co., river floodplain, 9 mi. W-NW of Doloroso, *Jones et al. 13529* (FSU, MISS, NCU). Amite Co., roadside of Longleaf Plantation, ca. 5 mi. S of Liberty, *Jones et al. 19946* (GA, MISS). Bolivar Co., 3.5 mi. W of Duncan on MS Hwy. 444, *Pullen 70420* (MISS). Calhoun Co., 6.9 mi. E of Bruce on MS Hwy. 32, *Pullen 70696* (MISS). Chickasaw Co., 4.7 mi. E of Vardaman on MS Hwy. 8, *Temple 3535* (GA, MISS, NCU). Clarke Co., 3 mi. S of Pachuta, *Ray 5072* (GA, GH, NCU, NY, TENN, USF). Clay Co., Tibbee Creek bottoms, ca. 3.8 mi. S of West Point on US Hwy. 45W, *Pullen 69839* (MISS). Coahoma Co., near Lyon, 1927, *Rhoades s.n.* (F, NY). De Soto Co., open R/W of US Hwy. 55 & adjacent Coldwater River bottoms, ca. 1 mi. N of Tate-De Soto Co. line, *Pullen 70877* (MISS). Forrest Co., Ragland Hills, Leaf River, *Rogers 3810* (MISS, VDB). Franklin Co., edge of Clear Springs Rec. Area, *Jones 10089* (MISS). George Co., banks of Cedar Creek, Agricola P.O., *Demaree 35758* (GH, SMU). Greene Co., along Leaf River on MS Hwy. 98, *Jones & Hudson 8486* (MISS). Hancock Co., along Jordan River S of Kiln, *Jones & Jones 14145* (MISS, TEX). Harrison Co., near Biloxi, *Tracy 6463* (GH, MO, MSU, NCU, NY, US, VINDOB). Holmes Co., ca. 2.5 mi. S of Tchula near open R/W of MS Hwy. 12, *Pullen 70402* (MISS). Humphreys Co., on MS Hwy. 12, 2.6 mi. NW of Holmes–Humphreys county line, *Pullen 69973* (MISS). Jackson Co., Pascagoula airport rd., *Jones & Jones 14941* (GH, MISS, NCU). Jasper Co., 6 mi. via rd. from Enterprise along Souinbuey Creek, *Jones 15162* (MISS, TEX). Jefferson Co., 6 mi. N-NW of Church Hill at base of loess bluffs, *Jones & Noble 10171* (MISS). Jones Co., 6.6 mi. NE of Moselle on MS Hwy. 11, *Raven 18569* (DS, NCU). Kemper Co., power line R/W, 2.9 mi. W of Scooba, Hwy. 16, *Jones 18867* (MISS, TENN). Lauderdale Co., RR tracks S of Lauderdale, *Jones 14995* (GA, MISS, SMU, USF). Leake Co., under power line, ca. 1 mi. N of Pearl River, S of Wiggins on Hwy. 13, *Jones et al. 18127* (MISS). Lincoln Co., 11 mi. W of Brookhaven, *Webster & Wilbur 3296* (GH, NY, SMU, US). Madison Co., 14 mi. SE of Canton at Ross Barnett Reservoir, *Jones 19454* (MISS). Monroe Co., ca. 3.5 mi. W of Amory, vicinity of Tombigbee River bridge on US Hwy. 278, *Pullen 671032* (MISS). Montgomery Co., 5.1 mi. E of Duck Hill on MS Hwy. 404, *Pullen 701013* (MISS). Neshoba Co., 5.1 mi. NW of Choctaw Indian Reservation, W of Philadelphia on MS

Hwy. 16, *Temple 11996* (MISS). Panola Co., 2.4 mi. W of Tallahatchie River bridge on MS Hwy. 6, *Temple 5893* (GA). Pearl River Co., 2 mi. W of Picayune, *Sargent 10226* (CAS, MO). Pike Co., 5 mi. SW of McComb, Percy Quin State Park, *Jones & Jones 19523* (MISS, VDB). Prentiss Co., 3.7 mi. E of Baldwyn on S side of MS Hwy. 366, *Temple 6212* (GA, MISS). Quitman Co., 3.5 mi. N of Tallahatchie–Quitman county line on MS Hwy. 3, *Pullen 641453* (GA, MISS). Rankin Co., ca. 3 mi. SE of Johns on MS Hwy. 18, *Temple 11960* (GA, MISS). Scott Co., edge of lake, Raworth Recreation Area, between Morton and Forest, *Jones et al. 17874* (FLAS, MISS). Sharkey Co., ca. 7 mi. W of Holly Bluff in Delta National Forest, *Pullen 691196* (MISS). Simpson Co., 2 mi. N of D'Lo on MS Hwy. 49, *Jones 14065* (MISS, VDB). Smith Co., 5.1 mi. S of Pulaski and N of Trenton on MS Hwy. 481 at stream, *Jones 19151* (MISS, SMU). Tishomingo Co., MS Hwy. 72 at Yellow Creek, *Coleman 48529* (TENN). Union Co., 5.7 mi. SE of Etta on county rd., around creek bridge, *Pullen 70842* (MISS). Washington Co., 1 mi. E of Longwood, *Pullen 65302* (MISS, NCU). Wilkinson Co., 8.4 mi. SW of MS Hwy. 33 near Crosby on MS Hwy. 563, *Temple 12148* (MISS). Winston Co., Nanih Waiya St. Pk., S-SE of Louisville, *Jones et al. 18231* (MISS, VDB). Yazoo Co., 3.5 mi. NW of jct. US Hwy. 49E on MS Hwy. 3, *Temple 10189* (GA, MISS). MISSOURI: Butler Co., swamps in Blue Spring, 1892, *Eggert s.n.* (MO). Cape Giradeau Co., 3 mi. W of Arbor on Hwy. 25, *Steyermark 64138* (F). Dunklin Co., near Campbell, 1893, *Bush s.n.* (GH, MO, ND, NY). Pemiscot Co., 7 mi. S of Portageville, *Steyermark 9131* (MO). Stoddard Co., woods bordering Swan Pond, T28N, R10E, Sect. 35, 4 mi. S of Advance, *Steyermark 66146* (MO). Sullivan Co., near Paw Paw, *Bush 152* (MO). Wayne Co., 3 mi. SE of Chaonia, T26N, R7E, Sect. 32 & part of 33, *Steyermark 6197* (F, MO). NORTH CAROLINA: Anson Co., Brown's Creek on NC Hwy. 74, W of Wadesboro, *Duke 54-111* (NCU). Beaufort Co., under bridge 300 yds. N of Wynns Service Station on US Hwy. 17, *Duke 54-176* (NCU). Bertie Co., under bridge of Conine Creek on US Hwy. 70 E of Williamston, *Duke 54-261* (NCU). Bladen Co., 2.9 mi. N of Clarkton on road to Bluefield, *Ahles & Leisner 33338* (NCU). Brunswick Co., 4 mi. S of jct. with Hwy. 17 on NC Hwy. 133, *McCrary & Ahles 1227* (NCU). Camden Co., ditch at Belgrade, *Duke 54-247* (NCU). Chatham Co., 7 mi. E of Pittsboro, RR R/W at US Hwy. 64 crossing, *Campbell 1046* (NCU). Chowan Co., 0.6 mi. W of Perquimans–Chowan county line on US Hwy. 17, *Ahles & Duke 47864* (NCU). Columbus Co., 2.3 mi. N of Tabor City on NC Hwy. 410, *Duke 54-91* (NCU). Craven Co., 0.8 mi. N of Hwy. 17 on Co. Rd. 1224 (rd. to Tuscarora), *Peng 3739* (MO). Cumberland Co., 1 mi. N of Beard, the 0.4 mi. W-NW, *Ahles & Leisner 33545* (NCU). Durham Co., jct. of Co. Rd. 1242 (Biscayne Rd.) and NC Hwy. 54, along New Hope Creek, *Boufford & Wood 18861* (MO). Edgecombe Co., beside Swift Creek on Hwy. 85, *Duke 54-71* (NCU). Gates Co., 1 mi. NE of Chowan River on NC Hwy. 158, *Beal 2132* (NCSC). Greene Co., 4 mi. W of Farmville on US Hwy. 70, *Duke 54-168* (NCU). Harnett Co., Byrd's Mill Pond, S of Bunn Level on NC Hwy. 15a, *Duke 54-149* (NCU). Hertford Co., 1.1 mi. NE of Como then 1.9 mi. E-NE on dirt rd., *Ahles & Duke 45982* (NCU). Hyde Co., 0.5 mi. N of Scranton Creek, on US Hwy. 264, *Duke 54-280* (NCU). Johnston Co., Neuse River, 3 mi. N-NE of Cox Mill, *Radford 27789* (NCU). Jones Co., 0.4 mi. W of Co. Rd. 1105 (Catfish Rd.) on Forest Service Rd. 172 (Murey Branch Rd.), E-SE of Maysville off NC Hwy. 58, *Peng et al. 3801* (MO). Lee Co., 2 mi. NW of Sanford along Big Buffalo Creek, *Houck 359* (NCU). Martin Co., 2.3 mi. SW of Robersonville, *Radford 39396* (NCU). Nash Co., near Moccasin Creek and US Hwy. 264 W of Middlesex, *Radford 44350* (NCU, US). Northampton Co., 1 mi. W of Margarettsville, then 0.3 mi. S, *Ahles & Haesloop 52529* (NCU). Pamlico Co., 5 mi. W of Grantsboro on NC Hwy. 55, *Duke 54-227* (NCU). Pasquotank Co., 1.5 mi. N of Nixonton by Halls Creek, *Ahles & Duke 51239* (NCU). Pender Co., 4 mi. W of Montague on Black River, *Radford et al. 7388* (NCU). Perquimans Co., 2 mi. E-NE of Chowan–Perquimans county line, *Ahles & Duke 48002* (NCU). Pitt Co., 2 mi. E of Pactolus near NC Hwy. 33, *Radford 39717* (TEX). Robeson Co., 4.7 mi. S of Fairmont on NC Hwy. 41, *Duke 54-143* (NCU). Rowan Co., 0.1 mi. N of Stanly–Rowan county line, *Ahles & Haesloop 57224* (NCU). Stanly Co., 3 mi. E of Richfield on NC Hwy. 49, *Duke 54-103* (NCU). Union Co., 3.5 mi. E of New Salem, *Ahles 34111* (NCU). Wake Co., 6.5 mi. S of Raleigh Yates Pond, *Beal 1837* (NCSC). Washington Co., 3.2 mi. NW of Creswell, *Radford 38902* (NCU). Wilson Co., 4.6 mi. W of Wilson, *Radford 40791* (NCU). OKLAHOMA: Atoka Co., 3.5 mi. SW of Atoka, *Cory 56815* (SMU). Choctaw Co., near Hugo, *Palmer 8348* (CAS, MO, NY, US). LeFlore Co., near Page at pond margin, *Stevens 2626* (DS, GH, MO, NY, US). Marshall Co., 2.5 mi. SE of Enos, Happy Hollow, near Lake Texoma, *Goodman 6696* (RSA, TEX). McCurtain Co., 3 mi. S and 1 mi. E of Eagletown, *Taxodium* swamp, *Waterfall 10406* (SMU). Sequoyah Co., 0.5 mi. SE of Blackgum on OK Hwy. 100, *Wallis 5565* (SMU). SOUTH CAROLINA: Aiken Co., North Augusta, near Savannah River, *Ahles & Crutchfield 55638* (NCU). Allendale Co., Coosawhatchie River, 3.4 mi. SE of Fairfax on County Hwy. 21, *Bell 5064* (NCU, USCH). Bamberg Co., Salkehatchie River on US Hwy. 321-301, NE side of river, *Ahles & Haesloop 30547* (NCU). Beaufort Co., 1.9 mi. W of Co. Hwy. 111 on Co. Hwy. 33, *Bell 3759* (NCU, U). Berkeley Co., Santee River, 3 mi. NE of Pineville, *Godfrey & Tryon 644* (CAS, DUKE, F, GH, MO, NY, TENN, US). Charleston Co., 24.5 mi. N of SC Hwy. 17, vicinity of Buck Hill Recreation Area, S of McClellenville, *Peng et al. 3896* (MO). Cherokee Co., 0.7 mi. S of US Hwy. 29A on dirt road along Broad River, *Ahles & Haesloop 31925* (NCU). Chesterfield Co., 1 mi. W of McBee in the Sandhills, *Godfrey 8025* (F, GH, MO, NY, TENN, US). Clarendon Co., NE shore of Lake Marion, ca. 4.5 mi. SW of St. Paul, off US Hwy. 15, *Bradley & Sears 3561* (MEXU, MISS). Colleton Co., 1.2 mi. W of Dorchester county line on SC Hwy. 61, *Raven 20461* (DS). Darlington Co., damp flats, *Smith 2001* (NCU). Dillon Co., Sweat Swamp, ca. 3 mi. N of Little Rock on Co. Hwy. 192, *Ahles & Leisner 32234* (NCU). Dorchester Co., 0.4 mi. N of Reevesville on Co. Hwy. 16, *Ahles & Leisner 31905* (NCU). Georgetown Co., 2.8 mi. NE of Yauhannah, Pee Dee River near US Hwy. 701, *Radford 28609* (NCU). Greenwood Co., 1.5 mi. N of Ninety Six, Wilson Creek near SC Hwy. 246, *Radford 26581* (NCU). Hampton Co., 0.8 mi. N-NW of Shirley on Co. Hwy. 20, *Ahles & Bell 18249* (NCU). Horry Co., along Waccamaw River at crossing of SC Hwy. 9, *Raven 18724* (DS, NCU). Jasper Co., roadside ditch at S end of Ridgeland, *Raven 18715* (DS, NCU). Kershaw Co., 8 mi. NW of Camden on Wateree River, *Radford 27668* (NCU). Marlboro Co., 9 mi. SW of Bennettsville, Pee Dee River, near US Hwy.

52, *Radford 15477* (CM, FLAS, NCU, SMU). McCormick Co., 6 mi. SE of Clarks Hill, Savannah River near SC Hwy. 28, *Radford 30647* (NCU, VDB). Orangeburg Co., 3.9 mi. S-SE of Eutawville on Co. Hwy. 104 along Sandy Run, *Ahles 35003* (NCU). Richland Co., 15 mi. below Columbia along Congaree River, 1965, *Batson s.n.* (USCH). Saluda Co., near US Hwy. 178 at Mayson, *Radford 26906* (NCU). Sumter Co., 4 mi. E-NE of Shiloh, Jordon Swamp, *Radford 27500* (FSU, NCU). TENNESSEE: Carroll Co., edge of cat-tail pool, *Svenson 4385* (GH). Crockett Co., Cypress Creek N of Bells, *Sharp & Clebsch 6754* (TENN). Franklin Co., near Huntland, *Svenson 10403* (GH). Grundy Co., N of Mt. View, *Godfrey 69774* (FSU, NCU). Hardeman Co., N of Middleburg, *Sharp & Clebsch 8208* (TENN). Henderson Co., Beech River SW of Chesterfield, *Sharp et al. 9289* (TENN). Lake Co., Reelfoot Lake, 1924, *Jennings & Jennings s.n.* (CM). Montgomery Co., 1.5 mi. NW Sadlersville by US Hwy. 41, *Kral 48384* (VDB). Obion Co., near Bayoudechien, Walnut Log, *Sharp & Clebsch 6207* (TENN). Shelby Co., McKellar Lake, Ensley Engineer yard, *Rogers 34826* (TENN). White Co., 9 mi. N of Sparta, swamp S of Cookeville, *Norris & Sharp 16241* (TENN). TEXAS: Angelina Co., near Redland, *Lewis & Oliver 5245* (DH). Bastrop Co., near Bastrop, *Tharp 224* (GH, NY, TEX). Bowie Co., near Texarkana, 1894, *Letterman s.n.* (F, MO, NY, TEX, US). Brazoria Co., Cockleburr Slough above bridge on Shell Rd., San Bernard Refuge, *Fleetwood 10159* (SMU). Brazos Co., Fish Lake behind Easterwood Airport, College Station, *Massey 309* (NCU, TAES, TEX). Cass Co., ca. 2.5 mi. SW of McLeod along Frazier Creek, *Correll 30113* (TEX). Fayette Co., near Muldoon, *Ripple 51-914* (TEX). Galveston Co., S edge of Alta Loma, *Correll & Correll 38997* (LL). Gonzales Co., *Bogusch 943* (TEX). Gregg Co., ponds along Sabine River S of Longview on TX Hwy. 149, *Correll & Correll 31856* (TEX). Grimes Co., Navasota Bottoms, 1927, *Parks & Cory s.n.* (TAES). Hardin Co., 16.5 mi. NW of Saratoga, *Kral 21046* (DH, DS, VDB). Harris Co., near Crosby, 1921, *Fisher s.n.* (DH, US). Henderson Co., 9.5 mi. S of Athens, *Shinners 19124* (SMU). Jackson Co., 8 mi. E of Edna, Navidad River floodplain, *Webster & Wilbur 3142* (SMU, US). Jasper Co., near Harrisburg, 1875, *Joor s.n.* (F). Lamar Co., ca. 5 mi. NE of Paris on TX Hwy. 195, *Correll 37518* (TEX). Liberty Co., 5.7 mi. E of Liberty, *Raven 19425* (DH, FLAS, NCU). Limestone Co., 4 mi. SE of Donie on Hwy. 80 & 0.5 mi. E on Hwy. 39, *Lipscomb 3088* (SMU). Marion Co., 9.6 mi. NW of Jefferson, *Shinners 30257* (SMU). Montgomery Co., 4.5 mi. E of Montgomery, 1950, *Henry s.n.* (CM). Nacogdoches Co., *Waller 254* (DH, TAES, TEX). Newton Co., E side of Bon Wier, *Kral 20731* (VDB). Orange Co., along Sabine River near bridge, E of Orange, *Correll 26792* (TEX). Panola Co., 8 mi. NE of Carthage, Sabine River, *Shinners 15656* (SMU, TAES). Polk Co., McCordell Lake, E of TX Hwy. 59, *Nixon et al. 5363* (NCU). Rains Co., 9.2 mi. S of Point, *Van Vleet 678* (SMU). Red River Co., ca. 7.5 mi. N of Clarksville along TX Hwy. 37, *Correll 37495* (NY, TEX). Titus Co., N of Winfield, *McGregor 750* (SMU). Upshur Co., 5 mi. N of Ore City, along Cypress Creek, *Correll 13171* (NY, SMU, TEX). Waller Co., near Hempstead, 1872, *Hall s.n.* (F, GH, NY, US). Wood Co., 4 mi. W of Mineola, *Kral 1239* (FSU). VIRGINIA: Greensville Co., SW of Haleys Bridge, Fontaine Creek, *Fernald et al. 6653* (GH). Nansemond Co., ca. 7 mi. E-NE of Suffolk, *Kral 13765* (FSU, VDB). Norfolk Co., S of North Landing, *Fernald & Long 4076* (GH, NY). Prince George Co., near Gary Church, *Fernald & Long 6307* (GH, NY). Princess Anne Co., near Rosemont, *Fernald & Long 4962* (GH, US). Southampton Co., near bridge over Three Creek, N of Drewryville, 1970, *Churchill s.n.* (MSU). Warwick Co., near Newport News, 1907, *Long & Bartram s.n.* (NY). York Co., E of Tabb's, *Fernald & Long 8787* (GH).

Ludwigia glandulosa is distinctive in being the only tetraploid species in sect. *Microcarpium* with cylindric capsules. The other three species with elongate capsules are the diploid, petaliferous, narrow-leaved *L. linearis*, *L. linifolia*, and *L. stricta*. Raven & Tai (1979) suggested that *L. linearis* is similar to *L. glandulosa* and might be directly related to it. The biosystematic study of Peng (1988), however, demonstrated that the genetic relationship between the diploid *L. linearis* and the tetraploid *L. glandulosa* is not any closer than that between *L. linearis* and other tetraploids. Furthermore, it has been shown that no extant diploids are involved directly in the formation of any tetraploid species in sect. *Microcarpium*.

Ludwigia glandulosa subsp. *glandulosa* is known to occur together with subsp. *brachycarpa*, *L. linearis*, *L. linifolia*, *L. microcarpa*, *L. pilosa*, *L. sphaerocarpa*, and *L. palustris* (sect. *Dantia*) in the field. It has been known to form natural hybrids with all but *L. microcarpa*, an extreme selfer, and the facultatively outcrossing *L. linifolia*. Attempts to synthesize *L. glandulosa* × *L. linifolia* in the experimental greenhouse also failed (Peng, 1988), presumably owing to incompatible genomes. Artificial hybrids between *L. glandulosa* subsp. *glandulosa* and *L. microcarpa*, however, were healthy and floriferous.

Duke (1955) was the first to record a natural hybrid population of *Ludwigia glandulosa* subsp. *glandulosa* × *L. pilosa*, although he did not fully describe the situation he observed. Tetraploid hybrids like this and others are usually fertile and are intermediate in such diagnostic characters as vestiture, sepal and bracteole length, capsule shape and size, seed surface pattern, and whether pollen is shed singly or as tetrads. Triploid natural hybrids involving *L. glandulosa* subsp. *glandulosa* and diploids like *L. linearis* and *L. palustris* may be floriferous but are highly sterile as to pollen and seeds. Their ovaries turn yellowish or pink and dehisce early. *Ludwigia glandulosa* subsp. *glandulosa* (stems erect, leaves alternate) × *L. palustris* (stems prostrate, leaves opposite) generally resembles *L. glandulosa* subsp. *glandulosa* but has slightly broader leaves and smaller flowers. The stems are erect and then prostrate and erect again in some cases; the leaves are alternate like *L.*

glandulosa subsp. *glandulosa*. By contrast, hybrids of *L. glandulosa* subsp. *glandulosa* and *L. linearis* are similar to *L. linearis*, having some yellow petals and narrow leaves. The number of petals on each flower varies from 0 to 4.

4b. Ludwigia glandulosa Walter subsp. **brachycarpa** (Torrey & A. Gray) Peng, Ann. Missouri Bot. Gard. 73: 490. 1986. Based on *L. cylindrica* Elliott β *brachycarpa* Torrey & A. Gray, Fl. N. Am. 1: 524. 1840, non *Jussiaea brachycarpa* Lam., Encycl. 3: 331. 1789. *L. glandulosa* Walter var. *torreyi* Munz, Bull. Torrey Bot. Club 71: 164. 1944, illeg. subst. LECTOTYPE: U.S.A. Texas: Austin Co., San Felipe, "third collection," 1833–1834, *T. Drummond 84* (GH; isolectotypes, GOET, K—2 sheets, W; Peng, Ann. Missouri Bot. Gard. 73: 490. 1986). Figure 42.

Stems sometimes reddish, 10–55(–90) cm tall. Cauline leaves linear-elliptic to linear, sometimes very narrowly elliptic, those on main stem 30–50(–70) mm long, 3–5(–10) mm wide, those on the branches 8–36 mm long, 2–3(–8) mm wide, sessile or with petioles up to 10 mm long. Sepals ovate-deltoid, the apex acute or short acuminate, 1.1–1.9 mm long, 1–1.75 mm wide. Petals 0. Anthers 0.3–0.5 mm long; filaments 0.55–1 mm long. Pollen grains shed as tetrads. Nectary disc obscurely minutely papillose. Style 0.35–0.75 mm long; stigma 0.2–0.35 mm across. Capsules 2–4 mm long, 1.3–2 mm thick, sessile or with pedicels up to 0.15 mm long. Bracteoles flanking capsule base, 0.35–0.75 mm long, 0.1–0.2 mm wide. Seeds 0.55–0.75 mm long, 0.3–0.4 mm thick, the surface cells oblong, elongate parallel to the seed length. Self-compatible. Gametic chromosome number, $n = 16$.

Distribution. Plants of *Ludwigia glandulosa* subsp. *brachycarpa* are usually found along ditches, in low meadows, coastal prairies, seeps in sandy woods, moist sinkholes in granites, and old clay fields. This subspecies occurs along the Gulf coast, from extreme southwestern Louisiana to Nueces County, Texas, and northward through eastern Texas to southcentral Oklahoma (Fig. 43). Flowering and fruiting from April to November.

Representative specimens examined. U.S.A. LOUISIANA: Calcasieu Parish, 1 mi. S of Holmwood, *Ewan 21343* (NO). Cameron Parish, 2 mi. W of jct. of State hwys. 82 & 27, *Peng et al. 4367* (MO). OKLAHOMA: Atoka Co., 6 mi. SE of Lane on OK Hwy. 3, *Massey & Massey 2496* (MO, NCU, SMU). Carter Co., N of Ardmore, *Goodman 5961* (GH, RSA, SMU). Coal Co., 5 mi. SE of Centrahoma on OK Hwy. 3, *Massey 2484* (NCU, SMU). Love Co., 5 mi. SE of Ardmore in Lake Murray State Park, *Crutchfield 3449* (LL). TEXAS: Aransas Co., near Lenoir's Landing, Copano Bay, *Correll & Correll 18905* (GH, LL). Bastrop Co., *Tharpe 870* (TEX). Brazoria Co., Columbia, 1980, *Bush s.n.* (MO, NY). Brazos Co., Fish Lake behind Easterwood Airport, *Massey & Reaux 586* (LL, NCU). Burnet Co., 2 mi. N of Marble Falls, Granite Mt., 1946, *Barkley & Copeland s.n.* (NY). Calhoun Co., Port O'Connor, 1930, *Tharpe s.n.* (TEX). Dallas Co., Dallas, 1877, *Reverchon s.n.* (NY). Denton Co., Lake Dallas Fish Hatchery, *McCart 1894* (NY, TEX). DeWitt Co., western part of county, 1941, *Reidel s.n.* (TEX). Fort Bend Co., 9.1 mi. N of Rosenberg on road to Fulshear, *Raven 19398* (DS, RSA, TEX). Galveston Co., 1942, *Nelson s.n.* (GH, MO, TEX). Gonzales Co., 7 mi. S of Gonzales, *Correll & Johnston 17481* (LL). Harris Co., 200 mi. S of TX Hwy. 59 near jct. with Santa Fe RR, 200 mi. N of Overhead Door Co., *Tranverse 1490* (F, SMU, TEX). Jasper Co., Harrisburg, 1875, *Joor s.n.* (LSU, US). Jefferson Co., on Hwy. 90, 12 mi. W of Beaumont, *Munz & Gregory 23458* (RSA). Lavaca Co., ca. 18 mi. SE of Yoakum, *Tharpe, Rogers & York 49177* (TEX). Limestone Co., ca. 5.5 mi. SE of Donie on 80 across Hwy. 39, *Lipscomb 2908* (SMU). Matagorda Co., near College Port, 1929, *Tharpe s.n.* (TEX). McLennan Co., MKT RR at Gapland crossing, *Smith 863* (TEX). Montague Co., 2 mi. NW of Stoneburg, *Shinners 26622* (SMU). Nueces Co., Mustang Island, ca. 3 mi. S of Port Aransas, *Jones 1837* (SMU). Red River Co., 1.5 mi. S-SW of Bogata, *Shinners 20405* (SMU). Refugio Co., Austwell, 1929, *Tharpe s.n.* (TEX). San Patricio Co., 3 mi. NE of Ingleside, *Jones 932* (SMU). Travis Co., Austin, *Tharpe 870* (TEX, US). Waller Co., Hempstead, *Hall 219* (F, NY, US).

Plants of *Ludwigia glandulosa* subsp. *brachycarpa* occur in the western range of the species and are frequently found in the same county as the typical subspecies, but mixed collections suggesting that they occur side by side are known only in the following: TEXAS: Fort Bend Co., 1 mi. NW of Arcola, water-filled roadside ditch of swampy brushlands, *Raven 19405* (DS, mixed collection of two plants of subsp. *glandulosa* and one plant of subsp. *brachycarpa*; FLAS, subsp. *brachycarpa* only).

Natural hybrid populations between these two subspecies are known in two cases from OKLAHOMA: Atoka Co., ca. 0.25 mi. S of small community of Boehler and SE of Atoka, *Taylor 20332* (VDB), and TEXAS: Galveston Co., ca. 2300 block of Broadway, San Leon, *Waller 3822* (GH). These hybrids are intermediate in stature, leaf shape and size, and (more diagnostically) in fruit size (4–5 mm long) and seed surface (which exhibits a mixture of columnar cells that are elongate, transversely elongate, and sometimes oblique to the seed length).

5. Ludwigia polycarpa Short & Peter, Transylv. J. Med. Assoc. Sci. 8: 581. 1835. *Is-*

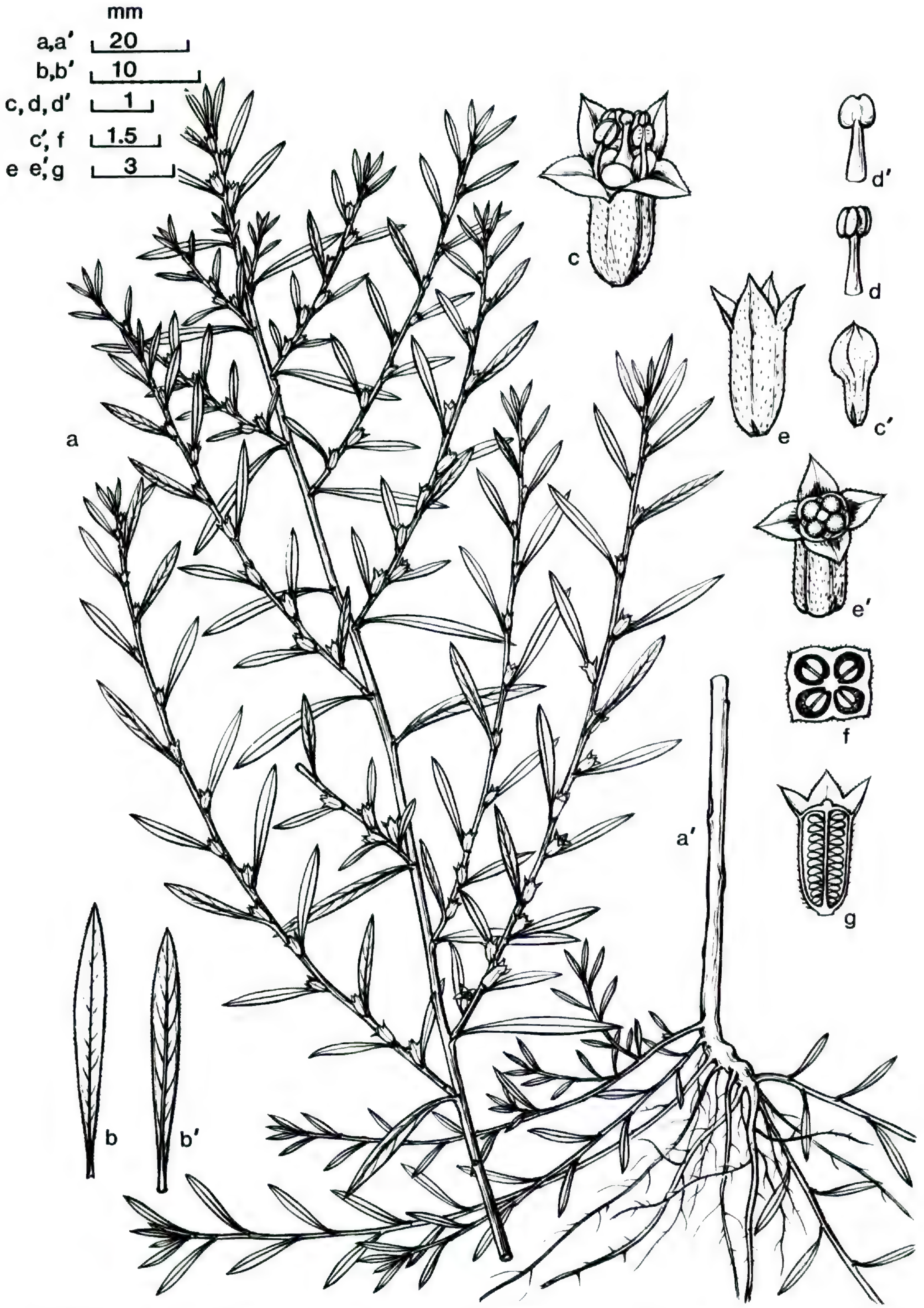

FIGURE 42. *Ludwigia glandulosa* subsp. *brachycarpa* (Louisiana: Cameron Co., *Peng 4367*, MO).—a. Habit, upper portion of erect stem.—a′. Lower stem with stolons.—b, b′. Adaxial and abaxial views of lower leaf.—c. Flower.—c′. Flower bud.—d, d′. Adaxial and abaxial views of stamens.—e. e′. Mature capsule.—f. Cross section of capsule.—g. Longitudinal section of capsule.

FIGURE 43. Distribution of *Ludwigia glandulosa* subsp. *glandulosa* (circles) and *L. glandulosa* subsp. *brachycarpa* (triangles).

nardia polycarpa (Short & Peter) Kuntze, Rev. Gen. Pl. 1: 251. 1891. LECTOTYPE: U.S.A. Kentucky: marshes around Louisville, s.d., *H. A. Griswold s.n.* (PH; isolectotypes, DWC, GH, NY, 2 sheets; lectotype here designated). Figure 44.

Plants glabrous. Stems erect, well branched, (10–)25–60(–85) cm tall, the leaf base decurrent and forming ridges 0.15–0.25 mm broad, these sometimes minutely strigillose; aerenchyma well developed on lower stems when submersed. Stolons short, several from the erect stem base, 2.5–15 (–22) cm long, 1–2.3 mm diam., usually seen only in late flowering season, frequently branching from the nodes; internodes short, leaves often clustered on stolon apex and overlapping, narrowly elliptic or oblanceolate, 7.8–20(–32) mm long, 2.4–8 (–12) mm wide, glabrous, the margin entire or remotely denticulate, papillose-serrulate; petioles 0–5 mm long. Cauline leaves very narrowly oblong-elliptic, 35–110 mm long, 4–10(–17) mm wide, the apex narrowly acute or acuminate, the margin entire, densely minutely papillose-serrulate except for the lowest ⅕, this usually smooth, hydathodal glands obscure, the base very narrowly cuneate or long attenuate into winged petiole 1–10 mm long. Stipules dark purplish, narrowly to broadly ovate, succulent, 0.15–0.35 mm long, 0.1–0.25 mm wide. Flowers many, sessile or nearly so in leaf axils, sometimes borne almost to the base of stems; flower-subtending leaves not reduced. Sepals greenish, triangularly ovate, the apex elongate acuminate, spreading horizontally with reflexed tips, 2.5–4.5 mm long, 1.5–3.2 mm wide, glabrous, the margin entire, minutely papillose-serrulate. Petals 0. Anthers 0.5–0.85 mm long; filaments yellowish green, 0.7–1.5 mm long, the base dilated. Pollen grains

FIGURE 44. *Ludwigia polycarpa* (Massachusetts: Franklin Co., 1949, *Delevoryas s.n.*, DS).—a. Habit, upper portion of stem.—a′. Stem base with newly formed stolons.—b. Leaf.—c. Portion of narrowly ridged branch.—d. Portion of branch with mature capsules.—e. Flower bud.—f. Flower.—f′. Partly dissected flower to show stigma, style, and nectary disc.—g, g′. Adaxial and abaxial views of stamens.—h. Sepal.—i. Bracteole.—j. Capsule.—k. Cross section of capsule.

shed as tetrads. Nectary disc yellowish green, raised 0.5–0.75 mm on ovary top, 1.8–3 mm across, 4-lobed, glabrous. Style yellowish green, 0.5–0.8 mm long, glabrous; stigma greenish yellow, cuboid, 0.4–0.8 mm long, distinctly 4-lobed on the apex. Capsules oblong-obovoid with constricted base, obscurely 4-sided with rounded corners, 4–7 mm long, 2.5–5 mm thick, glabrous to obscurely minutely strigillose; pedicels 0.1–0.3 mm long. Bracteoles flanking the capsules, attached 0.5–2.5(–3) mm from capsule base, linear-lanceolate with a swollen base, 3.5–6.5(–8) mm long, 0.4–1(–1.3) mm wide, the margin minutely papillose-serrulate. Seeds light brown, narrowly oblong with curved ends, 0.5–0.6 mm long, 0.2–0.3 mm wide, the surface cells elongate parallel to the seed length. Self-compatible. Gametic chromosome number, $n = 16$.

Distribution. Plants of *Ludwigia polycarpa* grow in ditches; on moist prairie; on alluvial ground of ponds, lakes, and rivers; in marshes; in swales; along edges of lagoons; and in low fallow fields. Contrary to all other species in sect. *Microcarpium*, *L. polycarpa* is centered primarily in the central Midwest, ranging from southcentral Missouri, eastern Kansas, eastern and northeastern Nebraska, northward and eastward across Iowa and southern Minnesota into central Wisconsin and the Upper Peninsula of Michigan. In the east, this species occurs in extreme southern Ontario and the eastern part of the Lower Peninsula of Michigan. *Ludwigia polycarpa* extends southward through western and southern Ohio, northcentral Kentucky, and western West Virginia. Scattered populations occur in central Virginia, southcentral Pennsylvania, Massachusetts, and Connecticut. A highly disjunct, presumably introduced population has been recorded from Kootenai County, Idaho (Fig. 45). Flowering from June to September; fruiting from July to October.

Representative specimens examined. U.S.A. CONNECTICUT: Hartford Co., *Bissell & Clark 245* (B, C, CAS, CM, DS, F, GA, GH, M, MO, NO, NY, S, TENN, TEX, US, USF, W). IOWA: Appanoose Co., 1896, *Fitzpatrick s.n.* (MO). Black Hawk Co., old creek bed, *Burk 847* (MO). Clinton Co., NW ¼ Sect. 6, Grant twp., *Cooperrider 2899* (NCU). Decatur Co., marshes, 1899, *Fitzpatrick s.n.* (F, MSU, NY). Emmet Co., wet ground, 1884, *Cratty s.n.* (DS). Fayette Co., borders of ponds, 1893, *Fink s.n.* (GH). Johnson Co., N of Homestead, 1924, *Shimek s.n.* (NY). Lee Co., ca. 1.25 mi. W-SW of Ft. Madison, *Davidson et al. 684* (TEX). Louisa Co., *Davidson 4035* (TEX). Palo Alto Co., 5 mi. E of Ruthven in a pond S of the viaduct over Hwy. 18, *Hayden 9416* (GH, MO, NY, US). Polk Co., *Van Bruggen 3152* (NY, SMU). Poweshiek Co., rich slough beside US Hwy. 6, about 1.5 mi. W of Victor, *Russell 815258* (USF). Story Co., Ames, 1877, *Arthur s.n.* (P). Warren Co., 1 mi. NW of Indianola, *Van Bruggen 3105* (?). Washington Co., 3 mi. S of Crawfordsville, *Wagenknecht 874* (F). Webster Co., Fort Dodge, 1904, *Somes s.n.* (NY). IDAHO: Kootenai Co., head of Fernan Lake, Coeur d'Alene, *Rust 1353* (NY, US). ILLINOIS: Adams Co., 1842, *Holtman s.n.* (CM). Champaign Co., near Urbana, *Jones 12683* (NY, SMU). Cook Co., Elk Grove Forest Preserve, *Kral 9384* (FSU, NCU, VDB). DuPage Co., W of Lacey road near the Milton–Lisle Township line NE of Lisle, *Swink 1828* (F). Gallatin Co., 1 mi. N of Shawneetown, *Evers 85336* (MO). Hancock Co., Augusta, 1847, *Mead s.n.* (F, MO). Henderson Co., Mississippi bottoms near Oquawka, s.d., *Patterson s.n.* (F, MO, US). Iroquois Co., 1888, *Moffatt s.n.* (NY). Lake Co., 5 mi. SW of Waukegan, *Kral 3324* (FSU). Massac Co., Mermet Lake, SW of Mermet, *Evers 85807* (DS). Menard Co., Athens, 1861, *Hall s.n.* (F, NY, GH). Ogle Co., Oregon, 1888, *Waite s.n.* (NY). Piatt Co., 1881, *Seymour s.n.* (USF). Pike Co., NW of Pleasant Hill, *Evers 93796* (NCU). St. Clair Co., vicinity of Kingshighway, *Neill 15378* (NCU, MO). Sangamon Co., Auburn, 1882, *Bigler s.n.* (GH). Stark Co., Wady Petra, *Chase 197* (F, GH, MSU). Will Co., 2 mi. SE of Custer Park, *Steyermark 64838* (F). Winnebago Co., 1858, *Bebb s.n.* (GH, UPS). INDIANA: Blackford Co., 2 mi. W of Mollie on S side of road, *Deam 325* (MO, US). Delaware Co., along NYC RR, ca. 3 mi. W of Yorktown, *Friesner 18365* (SMU, TEX, W). Fayette Co., *Gardner 545* (NY). Howard Co., 4 mi. NW of Kokomo, *EK 22* (US). Jackson Co., about 0.75 mi. S of Chestnut Ridge, *Deam 14039* (NY, S). Lake Co., Whiting, 1893, *Britton s.n.* (NY). Martin Co., old river slough just N of White River and W of road 45, *Tryon 4161* (DUKE). Newton Co., about 5.5 mi. SW of Lake Village, *Deam 56715* (CM, GH). Porter Co., Dune Park, *Lansing 1539* (F). Posey Co., in Scuffle pond, ca. 8 mi. SW of Mt. Vernon, *Kriebel 8378* (ND). Pulaski Co., ditch on Jasper-Pulaski game reserve, 1 mi. W Rd. 43, 1.5 mi. S Rd. 10, *Friesner 16176* (CAS, FLAS, NY). Randolph Co., Clarke, 1897, *Unbach s.n.* (US). Warrick Co., 6 mi. W of Boonville on the bank of Big Pigeon Creek, *Deam 24336* (GH). Wells Co., 1897, *Deam s.n.* (F). KANSAS: Douglas Co., 4 mi. SE Lawrence, *McGregor 15001* (US, NCU, SMU). Jackson Co., marshes, *Clothier 1141* (GH, MO, NY, US). Linn Co., 1 mi. S Boicourt, *Stephens 44334* (NCU). Miami Co., 1883, *Oyster s.n.* (CAS). KENTUCKY: Boone Co., pond about 1,000 ft. inland from Aurora ferry (just opposite Aurora, Indiana) along Hwy. ca. 2 mi. W of Petersburg, along Ohio River, *Thieret 50135* (VDB). Fayette Co., Lexington, *Short s.n.* (NY, GH). MAINE: Franklin Co., E side Pine Hill, Deerfield, *Ahles 64607* (DS, NCU, SMU). Hampshire Co., Hockanum Rd., Northampton, *Ahles 86398* (GA, SP). Middlesex Co., Winter pond, Winchester, *Raven 16514* (MO). MICHIGAN: Genesee Co., Linden Park, 1903, *Farwell s.n.* (DS). Houghton Co., near Houghton, 1916, *Dodge s.n.* (LL). Macomb Co., wet thicket W edge of woods, frequent, *Loughridge 4390* (GH, B). Monroe Co., along Detroit to Toledo RR between Stein and S Otter rds., 1972, *Churchill & Thompson s.n.* (MSU). Oakland Co., Hubbard marsh, 1916, *Chandler s.n.* (MSU, US). St. Clair Co., near Port Huron, 1893, *Dodge s.n.* (SMU, TEX, TENN, S). Tuscola Co., Akron Tp., 1895, *Davis s.n.* (S). Van Buren Co., Marsh Keeler, *Pepoon 619* (MSU). Washtenaw Co., 3 mi. W of Third Sister Lake, *Hermann 8357* (DS, F, MO, NY, US). Wayne Co., ca. 4 mi. out from Detroit, 1851, *Cooley s.n.* (MSU). MINNESOTA: Chisago Co., *Wis-*

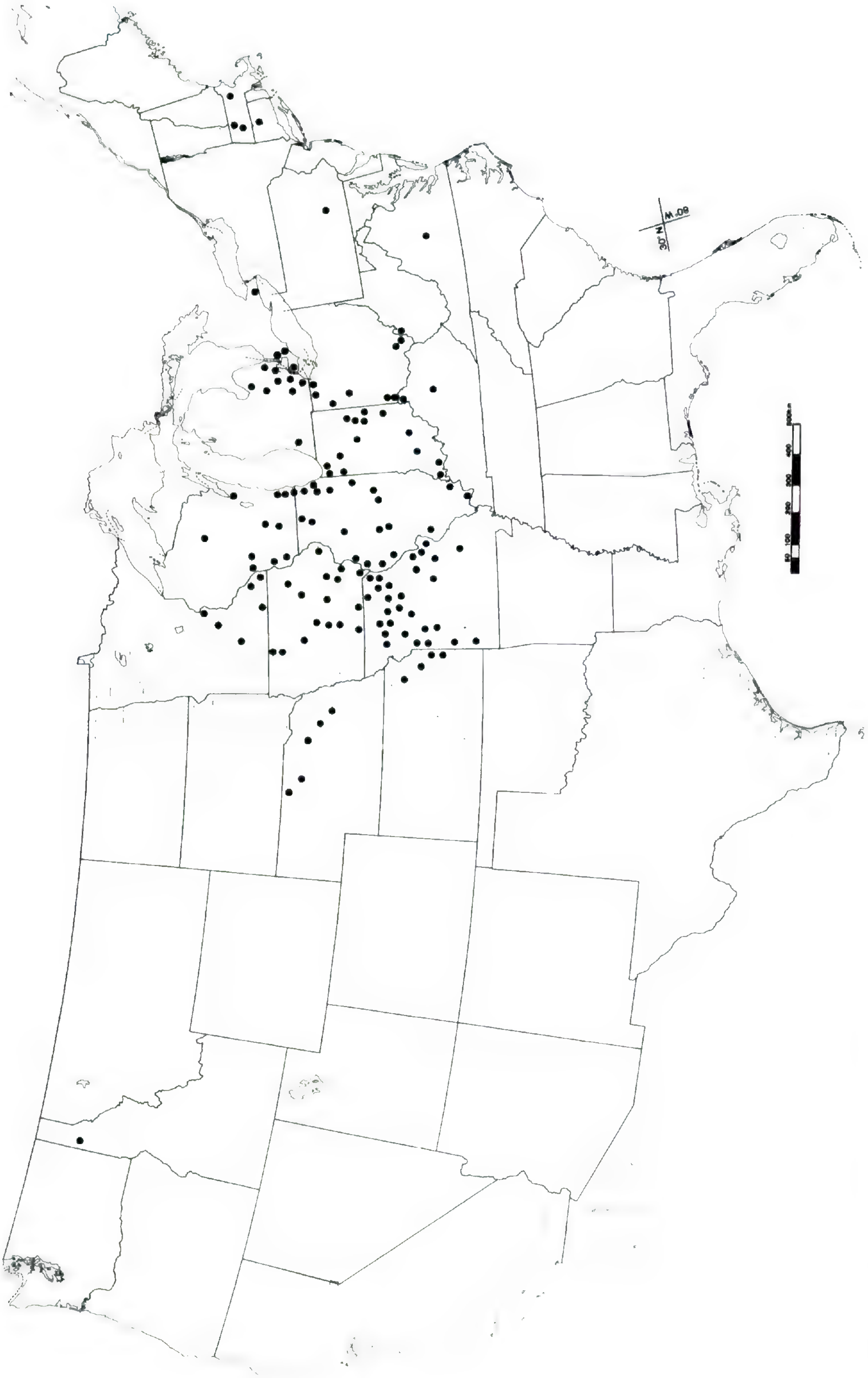

FIGURE 45. Distribution of *Ludwigia polycarpa*.

lizenus 503 (MO). Hennepin Co., near Minneapolis, 1892, *Burglehaus s.n.* (MO, MSU). Houston Co., along backwater of the Mississippi River, 2 mi. S of La Crescent, *Moore 26506* (CAS, EH, NCU). Mower Co., near Taopi, *Rosendahl et al. 7261* (GH). Nicollet Co., edge of the Red Rock outcrops 3–4 mi. W of Courtland, 1947, *Moore & Huff s.n.* (GH, US). Winona Co., river bank, 1897, *Holzinger s.n.* (NY). MISSOURI: Cass Co., in valley of Grand River, 3.5–4 mi. NW of Archie, *Steyermark 66785* (F, UPS). Chariton Co., Little Chariton River, 4 mi. NE of Keytesville, *Steyermark 26456* (MO). Clark Co., 1892, *Bush s.n.* (MO). Daviess Co., Old Grand River, S of Packwood Lake, 4.5 mi. W of Lock Springs, *Steyermark 74203* (F). DeKalb Co., between Clarksdale and Bayfield, *Steyermark 14943* (MO). Franklin Co., Shaw Arboretum, Pinetum Lake, *Dille 436* (MO). Grundy Co., Oxbow Lake in bottoms of E side of Thompson River, 13 mi. SW of Trenton, *Steyermark 68498* (F). Henry Co., Big Creek, 3 mi. SE of Hartwell, *Steyermark 7542* (F). Iron Co., Iron Mountain Lake, 1924, *Kellogg s.n.* (MO). Jackson Co., Sibley, *Bush 4173* (GH, MO, NY, SMU, US). Jasper Co., near Waco, *Palmer 18476* (NY). Johnson Co., Bear Creek, 3.5 mi. E of Warrensburg, along Hwy. 50, *Steyermark 24543* (F, NY, TENN). Knox Co., bottom woods along old channel of Salt River, 1.5 mi. SW of Locust Hill, *Steyermark 70647* (F). Lewis Co., Mississippi River bottoms, E of Shiloh church, along Doe Run, 7 mi. N of Canton, *Steyermark 74081* (F). Lincoln Co., W Fork of Cuivre River, 5.5 mi. SW of Davis, *Steyermark 72351* (F). Linn Co., Locust Creek, Pershing State Park, 4 mi. SW of Laclede, *Steyermark 40422* (F, MO). Livingston Co., Shoal Creek, 1 mi. NE of Dawn, *Steyermark 68458* (F). Macon Co., Chariton River, 5 mi. NE of New Cambria, *Steyermark 40580* (F, MO, US). Montgomery Co., ca. 1 mi. W-SW of Wellsville, *Gereau & Gu 1190* (MO). Osage Co., along Gasconade River on SW side, 8 mi. SE of Linn, *Steyermark 79318* (MO). Randolph Co., Silver Spring Creek, 2 mi. S of Huntsville, *Steyermark 9349* (MO). Ray Co., 1892, *Bush s.n.* (MO, NY). St. Charles Co., 3 mi. E of St. Peters, *Bauer 701* (F). St. Louis Co., Mississippi River near Baden, *Steyermark 8751* (MO). Saline Co., along road leading to bridge over Blackwater River, Sect. 32, 5 mi. NW of Ridge Prairie, *Steyermark 21527* (F, MO). Schuyler Co., N side of Rt. 4, in bottoms of Chariton River, just inside Schuyler County, just E of Livonia, *Steyermark 70272* (F). Shelby Co., alluvial woods along NW side of Salt River, 3.5 mi. N of Shelbina, *Steyermark 66574* (MO). Vernon Co., Clear Creek, 4–5 mi. W of Virgil City, *Steyermark 9688* (F). NEVADA: Brown Co., Ainsworth, *Clements s.n.* (GH, NY, US). Cherry Co., Valentine Lakes Refuge, *Tolstead 411242* (MO). Colfax Co., 1 mi. S of Schuyler on Hwy. 15, along bank of Platte River, *Churchill 4224* (NY). Holt Co., Ewing, 1893, *Bates s.n.* (TEX). Madison Co., 4 mi. S of Norfolk, *Conard s.n.* (TENN, W). OHIO: Auglaize Co., S shore of Grand Lake St. Mary's, 0.1 mi. E of Auglaize–Mercer county line, ca. 4 mi. SW of the town of St. Mary's, 1967, *Stuckey s.n.* (GH, NY, US, VDB). Butler Co., Oxford, 1898, *Moseley s.n.* (F). Fulton Co., 0.5 mi. E of Brailey, 1927, *Moseley s.n.* (US). Gaillia Co., swamp along Rt. 35, 2 mi. S Rio Grande, *Bartley 2279* (US). Hamilton Co., Turkey Bottoms, 1905, *Braun s.n.* (US). Jackson Co., Hammertown Lake, *Bartley 3024* (NY). Lucas Co., Toledo, 1878, *Sanford s.n.* (GH). Paulding Co., ca. 0.5 mi. W of Mandale, *Stuckey 6267* (SMU). PENNSYLVANIA: Dauphin Co., ca. 2 mi. E-SE of Millersburg, *Berkheimer 14541* (CM). VIRGINIA: Buckingham Co., Sprouses Corner (near Dillwyn), *Bartley & Pontius 539* (NY). WISCONSIN: Brown Co., Fort Howard, Elmore's, 1881, *Schuette s.n.* (F, GH, NY). Columbia Co., Portage, 1892, *True s.n.* (GH). Crawford Co., Prairie du Chien, 1861, *Hale s.n.*(?). Dane Co., Madison, *Watson s.n.* (NY). Grant Co., Wyalusing State Park, *Musselman 3825* (NCU). Kenosha Co., along Lake Michigan, just N of Illinois state line and E of RR, *Iltis 20258* (MO). La Crosse Co., young mixed hardwood forest bordered by a steep rocky rip-rap bank on W and a stagnant backwater pool on E, *Swanson 1887* (MO, NY). Lincoln Co., *Seymour 16321* (GH, MO). Milwaukee Co., 1882, *Hasse s.n.* (NY). Monroe Co., Hwy. 21 near Wyeville, *Hartley 8222* (GH). Racine Co., *Hale s.n.* (NY, US). WEST VIRGINIA: Mason Co., Point Pleasant, *Bartley & Pontius 476* (NY). CANADA. ONTARIO: Essex Co., Sandwich, *Macoun 44462* (CM, GH, F); 1 mi. SW of Windsor, *Rogers 9687* (MSU); near Amherstburg, 1892, *Macoun s.n.* (GH, NY, US). Kent Co., 11 mi. W-SW of Cedar Springs, 4 mi. S-SE of Merlin, N side Lake Erie, *Fosberg 39627* (C). Lambton Co., Pt. Edward, Lake Huron, *Macoun 44461* (F, GH, NY); *s.c. 188* (MO). Welland Co., Port Colborne, 1937, *Allen s.n.* (NCU).

Ludwigia polycarpa is the only species in sect. *Microcarpium* that occurs consistently north of 37°N, in the central Midwest of the United States. The report of Kral (1976) on the range extension of *L. polycarpa* to Covington Co., Alabama (*Kral 40992*, FLAS, GH, MO, NCU, NY, US, USF, VDB), was based on a pure F_1 stand of natural hybrids between *L. pilosa* and *L. glandulosa*.

Ludwigia polycarpa is therefore effectively isolated geographically from all other species in the same section except *L. sphaerocarpa*, which has a wide distribution throughout the Atlantic and Gulf coastal plains, also with scattered populations in the northeastern states as well as around the southern border of Lake Michigan (Fig. 45). Indeed, natural hybridization takes place where geographical isolation is not maintained, as is evidenced by the presence of fertile hybrid populations of *L. polycarpa* × *L. sphaerocarpa* found in Starke Co., Indiana (Peng, 1988). Furthermore, sterile, intersectional hybrids between *L. polycarpa* and the prostrate, opposite-leaved *L. palustris* (sect. *Dantia*), which is very widespread throughout the eastern half of the United States, are found in Ballard Co., Kentucky, the southern border of the range of *L. polycarpa* (Peng, 1988).

Herbarium specimens of *Ludwigia polycarpa* are rarely misidentified due partly to its geographical isolation and partly to its distinctive morphology. Plants of *L. polycarpa* are generally uniform and are characterized by having densely minutely papillose-serrulate leaf margins, elongate-acuminate sepals with reflexed tips, long bracteoles (3.5–6.5(–8) mm) attached above the capsule base, and the oblong-obovoid capsules that frequently exhibit reticulate markings along the rounded corners.

Plants of *Ludwigia polycarpa* produce stolons

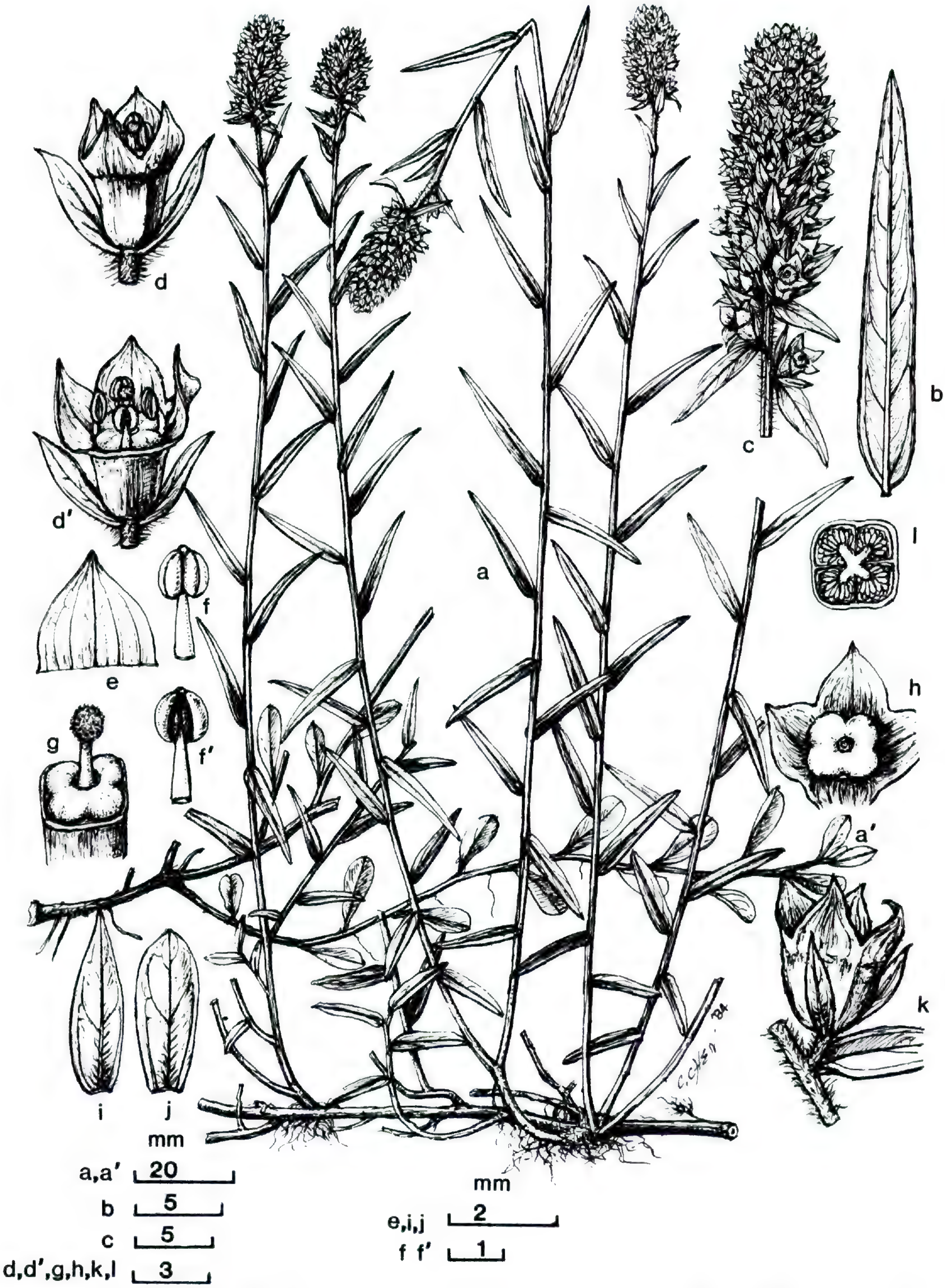

FIGURE 46. *Ludwigia suffruticosa*. All but a′ from Florida (Leon Co., *Godfrey 53576*, DUKE); a′ from Florida (Manatee Co., *Shuey 2024*, FLAS).—a. Habit, erect stems arising from horizontal rhizomes.—a′. Stolon.—b. Leaf.—c. Inflorescence.—d. Flower.—d′. Flower, a sepal removed to show stamens and pistil.—e. Sepal.—f, f′. Adaxial and abaxial views of stamens.—g. Nectary disc and pistil.—h. Nectary disc.—i. Bracteole.—j. Flower-subtending leaf.—k. Capsule.—l. Cross section of capsule.

from their lower nodes in late flowering season, like other species do. Their stolons, however, are much shorter, normally up to 15 cm, and their leaves, unlike those of any other species of sect. *Microcarpium*, are often densely congested and overlap at the apex of the sparsely leaved stolons. The modified stolon is comparable to the perennating turion of *Epilobium* (Keating et al., 1982), which apparently serves as an adaptation to the severe winter that plants of *L. polycarpa* have to endure in the northern states.

The short stolons are occasionally found growing from the nodes of aerial stems that have fallen to the ground. Such specimens include:

U.S.A. ILLINOIS: Riverside, *1886, Ohlendorf s.n.* (F): Western Springs, *Smith 676* (F). MISSOURI: Saline Co., Blackwater River, Sect. 32, 5 mi. NW of Ridge Prairie, *Steyermark 21527* (MO).

6. Ludwigia suffruticosa Walter, Fl. Carol. 90. 1788. *Isnardia suffruticosa* (Walter) Kuntze, Rev. Gen. Pl. 1: 251. 1891. *Ludwigia capitata* Michaux, Fl. Bor.-Am. 1: 90. 1803, nom. illegit., based on *L. suffruticosa* Walter. *Isnardia capitata* (Michaux) DC., Prodr. 3: 60. 1828. TYPE: U.S.A., "the Carolinas," s.d., *T. Walter* (type not seen, not located at BM). Figure 46.

Plants bearing rhizomes and stolons. Stems erect, unbranched or slightly branched, (16–)30–90 cm tall, glabrous except for the rachis and stem base, these often puberulous to densely hirtellous, the hairs 0.2–0.6(–0.8) mm long, aerenchyma in the lower part very rarely seen. Rhizomes 1–several, 6–55 cm long, 1.25–4.5 mm thick, often branched, glabrous to densely hirtellous, the leaves dark purplish, minute, scalelike, oblate or suborbicular, ca. 0.3–0.6 mm long, 0.6–0.9 mm wide, appressed. Stolons less commonly seen than rhizomes, 8–80 cm long, 1.1–2.2 mm thick, branched, glabrous to densely hirtellous, the leaves purplish, oblong or oblanceolate-elliptic to spatulate, 4–35 mm long, 1.6–15 mm wide, glabrous to pilose, the petioles 1–6 mm long. Cauline leaves green, lance-elliptic, lance-linear to linear, the lower ones shorter, oblong-oblanceolate to oblong or oblong-lanceolate, 25–95 mm long, (1–)3–9 mm wide, glabrous to ± pilose on those at stem base/peduncles, the apex manifestly elongate tapering into a sharp point or acute on lower leaves, the margin entire, hydathodal glands usually obscure, submarginal veins parallel to the midvein often prominent on the abaxial surface, the base rounded or obtuse, sessile. Stipules deltoid, 0.25–0.45 mm long, 0.15–0.4 mm wide. Flowers in racemose inflorescence 1–5(–12) cm long, 1–2 cm wide, terminal on the stems or branches; the subtending leaves much reduced and bractlike, lanceolate or lance-elliptic, 4–12(–18) mm long, 1.35–3.5(–4) mm wide, glabrous to hirtellous along margin and venation of the abaxial surface, especially on the lower half. Sepals whitish, broadly ovate or deltoid, ascending, 2.3–3.5(–4) mm long, 2.3–3.2(–3.8) mm wide, glabrous, apex acuminate, margin entire, base connate 0.6–1 mm above the ovary. Petals 0. Anthers 0.75–1(–1.3) mm long; filaments pale yellowish, 1.2–2 mm long, distinctly dilated toward the base. Pollen grains shed as tetrads. Nectary disc yellowish, raised 0.5–0.6 mm on top of the ovary, 1.8–3.1 mm across, the lobes obscure, glabrous. Style pale yellowish, 0.9–1.7 mm long, glabrous; stigma whitish, 0.4–0.75 mm long, 0.5–0.75 mm thick, distinctly 4-lobed on the apex. Capsules broadly obpyramidal with rounded corners, sometimes subspherical, 2.5–4.25 mm long, 2.5–4.5(–5) mm thick, glabrous or in a few cases minutely strigillose, the hairs ca. 0.05–0.1 mm long, pedicels 0.5–1.5(–2) mm long. Bracteoles flanking capsule base or on the short pedicel, 3.5–5(–6) mm long, (1.2–)1.4–2 mm wide, glabrous to pilose without, glabrous within. Seeds brown, elliptic oblong, curved on both ends, 0.5–0.6 mm long, 0.2–0.25 mm thick, surface cells nearly isodiametric. Self-compatible. Gametic chromosome number, $n = 16$.

Distribution. Plants of *L. suffruticosa* grow in sandy ditches, along river marshes, in meadows, in limestone sinks, in cypress swamps, and in moist pinelands. This species occurs along the Atlantic coast from southeastern North Carolina through eastern South Carolina, southern Georgia, and throughout the northern three-quarters of the Florida peninsula. To the west this species occurs through most of the Florida panhandle, extreme southeastern Alabama, and southern Georgia (Fig. 47). Flowering from May to September; fruiting from June to October.

Representative specimens examined. U.S.A. ALABAMA: Houston Co., Indigo Pond, SW of Cottonwood, *Kral 43405* (ENCB, MO, US, VDB). FLORIDA: Alachua Co., Gainesville, E of airport, 1937, *Murrill s.n.* (DUKE, MO). Bay Co., just S of Bay–Washington county line, *Adams 697* (DUKE, FLAS, FSU, GH, NCU, SMU, VDB). Bradford Co., Sampson City, 1946, *Dennison & Arnold s.n.* (FLAS). Brevard Co., N side of Cocoa, *Kral 5484* (NCU, NO, SMU). Charlotte Co., Caloosa Experimental Range, US Forest & Range Station, *Adams 235* (FSU, GA, GH). Citrus Co., 5 mi. S of Homosassa, *Kral 7771* (GA). Clay Co., Lake Brooklyn beside FL Hwy. 21, *D'Arcy 953* (C, FLAS). Collier Co., near Immokalee, *Craighead s.n.* (USF). Columbia Co., Lake City, 1893, *Rolfs s.n.*

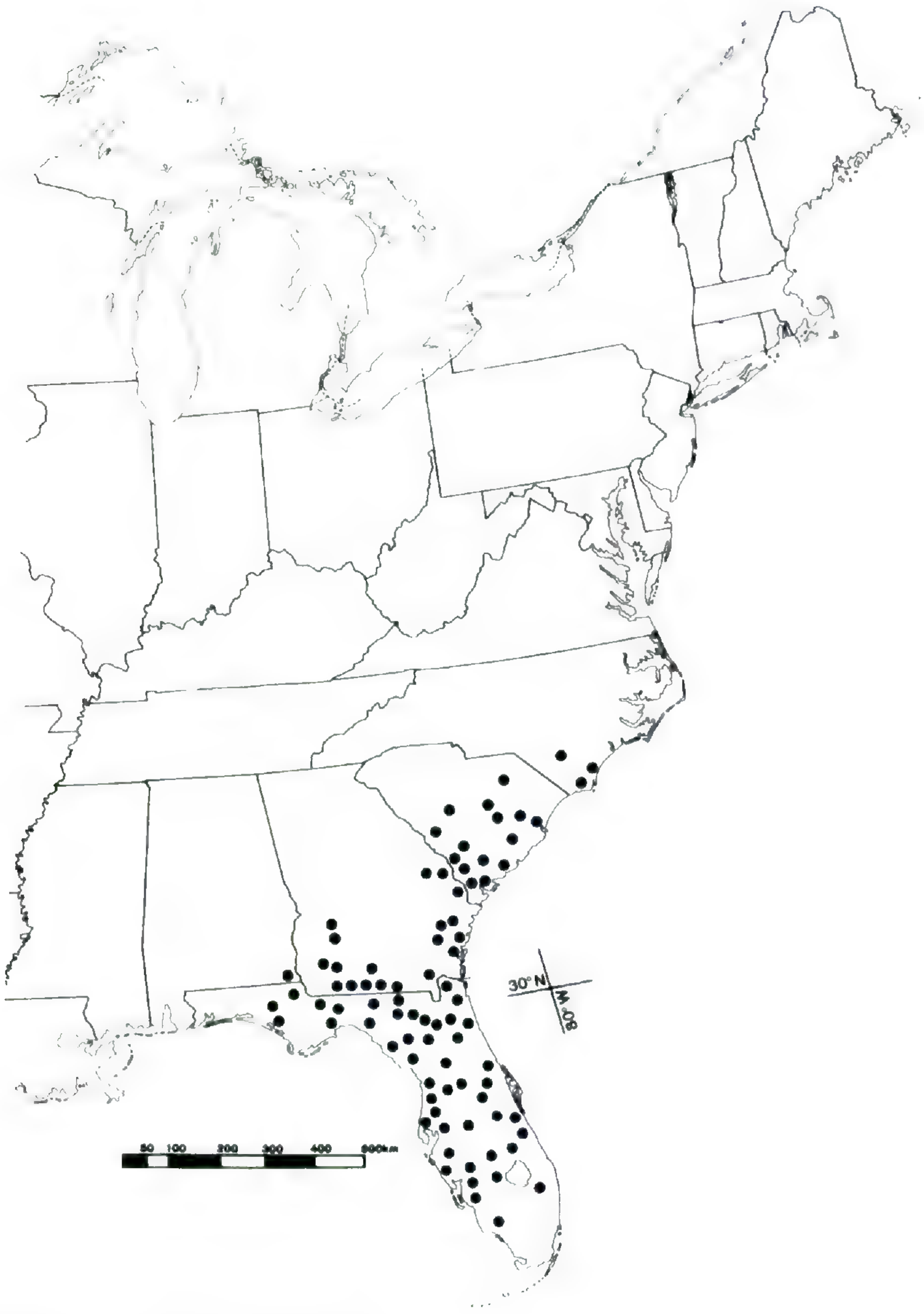

FIGURE 47. Distribution of *Ludwigia suffruticosa*.

(GA). De Soto Co., 4 mi. W-NW of Arcadia, *Kral 17965* (VDB). Dixie Co., 3.5 mi. N of Hines, 1937, *Pasture Survey s.n.* (FLAS). Duval Co., near Jacksonville, *Curtiss 5135* (GA, GH, JE, MSC, NY, US, W). Gadsden Co., 2.4 mi. N of Woodville, E side of US Hwy. 319, *Dress & Read 7736* (AAU, CAS). Gilchrist Co., 4 mi. E of Trenton, 1940, *West & Arnold s.n.* (FLAS). Glades Co., 6.4 mi. SE of jct. of FL Hwy. 29 and US Hwy. 27, *Raven 18678* (DS). Hamilton Co., 5 mi. E of Jasper, 1941, *West & Arnold s.n.* (FLAS). Hernando Co., *Cooley et al. 7068* (NCU, USF). Highlands Co., 10 mi. S of Lake Placid, *Brass 15203* (FLAS, GH, USF). Hillsborough Co., 1.5 to 1.7 mi. S of FL Hwy. 674 on the E side of Taylor Grill Dr., *Peng et al. 4327* (MO). Indian River Co., near Eau Gallie, *Curtiss 927* (CM, F, FLAS, GA, MO, NCU, NY, US). Jackson Co., near Dellwood, along FL Hwy. 69, *Hood 2759* (FLAS). Lake Co., vicinity of Eustis, *Nash 950* (F, GH, MO, MSU, NY, US). Lee Co., *Hitchcock 118* (F, GH, MO, NY, US). Leon Co., 6 mi. S of Tallahassee, *Godfrey 53576* (DUKE, FLAS, NY, SMU, USF, VDB). Levy Co., 5 mi. SE of Lebanon Station, *Kral 7807* (GA). Madison Co., 4 mi. N of Greenville on FL Hwy. 221, *Ramsey 104* (FSU, NCU, US). Manatee Co., 6.7 mi. W of jct. of FL Hwys. 64 and 675, E of Bradenton, *Perdue 1779* (C, FSU, GA, GH, LL, NCU, SMU, USF). Marion Co., Lake Kerr, 1935, *West & Arnold s.n.* (FLAS). Martin Co., Jonathan Dickinson State Park, W of Pinegrove Campground, *Popenoe 351* (FTG). Nassau Co., ca. 7 mi. SE of Yulee, *Kral 18629* (VDB). Okeechobee Co., US Hwy. 441, 20 mi. E of Kenansville, 1 mi. S of Osceola Co. line, *Clark 3477* (Duke). Orange Co., 5 mi. S of Oakland, *Kral 7735* (FLAS, GA, GH, US, USF). Osceola Co., W side of main road leading S through Poinciana S of US hwys. 17 & 92, *Wunderlin & Shuey 5779* (TENN, USF). Palm Beach Co., 2.0 mi. W of Lantana, *Howard 12960* (C, DS, DUKE, FLAS, GA, GH, MO, MSC, NO, NY, S, SMU, TENN, TEX, U, US, W). Pasco Co., 10 mi. E of Zephyrhills, *Kral 7264* (GH, NY, USF). Pinellas Co., FL Power right-of-way, Hwy. 19, 1 mi. N of Hwy. 588, *Genelle & Heming 2865* (TENN, USF). Polk Co., SE of Hesperides, ca. 8 mi. E of Lake Wales, off FL Hwy. 60, *Lakela 24806* (DS, USF). Putnam Co., *Martin & Copper 110* (FLAS, USF). St. Johns Co., Palm Valley, 1951, *Buker s.n.* (CM). Sarasota Co., 7 mi. N of S entrance of park, Myakka region, *Dodson 4515* (USF). Seminole Co., Prairie Lake, *Schallert 15229* (AAU, JE, U, WAG). Sumter Co., 3 mi. SW of Tarrytown, *Kral 7925* (FLAS, GH, USF).

Suwannee Co., 4 mi. E of Wellborn, *Wiegand & Manning 2202* (GH). Taylor Co., 3.2 mi. N of Shady Grove, *Raven 18619* (DS, NCU). Union Co., 1 mi. E of Worth Springs, *Murill 775*(?). Volusia Co., 3 mi. N-NW of DeLeon Springs, *Kral 1699* (CA, GH, USF, VDB). Wakulla Co., 0.5 mi. N of Ochlockonee River on US Hwy. 98, *Kral 3027*(?). Washington Co., 6 mi. S of Wausau, *Webster & Wilbur 3622* (GH, NY, SMU, US). GEORGIA: Baker Co., ca. 8 mi. SE of Milford, *Kral 20493* (VDB). Brooks Co., 12.5 mi. SE of Quitman, *Faircloth 3338* (GA, MO, NCU). Charlton Co., between Folkston and Mattox, *Correll 5517* (DUKE, FSU, GA, TENN). Cook Co., 7.6 mi. SE of Adel, *Faircloth 2927* (GA, NCU). Echols Co., 5.5 mi. S of Stockton on US Hwy. 129, *Norsworthy 162* (MO, NCU). Effingham Co., near Luciene Bay, *Eyles 6376* (GA). Glynn Co., St. Simons Island, 1946, *Ford & Thorne s.n.* (TENN). Grady Co., Susina Plantation, *White 180* (FSU). Jenkins Co., 2.5 mi. N of Millen, *Pyron & McVaugh 919* (GA). Lee Co., ca. 7 mi. N of Leesburg, *Cronquist 5445* (FLAS, GA, GH, MO, NY, SMU, US). Liberty Co., 7 mi. NE of Hinesville, *Wiegand & Manning 2201* (GH). Long Co., 3.8 mi. E-SE of Long–Tattnall county line on GA Hwy. 196 near RJ with GA Hwy. 261, *Faust & Jones 19981* (FSU, GA, VDB). Lowndes Co., 9.5 mi. SE of Valdosta, intersection of Southern RR and Howell Hwy., *Faircloth 2887* (GA, NCU). McIntosh Co., 1.8 mi. S-SW of N tip of Sapelo Island, *Duncan 20406* (CAS, DUKE, F, FLAS, GH, MISS, NCU, SMU, TENN, TEX, US, USF). Mitchell Co., *Duncan 6682* (GA). Screven Co., W of Blue Springs, *Duncan 5581* (GA, TENN). Sumter Co., S of Leslie, *Harper 484* (F, GH, MO, MSC, NCU, NY, S, US). Wayne Co., SE of Lindy's Bluff NE of Jesup, *Duncan 3759* (FLAS, GA, MISS, SMU, US, USF). NORTH CAROLINA: Brunswick Co., ca. 2 mi. W of NC Hwy. 133 off Co. Rd. 1536, Boiling Springs, *Bradley & Stevenson 3308* (BOON, C, ECUH, MEX, MISS, S, TEX, UNA, U, US, USCH, WCUH). Bladen Co., 2.5 mi. E of Elizabethtown, *Godfrey & Fox 49485* (DUKE, FSU, MO, NCSC, NY). New Hanover Co., Fort Fischer on the lower Cape Fear Peninsula, *Godfrey 4698* (GH, NLSC, NY, US). Orange Co., Taft, *Schallert 15229* (M). SOUTH CAROLINA: Aiken Co., Savannah River Plant, Ellington Bay, 1975, *Shealy s.n.* (USCH). Allendale Co., SE of Barton, *Ahles & Bell 15855* (CM, NCU). Bamberg Co., 1 mi. E of jct. of Co. Hwy. 59 and US Hwy. 601 on Co. Hwy. 59, S-SE of Bamberg, *Ahles & Haesloop 30589* (NCU). Beaufort Co., Bluffton, 1887, *Mellichamp s.n.* (US). Berkeley Co., 1 mi. N of Russelville, *Martin 48* (DUKE, GA, NY, TENN, US). Charleston Co., Adams Run, *Godfrey & Tryon 1565* (GA, NY, US). Clarendon Co., 1 mi. W of Davis Station, *Radford 28239* (FLAS, NCU, SMU). Colleton Co., E side of Walterboro, *Kral 19202* (VDB). Darlington Co., Hartsville, 1908, *Coker s.n.* (NCU, NY). Georgetown Co., 9 mi. N of Georgetown, *Godfrey & Tryon 337* (DUKE, F, GH, MO, NY, US). Hampton Co., 0.2 mi. N of Luray on US Hwy. 321, *Bell 5044* (USF). Jasper Co., NW of Tillman, *Ahles & Williamson 54838* (NCU). Lexington Co., Columbia, *Godfrey & Tryon 1241* (GH, US). Sumter Co., 1884, *Smith s.n.* (F, GH, US). Williamsburg Co., 6 mi. N of Kingstree, *Wiegand & Manning 2200* (GH).

Ludwigia suffruticosa is a very distinct species that has many features unique within sect. *Microcarpium*. Its leaves are rounded to obtuse at the base and clearly sessile. It has a very compact, racemose inflorescence at the very top of each erect stem, as is suggested by the name "*Ludwigia capitata*," an illegitimate synonym of *L. suffruticosa* Walter, coined by Michaux (1803). The stems are usually single or occasionally with one or two or more branches arising directly beneath the main inflorescence. These branches always rise above the main inflorescence and are each terminated by a smaller compact raceme. Furthermore, each flower is usually subtended by a reduced, bractlike leaf in addition to the bracteoles that flank the ovary. It is also the only species in sect. *Microcarpium* that perennates mainly by underground rhizomes. Stolons that float or send roots into mud, prevalent in many other species, are not common in *L. suffruticosa*. It is especially peculiar in having variously pubescent inflorescences and lower stems, stolons, and underground rhizomes but is otherwise completely glabrous in the middle—see below.

The flowers of this species are characteristically very compactly arranged into a raceme up to 5 cm long. The following specimens examined, however, have less compact and longer inflorescences but are otherwise typical of *Ludwigia suffruticosa*:

U.S.A. FLORIDA: Charlotte Co., Caloosa Forest/Expt. Area, Pasture 8, *Parrott 219* (DUKE, inflorescences 7 cm long). Hillsborough Co., Tampa, Gates Dr., in sandy field W of Gates Apts., *Dille 424* (MO, inflorescences up to 12 cm long, co-occurring with normal, compact-inflorescenced individuals (same locality, *Dille 423*, MO). GEORGIA: Wayne Co., in very sandy soil SE of Lindy's bluff, just NE of Jesup, *Dunkan 3759* (GH, inflorescences 8 cm long; NCU, inflorescences 10.5 cm long).

The distribution pattern of pubescence in plants of *Ludwigia suffruticosa* is peculiar and variable. The plants range from being completely glabrous to densely, minutely hirtellous with multicellular hairs up to 0.6(–0.8) mm long on rhizomes, stolons, stolon leaves, stem base, and basal leaves of the lower plant body and peduncles, pedicels, flower-subtending leaves, and bracteoles of the upper part but are completely glabrous in the middle part of the plant body. The capsules are usually completely glabrous. In the following specimens, however, erect, microscopic protuberances ca. 0.02–0.1 mm long are found evenly but not densely distributed on the fruit wall:

U.S.A. FLORIDA: Gilchrist Co., in swamps 4 mi. E of Trenton, 1940, *West & Arnold s.n.* (FLAS). Hillsborough Co., Tampa, Gates Dr. in sandy field W of Gates Apts., *Dille & Dille 424* (MO); in wet ground along SR-581, ca. 5 mi. N of Tampa, *Funk 72*; *Gregory 46*; *Kuczynski 48*; *Robbins 130*; *Rose 11*; *Willett 10* (all USF). Leon Co., bordering Lake Jackson on NW side, just N of route

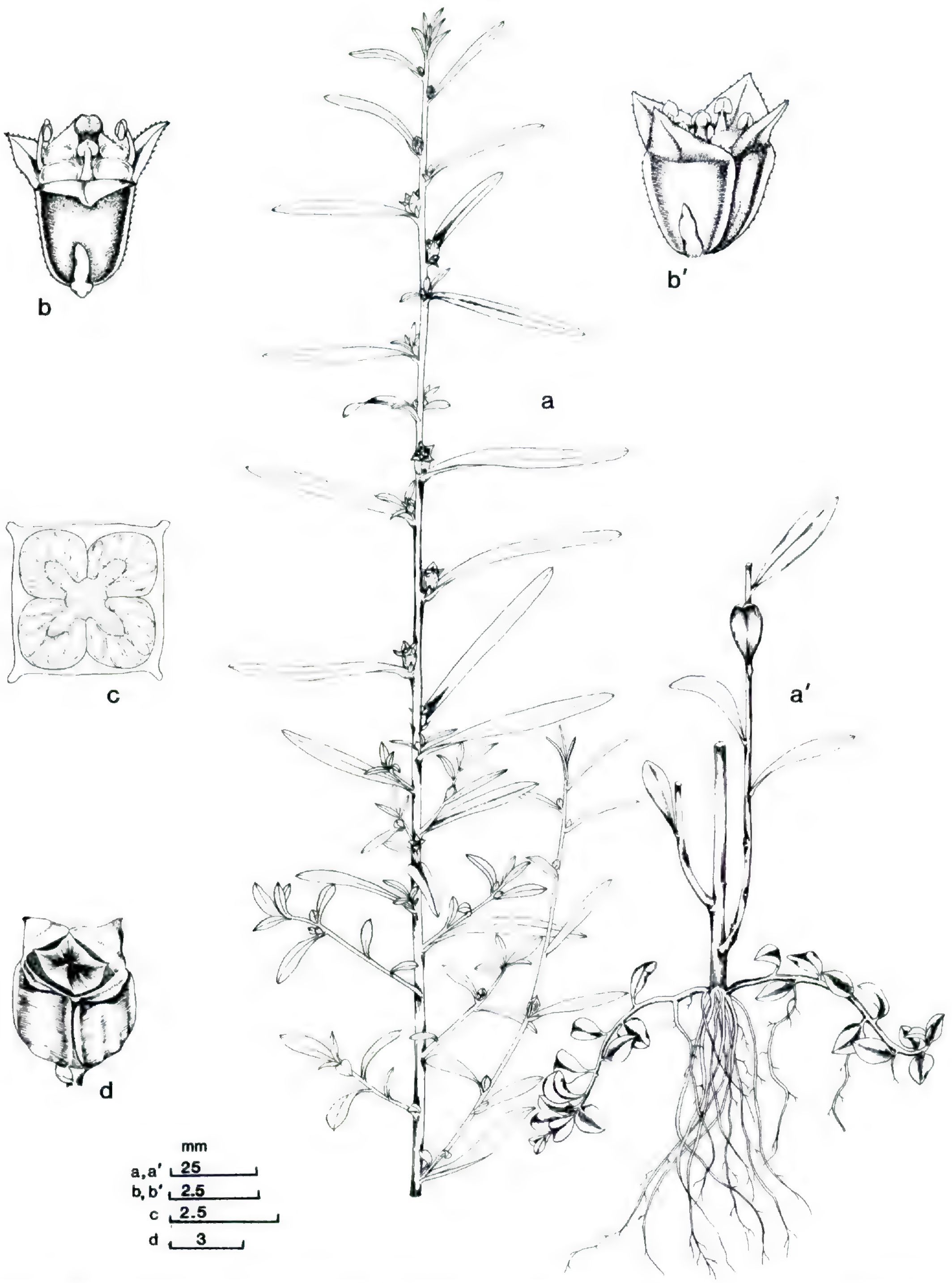

FIGURE 48. *Ludwigia lanceolata* (Florida: Highlands Co., *Peng et al. 4193*, MO).—a. Habit, erect stem.—a′. Stem base with stolons.—b, b′. Flower.—c. Cross section of capsule.—d. Dehiscent capsule.

27, NW of Tallahassee, *Anderson 4497* (GA, MO); on FL 363, 3 mi. N of Woodville, *Dille & Dille 421* (MO); Lake Jackson, adjacent to US 27, *Faircloth 246* (MO, NCU); shores of small pond, 6 mi. S of Tallahassee, *Godfrey 53576* (DUKE, FLAS, NCU, NY, SMU, USF, VDB); wet sands, exposed shores of sinkhole pond, by Spring Hill Rd., S of Tallahassee, *Godfrey 76066* (FSU); along US 319, ca. 5 mi. S of Tallahassee, *Henderson 63-1683* (TEX); margin of a small lake, along FL 271, ca. 5 mi. S of Tallahassee, *Henderson 67-1455* (VDB); near Lake Jackson, 8 mi. NW of Tallahassee, 1940, *Hocking s.n.* (FLAS). Orange Co., *Godfrey 57330* (FSU).

Polk Co., margin of a small lake, SE of Hesperides, ca. 8 mi. E of Lake Wales, off number 60, *Lakela 24806* (DS).

In a specimen collected from Florida (Leon Co., 4 mi. S of Tallahassee, on Rt. 369, 1950, *Sargent s.n.* (GA)) the capsule wall is minutely pilose with hairs ca. 0.4 mm long.

The sepals of *Ludwigia suffruticosa* are normally glabrous, but in the following specimen the sepals are minutely pilose:

U.S.A. FLORIDA: Duval Co., vicinity of Mayport & Jacksonville, 1870–1876, *Keeler s.n.* (NY).

Ludwigia suffruticosa, *L. alata*, *L. pilosa*, and *L. sphaerocarpa* are the species in sect. *Microcarpium* that do not undergo mechanical self-pollination. With its whitish creamy sepals, which are very showy in the dense flower aggregates, the cross-pollinating *L. suffruticosa* successfully attracts many insects, mostly bumblebees, honeybees, and wasps. It occurs with at least four species of *Ludwigia* (*L. alata*, *L. linearis*, *L. lanceolata*, and *L. pilosa*) in the field, hybridizing with all but *L. linearis*. These results are mirrored in the biosystematic study (Peng, 1988): artificial hybrids between *L. linearis* and *L. suffruticosa* are weak and inviable, whereas the other combinations that occur in nature have been synthesized successfully and were very vigorous in the experimental greenhouse.

Remarks on natural hybrids between *Ludwigia suffruticosa* and either *L. alata* or *L. lanceolata* are provided in the accounts of *L. alata* and *L. lanceolata*. Natural hybrid populations of *L. suffruticosa* × *L. pilosa* have previously been given a varietal status within *L. suffruticosa* (as *L. capitata* Michaux *β pubens*) by Torrey & Gray (1840), which was subsequently and incorrectly considered to be a synonym of *L. pilosa* by Munz (1944, 1965). The hybrids are densely hirtellous throughout, but the hairs are not as long as those of *L. pilosa*, and the sepals are neither cuspidate nor elongate-acuminate, but rather acuminate. Further, their stems are not well branched, their leaves are often long and narrow, their flowers are in more or less congested racemes on the upper part of the stem or branch, and the leaves that subtend their flowers are slightly reduced and bractlike. The combination of these characteristics clearly suggests that such plants represent hybrid populations of *L. suffruticosa* × *L. pilosa*. The possibility that *L. ravenii*, the only species other than *L. pilosa* that is consistently densely hirtellous, was involved in their parentage is reduced because it is rare and not known to occur with *L. suffruticosa*. Furthermore, the seed surface of the hybrid plants consists of subisodiametric cells, a characteristic of both *L. suffruticosa* and *L. pilosa*, but not of *L. ravenii*.

7. **Ludwigia lanceolata** Elliott, Sketch Bot. S.C. & Ga. 1: 213. 1817. *Isnardia lanceolata* (Elliott) DC., Prodr. 3: 61. 1828. TYPE: U.S.A. Georgia: in swamps, s.d., *J. E. Leconte s.n.* (holotype, CHARL; photographs, GH, MO; isotypes, P, PH). Figure 48.

Plants glabrous. Stems often brownish purple, erect, leafless below, branched above, 45–100 cm tall; aerenchyma well developed in lower stems when submersed in water; leaf bases slightly decurrent along the stems. Stolons up to 40 cm long, 2 mm thick, the leaves remote, 1–3 cm apart, purplish, rotund or elliptic to broadly elliptic, 5–27 mm long, 6–12 mm wide, apex rounded, obtuse or acute, base attenuate into winged petioles 2–10 mm long. Cauline leaves dark green, the lower ones sometimes purplish, leaves on the main stem elliptic, oblanceolate or narrowly oblanceolate, those on the branches usually much reduced, ranging from narrowly elliptic to very narrowly elliptic or linear; in general, leaves 20–75 mm long, 2–7.5 (–14) mm wide, apex acute to narrowly acute, margin entire with minute hydathodal glands, base narrowly cuneate or sometimes attenuate into a winged petiole up to 5 mm long. Stipules dark reddish purple, ovate to very widely ovate, succulent, 0.2–0.45 mm long, 0.15–0.25 mm wide. Flowers in upper leaf axils. Sepals greenish, shallowly triangular or deltate, ascending, 1.5–2.5 mm long, 1.8–3.3 mm wide, glabrous, apex acute to acuminate, minutely papillose along the margins. Petals 0. Anthers 0.4–0.6(–0.75) mm long; filaments nearly translucent, 1–1.4 mm long, dilated toward the base. Pollen grains shed as tetrads. Nectary disc yellowish green, raised 0.4–0.6 mm on ovary apex, 1.75–2.6 mm across, 4-lobed, glabrous. Style yellowish green, 0.5–0.7 mm long, glabrous; stigma yellowish, subglobose, 0.3–0.5 mm long, 0.7–1 mm thick. Capsules obpyramidal, winged on the corners, 3.5–5 mm long, 2.5–4.5 mm thick (as measured from wing to wing), glabrous, occasionally minutely strigillose, the wings 0.3–0.7 mm wide, usually minutely strigillose; pedicels up to 0.5 mm long. Bracteoles located at or slightly above capsule base and on 2 sides, variable in shape and size even in the same plant, ovate-elliptic to very narrowly elliptic, 1.5–4.3 mm long, 0.4–1.4 mm wide, margin minutely papillose, often with a distinct, rounded, swollen tissue 0.5–1 mm

FIGURE 49. Distribution of *Ludwigia lanceolata*.

across below the point of attachment. Seeds light brown, narrowly oblong with constricted ends, 0.65–0.75 mm long, 0.25–0.3 mm wide, the surface cells nearly isodiametric. Self-compatible. Gametic chromosome number, $n = 16$.

Distribution. Plants of *Ludwigia lanceolata* grow in ditches, low meadows, cypress swamps, moist pinelands, edges of pocosins, and on sandy peaty soil. This is a fairly uncommon species, with scattered populations occurring along the Atlantic coast of southern North Carolina, South Carolina, eastern and southern Georgia, and the Florida peninsula. This species reaches its western limit in the central panhandle of Florida (Fig. 49). Flowering from June to October; fruiting from June to November.

Representative specimens examined. U.S.A. FLORIDA: Brevard Co., Okeechobee region, *Fredholm 5987* (GH, MO, NY, US). Columbia Co., Lake City, *Nash 2502* (E, F, GH, MO, MSU, NY, US). De Soto Co., 5 mi. N of Arcadia, 1938, *West s.n.* (FLAS). Franklin Co., Apalachicola, *Chapman 4177* (GH, MO, NY, US, W). Gilchrist Co., 5 mi. E of Trenton, 1940, *West & Arnold s.n.* (FLAS). Hamilton Co., Cypress Swamp, 6 mi. E of Jasper, 1941, *West & Arnold s.n.* (FLAS). Highlands Co., on Co. Rd. S-634, 1 mi. W of US Hwys. 27 & 98, *Peng et al. 4183* (MO). Hillsborough Co., 1.5 to 1.7 mi. S of Hwy. 674, on E side of Taylor Gill Dr., *Peng et al. 4326* (MO). Jefferson Co., vicinity of Lloyd, *Godfrey & Houk 61411* (FSU). Madison Co., 8 mi. W of Greenville, *Kral 3741* (FSU, NY, USF). Marion Co., W of Lake Ocklawaha, *Martin & Cooper 877* (FLAS). Polk Co., 4.5 mi. E of Haines City, on FL 580, 1963, *Conard s.n.* (GH). Putnam Co., Fowlers Lake, 1935, *Weber s.n.* (FLAS). St. Johns Co., 5 mi. W of St. Augustine, *Godfrey & Reinert 61185* (FSU). Taylor Co., 1.2 mi. SE of Salem, *Godfrey 64738* (DS, FSU, LL, NCU). Volusia Co., ca. 4 mi. S jct. state 44 & 415, *Kral 18435* (VDB). Wakulla Co., Cow Swamp, Apalachicola National Forest, NW of Crawfordville, *Godfrey 64876* (FSU). GEORGIA: Glynn Co., St. Simons Isl., *Ford & Thorne 2788* (TENN). Long Co., 5 mi. W off US 301, on Hughes River Rd., *Bozeman & Radford 2042* (NCU). Lowndes Co., pine-barren pond S of Melrose, *Harper 1605* (E, F, GH, MO, MSU, NCU, NY, US). McIntosh Co., 1.25 mi. N of Fort Barrington,

TABLE 5. Comparison of *Ludwigia alata* with *L. lanceolata*.

Characters	*L. alata*	*L. lanceolata*
Stems	Often winged, sometimes obscurely so	Nearly smooth
Sepal		
Color	Whitish adaxially	Greenish adaxially
Length	Subequal to capsule	Shorter than capsule
Anther length (mm)	0.55–0.9	0.4–0.6(–0.75)
Filament length (mm)	1.1–1.7	1–1.4
Pollen grains shed	Singly	In tetrads
Nectary disc width (mm)	2–3.3	1.75–2.6
Style length (mm)	0.8–1.3	0.5–0.7
Breeding system	Obligate outcrossing	Modally autogamous
Capsule wall between the winged corners	Bulging out longitudinally in the central part	Smooth
Seed length/width ratio	Ca. 2	Ca. 2.4–2.8
Surface cells	Columnar	Suborbicular
Chromosome number	$n = 24$	$n = 16$

Cox Road, *Bozeman 2176* (FLAS, GA, NCU). NORTH CAROLINA: New Hanover Co., near Wilmington, 1867, *Canby s.n.* (NY). SOUTH CAROLINA: Beaufort Co., Bluffton, *Mellichamp s.n.* (NY).

Ludwigia lanceolata is interfertile with all seven other tetraploid members of sect. *Microcarpium*. However, it is most similar to the hexaploid *L. alata* in general aspects and fruit morphology, and is suspected to have been one of the parents of that species (Peng, 1988). For a detailed discussion of these two species, see remarks under *L. alata* and Table 5.

Ludwigia lanceolata has been found growing with *L. pilosa*, *L. suffruticosa*, both tetraploids, and with the diploid *L. linearis*. *Ludwigia alata* and *L. lanceolata* have not been found growing together, although they have overlapping ranges in the eastern and central Florida panhandle. It is worth noting that, although both species occur in generalized, wet habitats, such as the borders of ditches, ponds, and swamps, *L. lanceolata*, unlike *L. alata*, is not found in the limestone prairies and brackish marshes that prevail in the Everglades region of southern Florida. No hybrids have been observed, but they would be very difficult to detect without measuring pollen stainability or determining chromosome numbers.

Ludwigia lanceolata intergrades with *L. pilosa*, and fertile hybrids between them are frequent in nature. Such hybrids were named *L. simulata* by Small (1903). The type at NY (West Florida, *Biltmore Herbarium*) shows a combination of densely strigillose hairs and four-angled or barely winged capsules; it apparently arose following hybridization between a parent with strongly winged capsules (*L. alata* or *L. lanceolata*) and one that was pubescent (*L. pilosa*, *L. ravenii*, or *L. sphaerocarpa*). The isodiametric seed surface cells, combined with the fact that these plants shed their pollen grains as tight tetrads clearly suggest *L. lanceolata* and *L. pilosa* as the parents. Two other collections identified as this hybrid are also from Florida:

U.S.A. FLORIDA: Franklin Co., Apalachicola, *Chapman s.n.* (F, US). Highlands Co., Bear Point, Lake Childs, *Brass 15532* (GH, US).

Ludwigia lanceolata also intergrades with *L. suffruticosa*. For example, putative parents and introgressed hybrid populations were found in the same sandy ditch by a prairie in Hillsborough Co., Florida (*Peng 4324*, *4328*, MO). The leaves of the hybrids were narrow like those of *L. suffruticosa*, but the stems were well branched above the middle. The flowers are produced in somewhat congested racemes at the top of each branch, and the capsules were obpyramidal and weakly four-angled. *Peng 4324* had 85% stainable pollen and formed 16 bivalents in meiosis.

8. **Ludwigia alata** Elliott, Sketch Bot. S. C. & Ga. 1: 212. 1817. *Isnardia alata* (Elliott) DC., Prodr. 3: 61. 1828. LECTOTYPE: U.S.A. South Carolina: Charleston Co., found in damp places on Sullivan's Island, in the wooded part of the island, July–Sep., s.d., *S. Elliott s.n.* (PH; no authentic material found in Elliott's herbarium at CHARL, so sheet from PH selected as lectotype). Figure 50.

Plants glabrous. Stems erect or somewhat sprawling, 40–120(–160) cm tall, branched above, aerenchyma distinct in lower parts when sub-

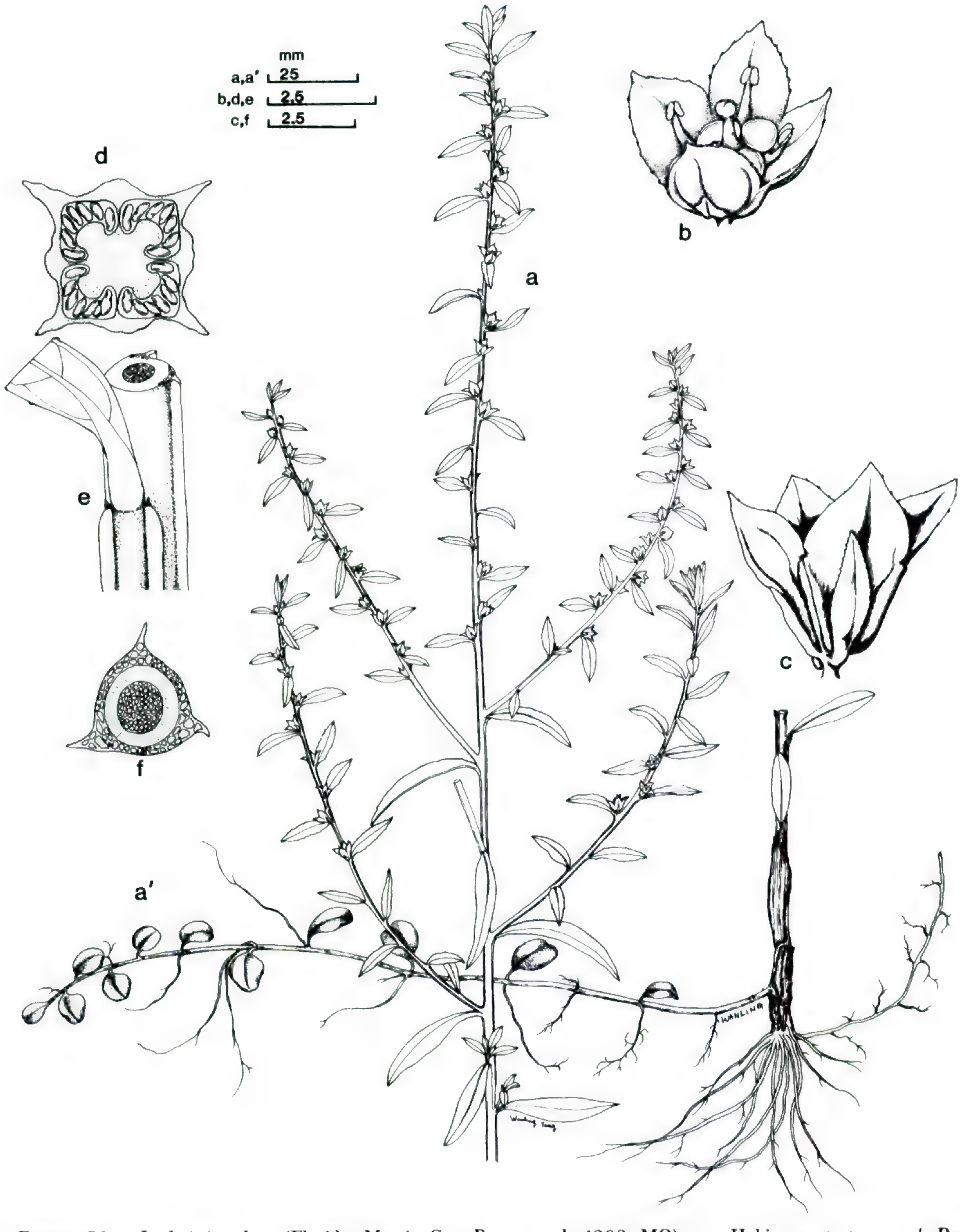

FIGURE 50. *Ludwigia alata* (Florida: Martin Co., *Peng et al. 4203*, MO).—a. Habit, erect stem.—a'. Basal stolon.—b. Flower.—c. Capsule.—d. Cross section of mature capsule.—e. Branch, showing decurrent leaf base.—f. Cross section of stem.

mersed, slightly to distinctly winged, the wings up to 1.8 mm broad. Stolons several from lower nodes, often seen in the flowering season, 8–65(–95) cm long, 0.7–2.5 mm diam., the leaves often purplish, especially on the abaxial surface, variable in shape, ranging from orbicular, rotund, oblanceolate to (broadly) elliptic, 4–26 mm long, 4–15 mm wide, base attenuate into petioles 1.5–10 mm long. Cauline leaves lance-elliptic, very narrowly elliptic to linear (those of lower stems sometimes oblanceolate or oblance-elliptic), 18–100 mm long, 2–12.5 (–20) mm wide, those on the branches that subtend

flowers often 2–4 times smaller than those on the main stem, the apex acute to narrowly acute, margin with remote but pronounced hydathodal glands, very occasionally minutely papillose-serrulate on the upper margin, base narrowly cuneate or narrowly acute, sessile or with petioles up to 3 mm long. Stipules dark brownish purple, triangular-ovate or lanceolate, succulent, 0.2–0.4 mm long, 0.1–0.3 mm wide. Flowers in upper leaf axils, sometimes rather congested and in an inflorescencelike arrangement. Sepals creamy white within, the apex pale green, broadly ovate-deltate and boat-shaped, flaring outward, apex acute or acuminate, 2–4 mm long, 1.6–4 mm wide, margin smooth or minutely papillose-serrulate. Petals 0. Anthers 0.55–0.9 mm long; filaments nearly translucent, 1.1–1.7 mm long, slightly dilated toward the base. Pollen grains shed singly. Nectary disc bright yellow, square with rounded corners, raised 0.5–0.8 mm on top of the ovary, 2–3.3 mm across, prominently 4-lobed, glabrous. Style pale green, 0.8–1.3 mm long, glabrous; stigma light yellowish, subglobose, 0.25–0.75 mm across, shallowly 4-lobed on top. Capsules glabrous, obpyramidal, winged on the corners, 3–5 mm long, 2.8–4.5 mm wide (including both wings), the wings ca. 0.5–0.9 mm broad, smooth or minutely papillose, central portion on each side of the wall often somewhat bulging longitudinally, sessile or with pedicels up to 0.8 mm long. Bracteoles flanking capsule base, lance-elliptic or narrowly so, 2.4–4.7 mm long, 0.6–1.5 mm wide, glabrous, margins minutely papillose or smooth. Seeds light brown, ellipsoid, slightly curved on both ends, 0.6–0.7 mm long, 0.3–0.35 mm wide, the surface cells elongate transversely to the seed length. Self-compatible. Gametic chromosome number, $n = 24$.

Distribution. The habitats of *L. alata* include ditches; shores of ponds and lagoons; peaty or sandy swales; open cypress swamps; sandy borrow pits in open pine woods; swampy, flat outcrops of oolitic rocks; wet savannas; tidal flats; brackish marshes; sandy beach strands; and hammocks. This species occurs along the eastern Coastal Plain from southeastern Virginia through eastern North Carolina, with sporadic populations in eastern South Carolina and Georgia; it reaches its southern limit at localities scattered throughout the Florida peninsula. To the west this species extends along the Gulf Coast through the Florida panhandle into southern Alabama, Mississippi, and extreme eastern Louisiana (Fig. 38). Proctor (1982) reported disjunct populations from Jamaica. Flowering from June to October; fruiting from July to November.

Representative specimens examined. U.S.A. ALABAMA: Baldwin Co., ca. 7 mi. W of Gulf Floors, *Kral 32612* (MO, SMU, VDB). FLORIDA: Bay Co., ca. 10 mi. W-NW of Mexico, *Kral 22985* (VDB). Brevard Co., SW shore of Lake Poinsett, 0.5 mi. N of St. Johns River inlet, *Kral 5335* (DS, FSU, NCU, NO, SMU). Broward Co., near E gate of Alligator Alley, *Lakela & Meaghen 31895* (NCU, NY, USF). Citrus Co., Chassahowitzka, *Genelle & Fleming 1551* (GA, USF). Collier Co., 4.8 mi. W of Monroe Station on N side of US Hwy. 41, *Peng et al. 4242* (MO). Dade Co., 2.5 mi. W of Pinelands, on main road of Everglades National Park, between Pinelands and Pa-Hay-Okee Overlook, *Peng et al. 4205* (MO). Dixie Co., 3 mi. SE of Hines, *Kral & Redfearn 3040* (FSU, NY, USF). Duval Co., near Jacksonville, *Curtiss 929* (C, F, FI, FLAS, GA, GH, MO, MSU, NY, P, US). Escambia Co., inland from Gulf Beach, SW Pensacola, *Kral 17602* (VDB). Franklin Co., 38.8 mi. W of jct. (one that is closer to St. Teresa Beach) of US Hwys. 98 & 319, *Peng et al. 4344* (MO). Gulf Co., 2 mi. E of Mexico Beach, *Godfrey & Henderson 62980* (FSU, LL). Hendry Co., *Atwater M-74* (FLAS). Hernando Co., Weekiwachee River, below the Springs, *Godfrey & Hawk 63101* (FSU). Hillsborough Co., Tampa, 1876, *Garber s.n.* (F, US). Lee Co., Myers, *Hitchcock 113* (F, GH, MO, NY, US). Levy Co., near Yankeetown, *Cooley et al. 6971* (FSU, NCU, USF, VDB). Manatee Co., north fork of Manatee River, S of State Rd. 62 and SW of Duette, *Shuey 1768* (USF). Marion Co., Rainbow River, between Dunellon and Rainbow Springs, *Godfrey 63112* (FSU, MO). Martin Co., jct. of Hwy. C-708 and FL Hwy. 76, on S side of ditch on Hwy C-708, *Peng et al. 4203* (MO). Monroe Co., ca. 8 mi. N-NW of Card Sound from Florida City of Key Largo, *Ferborgh & Brockman 287* (FSU). Okaloosa Co., Santa Rosa Island, W of Destin, *McDaniel 4978* (FSU). Orange Co., Killarney, 1889, *Veslulund s.n.* (S). Palm Beach Co., SW of headquarters of Loxahatchee National Wildlife Refuge, ca. 10 mi. W of Gulf Stream, 1970, *Poltevint s.n.* (FLAS). Pinellas Co., Clearwater, *Rolfs 592* (F). Polk Co., near N end of Lake Pierce, 1963, *Conard s.n.* (FLAS). Putnam Co., 0.5 mi. N of Welaka, 1940, *Laessle s.n.* (FLAS). Santa Rosa Co., Blackwater River, vicinity of Milton, *Godfrey 75471* (FSU). Seminole Co., 2 mi. E of Geneva, *Kral 5091A* (FSU, SMU). Taylor Co., ca. 20 mi. NW of Cross City, *Godfrey & Houk 60297* (DUKE, FSU, LL, MSU, NCU, SMU). Volusia Co., 4 mi. S of jct. FL Hwys. 44 and 415, *Kral 18436* (VDB). Wakulla Co., St. Marks Wildlife Refuge, *Godfrey 55760* (FLAS, FSU, GA, GH, NY, S, SMU, TENN, UNA, USF). GEORGIA: Camden Co., White Oak River, 1902, *Harper s.n.* (F, GH, MO, NY, US). LOUISIANA: St. Tammany Parish, ca. 2.25 mi. S of LA Hwy. 90, between West Pearl River and Mill Bayou, *Darwin & Sundell 676* (NO). MISSISSIPPI: Hancock Co., S of Kiln off MS Hwy. 45, *Rogers 1595* (NCU). Harrison Co., Ship Island, *Tracy & Lloyd 230* (E, F, GH, MO, MSC, NY, US). Jackson Co., Horn Island, *Godfrey & Channel 53720* (DUKE, FSU, GH, NY). NORTH CAROLINA: Brunswick Co., Long Beach, *Godfrey 48436* (FSU). Camden Co., E side of Pasquotank River on US Hwy. 158, E of Elizabeth City, *Bozeman & Radford 11531* (C, CM, FLAS, NO, SMU, TENN, TEX, U, UNA, USCH, WCUH, East Carolina Univ. herbarium). Carteret Co., SE of Mullet Pond on Shackleford Banks, *Anderson 408* (DUKE, SMU). Craven Co., New Bern, *Kearney 1961* (US). Currituck Co., Northwest River, near Moyock, *Blomquist 14379* (DUKE). Dare Co., 6 mi. S of Buxton, *Radford et al.*

7593 (GH, NCU). Gates Co., near Sunbury, s.d., *Le Conte s.n.* (NY). Hyde Co., Ocracoke Island, *Kearney 2325* (US). New Hanover Co., Wrightsville Sound, 1963, *Ahles & McCrary s.n.* (NCU). Onslow Co., Bear Island or Hammock Beach State Park, W quarter of island, *Wilbur 9576* (DUKE). SOUTH CAROLINA: Charleston Co., Santee River, N of McClellanville, *Godfrey & Tryon 718* (GH). Horry Co., Myrtle Beach, 70th Ave. N & US Hwy. 17, *Raven 18719* (DS, NCU). Jasper Co., 0.4 mi. SW of Neue River on SC Hwy. 170, *Ahles & Bell 18134* (NCU). VIRGINIA: Norfolk Co., Northwest River below Northwest, *Fernald & Long 14965* (C, GH, S). Princess Anne Co., along Blackwater River, SW of Pungo Ferry, *Fernald & Long 13981* (GA, GH, MO, NY, SMU, TENN, TEX, US). JAMAICA: Hanover Co., in the Great Morass, ca. 1.9 mi. SW of Logwood, *Proctor 37134* (FTG, GH, IJ, MO). Westmoreland Co., ca. 2.7 mi. N-NE of Negril, inland from milepost 23, *Proctor 37733* (F, FTG, IJ).

Ludwigia alata has been confused with *L. lanceolata* (Long & Lakela, 1976; Raven & Tai, 1979; Godfrey & Wooten, 1981; Wunderlin, 1982; Clewell, 1985), owing to their similarity in being glabrous, apetalous, and most notably, in having winged, obpyramidal fruits, a character not shared by other species of sect. *Microcarpium*. Raven & Tai (1979) reported the chromosome numbers of *L. alata*. They reported tetraploid counts of $n = 16$ and hexaploid counts of $n = 24$ as a result of not differentiating *L. lanceolata* from *L. alata*. It has now become clear that *L. alata* is a hexaploid and *L. lanceolata* is a tetraploid (Peng, 1988). In my biosystematic study (1988), I reported that reciprocal artificial hybrids between the two species exhibit a modal meiotic configuration of 16 bivalents and 8 univalents, which suggests that they have two genomes in common. Similar results were obtained when the hexaploid *L. alata* was crossed with any of the other tetraploid species of sect. *Microcarpium*. Cytogenetic and morphological data suggest that *L. alata* may have originated following hybridization between the tetraploid *L. lanceolata* and the diploid *L. microcarpa* or populations ancestral to them (Peng, 1988).

Despite their superficial resemblance, *Ludwigia alata* differs sharply from *L. lanceolata* in that the pollen grains are shed singly in *L. alata* and as tetrads in *L. lanceolata* (Praglowski et al., 1983), and the seed surface cells are columnar in *L. alata* vs. suborbicular in *L. lanceolata*. Other characters used by monographers to differentiate the two species include seed shape (ovoid in *L. alata* vs. cylindric in *L. lanceolata*) and sepal shape and size (slightly longer in length than width and nearly as long as the capsule in *L. alata* vs. about as long as wide, shorter than the capsule in *L. lanceolata*) (Small, 1933; Munz, 1944, 1965). These characters, however, are not always clear and reliable.

The leaf base is usually decurrent in *Ludwigia alata*, resulting in the winged stem. The wings are up to 1.8 mm wide in extreme cases. In *L. lanceolata*, by contrast, the stems are nearly smooth. However, the character of the winged stem in *L. alata* is too variable to be diagnostic.

Ludwigia alata has, like all other tetraploids of the section, lost its petals in the course of evolution. In a specimen collected from Duval Co., Florida (*Creager 639*, NCU), one vestigial petal is present on a single flower. Progeny of *Peng 4205* collected from Dade Co., Florida, exhibited minute, vestigial petals on some flowers, too, in greenhouse cultivation. Although normally lacking petals, *L. alata* has whitish sepals that flare outward. This character, along with the fact that the distance between the androecium and the gynoecium is such that mechanical self-pollination cannot usually occur, indicates that *L. alata* is an obligate cross-pollinator. By contrast, *L. lanceolata* has greenish, ascending sepals and is modally self-pollinating. *Ludwigia alata* and *L. lanceolata* are compared in Table 5.

Ludwigia alata occurs with *L. curtissii*, *L. linifolia*, *L. microcarpa*, *L. pilosa*, *L. simpsonii*, and *L. suffruticosa*. Natural hybrids between *L. alata* and *L. pilosa*, and between *L. alata* and *L. suffruticosa*, all of which require insect vectors to effect pollination, are abundant. (See Peng [1988] for voucher information of such natural hybrids.) The hybridity of field populations of *L. alata* × *L. pilosa* is initially suggested by the combination of the winged ovaries/capsules and minute, uniform pubescence found in these plants. Of the 15 taxa in sect. *Microcarpium*, only *L. alata* and *L. lanceolata* have winged capsules, and they are glabrous. *Ludwigia pilosa* and *L. ravenii* are consistently pubescent, and *L. sphaerocarpa* is variable in vestiture; none of them has winged capsules. The parentage of the hybrids between *L. alata* ($n = 24$) and *L. pilosa* ($n = 16$) is further verified by (1) their reduced level of stainable pollen (ca. 45–70%, which is indicative of a heteroploid cross), and (2) a mixture of columnar and isodiametric cells and some other irregular cells on their seed surface (among the pubescent putative parental species, only *L. pilosa* differs significantly in the seed surface pattern from *L. alata*).

Natural hybrids between *Ludwigia suffruticosa* ($n = 16$) and *L. alata* ($n = 24$) are difficult to recognize in the field. They are very similar to *L. alata* in general aspect, having winged capsules and slightly winged stems, as well as pollen grains shed singly. However, they differ from *L. alata* in that their stems are less branched; their flowers are borne only in the upper leaf axils of each

branch; their capsules are smaller, presumably as a result of reduced seed set; and their seed surface consists of a mixture of many columnar but relatively shorter cells, as well as somewhat isodiametric cells (typical of *L. suffruticosa*), and is irregular.

9. Ludwigia sphaerocarpa Elliott, Sketch Bot. S. C. & Ga. 1: 213. 1817. *Isnardia sphaerocarpa* (Elliott) DC., Prodr. 3: 61. 1828. *Ludwigia sphaerocarpa* Elliott var. *typica* Fern. & Griscom, Rhodora 37: 174. 1935. TYPE: U.S.A. South Carolina: Orangeburg Co., in swampy grounds near Orangeburg, flowers in August, s.d., *S. Elliott s.n.* (holotype, CHARL; photographs, GH, MO; possible isotype, PH). Figure 51.

Ludwigia sphaerocarpa Elliott var. *deamii* Fern. & Griscom, Rhodora 37: 174. 1935. TYPE: U.S.A. Indiana: Porter Co., low border of Lake Walker, NW of Baileytown, 23 Aug., 1925, *C. C. Deam 42350* (holotype, GH).

Ludwigia sphaerocarpa Elliott var. *jungens* Fern. & Griscom, Rhodora 37: 174. 1935. TYPE: U.S.A. Virginia: Princess Anne Co., Cape Henry, pool in sandy barrens, 23 Sep., 1933, *M. L. Fernald & L. Griscom 2862* (holotype, GH).

Ludwigia sphaerocarpa Eliott var. *macrocarpa* Fern. & Griscom, Rhodora 37: 174. 1935. TYPE: U.S.A. Massachusetts: Plymouth Co., Lakeville, stony shore of Quitacas Pond, 27 Aug., 1899, *W. P. Rich s.n.* (holotype, GH).

Stems erect, well-branched, (40–)60–110 cm tall, glabrous to densely strigillose; aerenchyma often very prominent in the lower part. Stolons many, up to 90 cm long, 2–3.5 mm thick, floating, sometimes branched, the leaves purplish, narrowly elliptic or oblanceolate, sometimes spatulate, 9–30 mm long, 4–8(–13) mm wide, glabrous to densely strigillose, apex acute or obtuse, margin with distinct hydathodal teeth or sometimes subentire, base attenuate into ± winged petiole 1.5–3 mm long. Cauline leaves narrowly elliptic or lanceolate to sublinear or linear, those on the main stem (26–)60–100 mm long, 4.5–11(–16) mm wide, those of the branch 20–50(–60) mm long, 2.5–5(–6) mm wide, glabrous to densely strigillose, apex acute to very narrowly acute, margin entire, hydathodal glands often visible in main cauline leaves, base attenuate or narrowly cuneate into petioles 1–4(–10) mm long. Stipules reddish purple, lanceolate or deltoid, 0.15–0.4 mm long, 0.1–0.2 mm wide. Flowers in upper leaf axils, lax to very crowded on branches. Sepals green without, yellow within, ovate-deltoid, ascending, 2–3.5(–4) mm long, 1.6–3(–3.3) mm wide, glabrous to densely strigillose on both surfaces, apex acuminate, margin entire. Petals 0. Anthers 0.5–0.8 mm long, filaments yellow, 1–1.7 mm long, slightly dilated toward base. Pollen grains shed as tetrads. Nectary disc bright yellow, raised 0.4–0.6 mm on ovary apex, 1.5–3 mm across, 4-lobed, glabrous to short hirtellous between the lobes. Style yellow, 0.55–1(–1.25) mm long, glabrous to strigillose, especially below. Stigma yellow, subglobose, 0.35–0.5 mm long, 0.4–0.7 mm thick. Capsules sometimes pinkish, subglobose, (1.8–)2–4(–4.5) mm long, 2–4 mm thick, glabrous to densely strigillose, pedicels 0.5–1.2(–2.3) mm long. Bracteoles subopposite on short pedicel, rarely flanking capsule base, linear to very narrowly lanceolate, rarely lanceolate, 0.5–1.5 mm long. Seeds brown to light brown, elliptic, 0.45–0.7 mm long, 0.25–0.35 mm wide, the surface of a mixture of columnar cells, these elongate and transversely elongate to the seed length, sometimes oblique, the orientation of cells often variable from seed to seed. Self-compatible. Gametic chromosome number, $n = 16$.

Distribution. Plants of *L. sphaerocarpa* grow in drainage ditches, on stream or pond shores, and in river marshes, swales, swamp forests, edges of limestone sinks, peaty bogs in pastures, and interdunal marshes. This species has an extensive distribution along the Atlantic coast, ranging from Massachusetts to northcentral Florida. To the west it extends through the panhandle of Florida, southwestern Georgia, southeastern Alabama, central and southwestern Louisiana, and reaches eastern Texas. Disjunct populations occur in southcentral Tennessee, extreme southwestern Indiana, along Lake Michigan in northeastern Illinois and northwestern Indiana, and in westcentral New York (Fig. 52). Flowering from June to September; fruiting from August to November.

Representative specimens examined. U.S.A. ALABAMA: Covington Co., Blue Pond, Conecuh National Forest, SW of Andalusia, *Kral 44739* (ENCB, GA, GH, MO, SMU, US, VDB). Elmore Co., ca. 5.5 mi. E-SE of jct. with US Hwy. 231 & Co. Rd. 4, *Wiersema 325* (UNA). Geneva Co., 1 mi. SW of Hartford, *McDaniel 7654.* CONNECTICUT: Middlesex Co., Killingworth, *Eames 11046* (GH). New London Co., Groton, *Enequist 299* (NY). New Haven Co., N Guilford, 1906, *Bartlett s.n.* (GH). DELAWARE: Kent Co., Felton, 1873, *Canby s.n.* (F). New Castle Co., Townsend, 1862, *Canby s.n.* (NCU). Sussex Co., Ellendale, *Commons s.n.* 1892 (GH, NY). FLORIDA: Dixie Co., 4 mi. N of Suwannee, *Godfrey 56178* (FSU, GA, GH, NY, TENN, USF). Flagler Co., near Korona, 1944, *Butts s.n.* (GH). Franklin Co., 0.5 mi S of the mouth of the Ochlockonee River, *Godfrey 54110* (FSU, GH, NY). Gilchrist Co., 4 mi. E of Trenton, 1940, *West & Arnold s.n.* (FLAS). Holmes Co., just E of Westville, *Godfrey 59013* (FSU, in 2 sheets). Jackson Co., Lake Seminole, Wildlife Refuge Area, *Monoson 55* (GH). Jefferson Co., ca. 4 mi. E of Wacissa, *Godfrey 63173* (FSU). Leon

FIGURE 51. *Ludwigia sphaerocarpa.* All but a′ from South Carolina (Jasper Co., *Peng et al. 3986*, MO); a′ from South Carolina (Jasper Co., *Boufford et al. 21650*, MO).—a. Habit, erect stem.—a′. Basal stolon.—b. Flower.—c, c′. Adaxial and abaxial views of stamen.—d. Fruit.—e. Cross section of fruit.

FIGURE 52. Distribution of *Ludwigia sphaerocarpa*.

Co., 2 mi. SE of Tallahassee, *McDaniel 3708* (FSU). Madison Co., 6 mi. E of Greenville, *Wiegand & Manning 2199* (GH). St. Johns Co., 1.9 mi. N of jct. of FL 207 and C-305, on FL 207, *Peng et al. 4159* (MO). Taylor Co., 1.2 mi. SE of Salem, *Godfrey 64726* (DS, LL, NCU). Volusia Co., 2 mi. N of Barberville, 1943, *West & Arnold s.n.* (FLAS). Wakulla Co., 6 mi. E of Sopchoppy along Ochlockonee River, *Morar 28* (DUKE, FLAS, FSU, MSC, US). Washington Co., *Curtiss 925* (C, F, GH, NCU, NY, S, UPS, US). GEORGIA: Baker Co., SW corner, *Duncan 4055* (GA). Burke Co., near Shell Bluff, *Eyles 6478* (GA). Decatur Co., along Hwy. 97, 1.3 mi. S-SW of Faceville, *Thorne & Davidson 17147* (FSU, GA). Dooly Co., 2 mi. N of Pinehurst, *Kral 51611* (VDB). Emanuel Co., 0.8 mi. S of Interstate 16 on US 1, on Ohoopee River, *Peng et al. 4026* (MO). Lee Co., W of Leesburg by GA Hwy. 32, *Kral 56334* (VDB). Long Co., 1.5 mi. SW of jct. of US 301 and 25, and GA 99, on US 301 and 25 near Altamaha River, *Peng et al. 4115* (MO). Lowndes Co., near Valdosta, *Curtiss 6710* (GA, GH, MO, NY). Mitchell Co., 5 mi. N of Camilla, *Thorne 5792* (GA). Seminole Co., Ray's Lake, lots 99 and 102, Dist. 21, *Thorne & Davidson 16764* (FLAS). Sumter Co., *Harper 553* (F, GH, MO, NY, US). ILLINOIS: Cook Co., Chicago, 1860, *Scammon s.n.* (F). INDIANA: Jasper Co., ca. 1.8 mi. S of Co. Rd. 10 and 0.8 mi. W of Co. line, *Friesner 22974* (FLAS, LL, S, SMU). Lake Co., Pine, 1896, *Unbach s.n.* (DS, F, MSC, NY, S, US). Porter Co., Wilson (Dune Park), 1958, *Bennett s.n.* (F, NY, SMU, W). Posey Co., Scuffle Pond in the Nolta Erwin Woods, ca. 8 mi. SW of Mt. Vernon, *Deam 59451* (NY). Starke Co., SW corner of Bass Lake, *Friesner 16306* (GH, MO, SMU). LOUISIANA: Cameron Parish, Lacassine Wildlife Refuge, *Thieret 16410* (DUKE, GA, MO, SMU). Rapides Parish, Red River, 1840, *Hale s.n.* (US). MARYLAND: Wicomico Co., Salisbury, 1889, *Canby s.n.* (NY). Worcester Co., 15 mi. N of Berlin, *O'Neill 7489* (CAS, DS, F, ND, NY). MASSACHUSETTS: Middlesex Co., Concord River, Bedford, 1908, *Fernald s.n.* (GH). Plymouth Co., Middleboro Ponds, Lakeville, *Churchill 595* (MO). Suffolk Co., near Boston, 1830, *Greene s.n.* (NY). NEW JERSEY: Atlantic Co., Hammonton, *Gershay 505* (GH). Burlington Co., Atsion, *Fogg 4697* (GH, TENN). Cape May Co., Bennett, 1913, *Stone s.n.* (NY). Cumberland Co., 1902, *Holmes s.n.* (FLAS, GA). Gloucester Co., Nortonville, *Lippincott 42* (GH). Middlesex Co., Spotswood, *Taylor 2586* (NY). Morris Co., Denmark Pond, *Mackenzie 4758* (MO, NY, S). Sussex Co., Hopkins Corners, 3 mi. NE of Lafayette,

1935, *Edwards s.n.* (NY). NEW YORK: Queens Co., N of Jamaica, Long Island, 1900, *Bicknell s.n.* (NY). Richmond Co., Staten Island, 1879, *Briton s.n.* (GH). Suffolk Co., Long Island, Long Pond, Sag Harbor, *Muenscher & Curtiss 6357* (GH, NY, US). Ulster Co., Esopus Pond, *Muenscher & Curtis 5779* (GH). Westchester Co., Lake Mohegan, 1887, *Martens s.n.* (C, DUKE, F, GH, NY, US). Yates Co., s.d., *Sartwell s.n.* (US). NORTH CAROLINA: Dare Co., along Hwy. 345, 3.75 mi. N of Wanchess, Roanoke Island, *Radford & Stewart 895* (NCU). Hoke Co., 4 mi. SW of Ashley Heights, *Ahles 36372* (NCU). Johnston Co., 5 mi. S-SW of Princeton, *Radford 27780* (CM, GH, FLAS, NCU, NY, SMU, TENN, VDB). Washington Co., 3.6 mi. S of Cherry, *Radford 38909* (NCU). PENNSYLVANIA: Bucks Co., Bristol, 1864, *Porter s.n.* (P). Westmoreland Co., 1878, *Pierron s.n.* (JE). RHODE ISLAND: Washington Co., Worden's Pond, South Kingstown, 1931, *Collins s.n.* (GH). SOUTH CAROLINA: Aiken Co., 1.4 mi. E of Monetta on SC Hwy. 39 and 0.2 mi. N on SC Hwy. 266 (near Williams Cemetery), *Massey & Massey 2995* (MO, NCU). Bamberg Co., 4 mi. SW of Denmark on Co. Rd. 26, *Ahles 37601* (NCU). Barnwell Co., Savannah River Operations Area of the Atomic Energy Comm., 1964, *Kelley s.n.* (USCH). Berkeley Co., 10.3 mi. W of Pineville on SC Hwy. 45, *Ahles & Baird 54901* (NCU). Calhoun Co., Riley, along US Hwy. 601, *Ahles 35324* (NCU). Clarendon Co., 13 mi. SW of Manning, *Godfrey & Tryon 1457* (DUKE, F, GH, MO, NY, US). Colleton Co., 4.2 mi. E of Smoaks on SC Hwy. 217, *Ahles & Bell 17889* (NCU). Dorchester Co., along US Hwy. 15, N of SC Interstate 15, *Leonard & Radford 1988* (NCU). Hampton Co., 2.1 mi. S of Gifford on US Hwy. 321, *Bell 3948* (NCU, USF). Jasper Co., 6.6 mi. N of SC Hwy. 46 on US Hwy. 17, N of Hardeeville, *Peng et al. 3986* (MO). Kershaw Co., Adams Millpond, 2.5 mi. NE of US Hwy. 1 at Camden, on SC Hwy. 15, *Radford et al. 11388* (B, BOON, DS, East Carolina Univ. Herb., MEX, MISS, NCU, S, TEX, UNA, WCUH). Lee Co., McGurts Creek, near US Hwy. 15 at Mechanicsville, *Radford 27252* (FSU, NCU). TENNESSEE: Coffee Co., Goose Pond on AEDC land along access hwy., 1973, *DeSelm et al. s.n.* (TENN). Franklin Co., ca. 8 mi. W of Winchester, 1976, *Kral s.n.* (VDB). VIRGINIA: Greensville Co., *Cephalanthus* swamp, ca. 1 mi. N of Skipper's, *Fernald & Long 8788* (GH). Isle of Wight Co., Cat Pond, S of Berns Church, *Fernald & Long 7547* (GH, MO). Nansemond Co., ca. 7 mi. E-NE of Suffolk, *Kral 13766* (FSU, VDB). Norfork Co., Lake Drummond, Great Dismal Swamp, W of Wallaceton, *Fernald & Long 13402* (GH, MO, NY, SMU, TENN, US). Princess Anne Co., E of T-1, N of RR, near picnic shelter, *Egler 40281* (NY). Sussex Co., N of Stony Creek, *Fernald & Long 8790* (GH). York Co., NW of Grafton, *Fernald & Long 7548* (GH, NY, US).

Ludwigia sphaerocarpa is highly polymorphic. Its variability is largely the result of its wide geographic (and latitudinal) range, the sporadic, semi-isolated distribution of the populations, the interaction of differential adaptation and genetic drift made possible by its pattern of distribution, and its possible hybrid nature (see below). Hybridization with *L. pilosa* in regions where their ranges overlap apparently provides an important source of variability in *L. sphaerocarpa*.

Populations of this species consist of individuals that vary in overall pubescence, leaf shape and size, fruit size, and density of fruits on branches. Fernald & Griscom (1935) recognized var. *jungens*, var. *macrocarpa*, and var. *deamii* based on various combinations of these characters. In their treatment, the varieties were separated as follows:

Rameal leaves strongly reduced, glabrous or pubescent, lanceolate.
- Mature hypanthium small, 2.5–3.2 mm long, 2.8–4 mm broad, averaging broader than long.
  - Hypanthium pubescent; leaves narrowly lineear-lanceolate and attenuate ..... var. "*typica*" [var. *sphaerocarpa*]
  - Hypanthium, branches, and leaves pubescent; leaves more broadly lanceolate, not attenuate ..... var. *jungens*
- Mature hypanthium larger, 3.5–4.6 mm long, 3.2–4 mm broad, averaging longer than broad ..... var. *macrocarpa*

Rameal leaves scarcely smaller than the primary ones, pubescent, narrowly oblong; stems pubescent; hypanthium pubescent, 3 mm long, about as wide ..... var. *deamii*

In his revisions of the New World species of *Ludwigia*, Munz (1944, 1965) reduced var. *deamii* to synonymy under var. *jungens* and presented the following key to the varieties:

Fruit crowded on branches, 3.5–4.5 mm long, not as wide. Massachusetts to New Jersey ..... var. *macrocarpa*

Fruit not crowded on branches, 2–3.2 mm long, usually wider.
- Main stems and leaves usually glabrous; principal leaves linear-lanceolate and over 7 cm long. Rhode Island to Florida ..... var. *sphaerocarpa*
- Main stems and leaves pubescent to strigose, lanceolate, usually less than 7 cm long. New Jersey to North Carolina, Michigan, and Indiana ..... var. *jungens*

A study of numerous herbarium specimens not available to Fernald & Griscom (1935) and Munz (1944, 1965) has revealed that correlations between these characters are not consistent; they often intergrade. Indeed Munz (1944) noted that "var. *typica* (the typical variety) and var. *jungens* intergrade freely." Under *Ludwigia sphaerocarpa* var. *macrocarpa*, he also wrote, "New Jersey material is sometimes difficult to distinguish from var. *typica* (the typical variety)." In my opinion, it is best to treat *L. sphaerocarpa* as representing an assemblage of variable populations without recognizing the infraspecific taxa. These populations share the following diagnostic characters: subglobose capsules, diminutive bracteoles (shorter than 1.5 mm long), and ovate-deltoid, yellowish, conspicuous sepals.

It is also of interest to note that, although the seed surface cell pattern is generally very regular within populations of members of *Ludwigia* sect. *Microcarpium* (Figs. 19–28, 30–34), this is not the case for *L. sphaerocarpa* (Fig. 29). The seed surface is arranged in columnar cells both transversely elongate and parallel to the seed length, the former alignment often predominating in the central part of the seeds. Seeds with variously oriented surface cells are also seen in some populations. Comparison of the seed surface pattern in populations of *L. sphaerocarpa* with that of various artificial hybrids strongly suggests that earlier hybridizations within the interfertile tetraploid group of sect. *Microcarpium* may have resulted in this widespread series of populations that are more or less stabilized in some of their characteristics, and such hybridizations may still be contributing to the variability of this series of populations.

The biosystematic study of *Ludwigia* sect. *Microcarpium* (Peng, 1988) demonstrated that hybrids between species that differ in their seed surface cell pattern always show a mixture of cell types or cells of intermediate shapes and sometimes of randomly oriented cells. Similarly, hybrids resulting from crossing a densely hirtellous species with a glabrous one always exhibit minutely villous or strigillose pubescence. Of the tetraploid *Ludwigia* taxa that are interfertile with *L. sphaerocarpa*, *L. ravenii* and *L. glandulosa* subsp. *brachycarpa* are the only ones with columnar seed surface cells elongate transversely to the seed length, whereas *L. polycarpa* and *L. glandulosa* subsp. *glandulosa* are the only taxa with columnar seed surface cells elongate parallel to the seed length. Both subspecies of *L. glandulosa*, having narrow, subcylindrical capsules, are unlikely to be parents of *L. sphaerocarpa*. In seed surface pattern and overall pubescence, *L. ravenii* (densely hirtellous) and *L. polycarpa* (glabrous) seem to be suitable parental candidates. However, that they both have oblong-obovoid capsules and are highly autogamous, in contrast to subglobose capsules and outcrossing habit of *L. sphaerocarpa*, renders it unlikely that they have been involved directly in the formation of *L. sphaerocarpa*. One or possibly both parents of *L. sphaerocarpa* are likely extinct.

The morphological variation in *Ludwigia sphaerocarpa* is further complicated by its frequent natural hybridization with *L. pilosa*, which has apparently resulted in many hybrid swarms or introgressed populations. These plants generally exhibit varying degrees of intermediacy in diagnostic characters such as seed surface pattern, overall pubescence, bracteole size, sepal shape and size, and leaf shape. The following specimens show intermediacy in at least two of the above characters or a combination of some of the diagnostic features of *L. pilosa* with some of those of *L. sphaerocarpa*:

U.S.A. ALABAMA: Escambia Co., 2.5 mi. N of Atmore Prison, off Hwy. 21, *Harvey 275* (UNA). FLORIDA: Citrus Co., 5 mi. S of Homosassa, *Kral 7772* (FLAS, GH, NCU, US, USF, VDB). Columbia Co., 2.5 mi. N of Ellisville, along U.S. Hwy. 41, *Raven 18634* (DS). Dade Co., near Lake Okeechobee, *Fredholm 6182* (GH, NY, US). Duval Co., near Jacksonville, *Curtiss 4324* (DS, ND, NY, US), *Curtiss 5214* (GH). Highlands Co., S end of Lake Istokpoga, *Raven 18683* (DS, NCU); E of Sebring, Carter Creek Swamp, 1948, *Garrett s.n.* (FLAS); 2 mi. S of Parker Islands, *Brass 15325* (US). Hillsborough Co., River State Park, along U.S. Hwy. 301, 1978, *Rochow & Lopez s.n.* (USF); 1 mi. N of bridge on Tarpon Springs–Lake Fern Road, *Poppleton 699* (DS). Lake Co., in the vicinity of Eustis, *Nash 1041* (F, GH, MO, MSC, NY, PH, S, US). Madison Co., 6.8 mi. W of Greenville, along U.S. Hwy. 90, *Raven 18629* (DS); 10 mi. S of Greenville, *Kral 3769a* (FSU, GA, GH, NY, SMU, TENN, UNA, USF). Manatee Co., NE of intersection of state roads 62 & 39, *Shuey 1712* (USF). Polk Co., ca. 3.3 mi. SW of Polk City, along FL Hwy. 33, *Smith & Myint 586* (FLAS, FSU, NCU). St. Johns Co., St. Augustine, 1875, *Reynolds s.n.* (F, FLAS, MO, NY—2 sheets, PH); 1876, *Garber s.n.* (FLAS). Wakulla Co., vicinity of Panacea, *Godfrey 60276* (FSU). GEORGIA: Colquitt Co., 8 mi. NE of Moultrie, *Kral 15008* (VDB). Emanuel Co., 0.8 mi. S of Interstate 16 on U.S. Hwy. 1, *Peng et al. 4025* (MO), *Peng et al. 4026a* (MO). Richmond Co., Augusta, Sanitary Dairy Pond, 1924, *Hildebrand s.n.* (DUKE). Wilcox Co., 10.9 mi. NNW of Abbeville, *Hardin & Dunkan 14246* (GA). NORTH CAROLINA: Robeson Co., ca. 1.5 mi. S of Luberton, *Kral 19030* (VDB, mixed with *L. pilosa*). SOUTH CAROLINA: Aiken Co., 1869, *s.c., s.n.* (US); Beaufort Co., St. Helena Island, 1884, *Cuthbert s.n.* (FLAS). Colleton Co., 4.2 mi. E of Smoaks, *Raven 18718* (DS, 2 sheets, NCU). TEXAS: Freestone Co., 5 mi. SE of Dew, on Hwy. 75, *Correll 35249* (LL); 15 mi. SE of Fairfield, *Kral 111* (FSU). Gonzales Co., Ottine, 1936, *Tharp s.n.* (MO, SMU, TEX). Harris Co., Gosby, 1923, *Fischer s.n.* (S, US); Humble, *Tharp 4518* (MO); Sheldon, *Reverchon 2301* (MO). Hardin Co., 1937, *Tharp s.n.* (TEX). Nacogdoches Co., Nacogdoches, *Waller 273* (SMU, TAES). Orange Co., 1.7 mi. N of Mauriceville, *Shinners 25116* (SMU). Wood Co., 2 mi. N of Mineola, *Correll 35021* (LL); Lake Ellis, *Lundell & Lundell 11748* (LL, SMU).

Some of the above putative hybrid populations are from central and southern Florida, where neither typical *Ludwigia pilosa* nor *L. sphaerocarpa* occur (Peng, 1988, fig. 22). This suggests that their physiological characteristics, and thus their ecological tolerances, may differ from those of the parents in such a way as to allow them to occur in novel habitats and areas where neither of their parents can survive.

The following collections are unusual in being densely hirtellous (having erect hairs ca. 0.4–0.8

mm long), but they are otherwise typical of *Ludwigia sphaerocarpa*. They may represent introgressants between *L. sphaerocarpa* and either *L. pilosa* or *L. ravenii*.

U.S.A. FLORIDA: Flagler Co., vicinity of Andalusia, *Godfrey & Reinert 61149a* (FSU). SOUTH CAROLINA: Beaufort Co., 0.8 mi S of Yemassee on Co. Rd. 3, *Bell 4703* (NCU); *Raven 18716* (DS, FLAS, TEX). Hampton Co., 0.8 mi. NNW of Shirley on Co. Rd. 20, *Bell & Ahles 18254* (NCU). Jasper Co., 5 mi. S of Ridgeland, on U.S. Hwy. 17, *Dille & Dille 346* (MO); 7 mi. N of Hardeeville, on U.S. Hwy. 17, *Dille & Dille 349* (MO). TEXAS: Angelina Co., N of Boykin Springs, Angelina National Forest, *Correll 34910* (LL). Hardin Co., between Silsbee and Kountze, S of Hwy. 418, SW of county dump grounds, *Amerson & Watson 228* (LL). Harris Co., Humble, *Tharp 4518* (US). Montgomery Co., 12 mi. W of Cleveland, *Kral 21041* (DS, VDB—2 sheets).

Plants of the following collections were found to have one to three vestigial, yellow petals in some of the flowers:

U.S.A. FLORIDA: Flagler Co., near Korona, 1944, *Butts s.n.* (GH). Wakulla Co., on U.S. 98, 5 mi. W of FL 59, *Dille & Dille 401* (MO). NEW YORK: Suffolk Co., Long Pond, Sag Harbor, *Muenscher & Curtis 6357* (NY).

Judged by their morphology as well as their full seed set, these plants are more likely to be mutants showing an ancestral trait rather than hybrids between *Ludwigia sphaerocarpa* and one of the petaliferous species of sect. *Microcarpium*.

Almost all populations of *Ludwigia sphaerocarpa* are at least sparingly strigillose, especially on the ovary/capsule walls. The following two glabrous collections from Louisiana are exceptional:

U.S.A. LOUISIANA: Cameron Parish, in "The Pool," Lacassine Wildlife Refuge, *Thieret 16410* (DUKE, GA, MO, SMU). Rapides Parish, Red River, 1840, *Hale s.n.* (US).

They seem to parallel the glabrous variants of *Ludwigia linearis* (see above) in which a few glabrous plants may grow intermixed locally with densely strigillose individuals.

Ludwigia sphaerocarpa is one of the few species in sect. *Microcarpium* in which the distance between the androecium and the gynoecium is such that self-pollination is impossible without the intervention of pollen vectors. Although the flowers of *L. sphaerocarpa* are apetalous, their sepals are adaxially yellowish. This, along with the bright yellow nectary disc, which produces copious nectar, attracts many insects to the flowers of this apparently largely outcrossing species.

In the field, *Ludwigia sphaerocarpa* grows with *L. glandulosa*, *L. linearis*, *L. microcarpa*, *L. pilosa*, and *L. polycarpa* and hybridizes with all but the small-flowered, modally selfing *L. microcarpa*. The natural hybrids generally exhibit intermediate morphology, most notably in fruit shape and size, bracteole length, overall pubescence, and seed surface cell pattern. The fruits are plump and contain abundant seeds in homoploid (tetraploid) hybrids. In the heteroploid (triploid) *L. sphaerocarpa* ($n = 16$) × *L. linearis* ($n = 8$), one to four petals were present in most flowers, and seed set was negligible.

In the experimental greenhouse, artificial hybrids have been synthesized between *Ludwigia sphaerocarpa* and the diploid *L. linearis*, *L. microcarpa*, the tetraploid *L. glandulosa*, *L. polycarpa*, *L. suffruticosa*, *L. lanceolata*, *L. pilosa*, the hexaploid *L. alata*, and the octoploid *L. curtissii* (Peng, 1988).

10. Ludwigia pilosa Walter, Fl. Carol. 89. 1788. *Isnardia pilosa* (Walter) Kuntze, Rev. Gen. Pl. 1: 251. 1891. TYPE: U.S.A., "the Carolinas," s.d., *T. Walter 658* (holotype, BM, Walter Herbarium p. 66; photograph, MO). Figure 53.

Ludwigia rudis Walter, Fl. Carol. 89. 1788. TYPE: U.S.A. "the Carolinas," s.d., *T. Walter s.n.* (type not found at BM, Walter Herbarium; possible isotype, P ("No. 3"); photograph, MO).

Ludwigia hirsuta Lam., Encycl. 3: 614. 1792. TYPE: U.S.A. South Carolina: 1785–1792, *J. Fraser s.n.* (holotype, P; photographs, GH, MO).

Ludwigia mollis Michaux, Fl. Bor.-Am. 1: 90. 1803. *Isnardia mollis* (Michaux) Poiret in Lam., Encycl. Suppl. 3: 188. 1813. TYPE: U.S.A. South Carolina: wet places, 1785–1796, *A. Michaux s.n.* (holotype, P; photographs, GH, MO; possible isotype, PH).

Plants hirtellous throughout. Stems much branched, 40–120 cm tall, often with prominent aerenchyma below when submerged in water, the hairs 0.25–0.95 mm long, translucent or spotted with light brown pigments. Stolons up to 2.5 m long, creeping in mud or floating in water, occasionally bearing flowers and fruits, the leaves obovate or elliptic to orbicular, 6.5–20 mm long, 5–11 mm wide, densely hirtellous to nearly glabrous, margin with distinct hydathodal teeth, petioles 2–7 mm long. Cauline leaves (upon drying) usually brownish green adaxially, brown abaxially, elliptic or lance-elliptic to very narrowly so, 15–80(–100) mm long, 3–12(–14) mm wide, those on the main stem usually 1.5–4 times longer than those on the branches, the veins reddish, the hairs 0.3–0.5 mm long, apex acute or narrowly acute, margin entire, hydathodal glands obscure, base acute to narrowly acute or attenuate, sessile or with petioles up to 2(–10) mm long. Stipules brownish purple, ovate to lanceolate, 0.2–0.25 mm long, up to 1 mm

FIGURE 53. *Ludwigia pilosa* (South Carolina: Berkeley Co., *Peng 4397*, MO).—a. Habit, erect stem.—a′. Basal stolons.—b. Cauline leaf.—b′. Stolon leaf.—c. Flowering branch.—d. Flower bud.—e. Flower.—f. Flower, partly dissected to show stigma, style, and disc.—g. Sepal.—h, h′. Adaxial and abaxial views of stamen.—i. Fruit.—j. Cross section of capsule.

wide, usually obscured by hairs on the stem. Flowers usually congested in upper leaf axils. Sepals very conspicuous, creamy white within, usually also tinged with pink along the main veins and edges, occasionally reddish when grown in exposed sites, ovate-triangular or triangular, with 3 parallel main veins that are usually raised and prominent on the adaxial surface, apex elongate acuminate to subcuspidate, ascending with reflexed tips, 3.5–5.5 (–6) mm long, 2–4 mm wide, densely hirtellous within. Petals 0. Anthers 0.6–0.9(–1.3) mm long; filaments yellowish, 1.5–2.5 mm long, distinctly dilated below. Pollen grains shed as tetrads. Nectary disc bright yellow, turning black upon drying, raised 0.3–0.75 mm on top of the ovary, 2–3.8 mm across, indistinctly 4-lobed, densely hirtellous around the style base and often sparsely hirtellous between the lobes. Style 1–2 mm long, sparsely to densely hirtellous, especially below; stigma 0.3–0.6 mm thick. Capsules subglobose or sometimes oblong-obovoid with rounded corners, 3–5 mm long and 3–4.5 mm thick, densely hirtellous, sessile or with pedicels up to 1 mm long. Bracteoles flanking the capsules, attached 1–2.25 mm above capsule base, linear-lanceolate or narrowly elliptic, hirtellous, 3–6.5(–7.2) mm long, 0.25–1.5(–1.7) mm wide. Seeds brown, elliptic oblong or oblong ovoid, slightly curved on both ends, 0.5–0.7 mm long, 0.25–0.35 mm thick, the surface cells nearly isodiametric. Self-compatible. Gametic chromosome number, $n = 16$.

Distribution. Plants of *Ludwigia pilosa* are frequently found in roadside ditches, in river marshes, in swales in sandy pine flats, at edges of pocosins, in peaty bogs, in low grassy savannahs, and in swamp forests. This species is distributed along the Atlantic coast of extreme southeastern Virginia, eastern and central North and South Carolina, southern Georgia, and northern Florida. It extends westward through the Florida panhandle, southern Alabama, Mississippi, and Louisiana, reaching eastern Texas. A disjunct population occurs in northern Alabama (Fig. 54). Flowering from late June through September; fruiting from late July through November.

Representative specimens examined. U.S.A. ALABAMA: Baldwin Co., Fort Morgan Peninsula, *Demaree 35917* (FSU, GH, SMU, USF, VDB). Barbour Co., ca. 5 mi. N of Eufaula on AL I-65, Cowickee Creek camp by Lake Eufaula, *Kral 33185* (VDB). Butler Co., ca. 11 mi. N of Georgiana by AL I-65, *Kral 40892* (VDB). Covington Co., ca. 8 mi. S of Opp, by US Hwy. 331, *Kral 32063* (SMU, VDB). Crenshaw Co., near Dozier, *Reed 2052* (TEX). Dale Co., near Clayhatchee, *Kral 22079* (DS, VDB). Dallas Co., just W of Selma, by Hwy. 22, *Perdue 4155* (FSU, VS). Elmore Co., W side of Elmore, by Mortar Creek, *Kral 40808* (VDB). Escambia Co., 1.3 mi. E of Wawbeek, *Kral 33831* (MO, VDB). Geneva Co., 3.2 mi. S of Hartford on AL Hwy. 167, *Kral 36728* (VDB). Houston Co., just E of jct. S of Spring Hill Church, Cypress Creek Swamp, *Clark 7343* (NCU). Lowndes Co., 10 mi. E of Minter, near Fostoria, *Kral 48927* (VDB). Macon Co., *Earle & Earle 49* (GH, MO, ND-G, NY, US). Madison Co., *Earle & Earle 49* (GH, MO, NY, US). Mobile Co., on Hollinger's Island, *Harper 4087* (GA, MO, NCU, NY, UNA, US, VDB). Pike Co., Spring Hill, *Bush 339* (S). Washington Co., 3.1 mi. S of St. Stevens, *Kral 37234* (FSU, VDB). FLORIDA: Alachua Co., near Waldo, 1936, *Survey s.n.* (FLAS). Bay Co., near Long Beach, *Godfrey & Kral 55075* (FSU, NCU). Bradford Co., near US Hwy. 301, *Radford 8245* (NCU). Calhoun Co., 10 mi. S of Blountstown, *Adams 700* (FLAS, FSU, GH, NY, SMU, VDB). Clay Co., 2.7 mi. S of Cove Springs along US Hwy. 17, *Raven 18686* (DS). Columbia Co., 3.6 mi. NE of Lake City, Osceola National Forest, *Perdue 1824* (C, FSU, GA, GH, NCU, SMU, TEX, USF). Duval Co., near Jacksonville, *Curtiss 924* (CM, F, FLAS, GA, GHM, MO, MSU, NY, US). Escambia Co., near Pensacola, *Burkhalter 2919* (FLAS). Franklin Co., 38.8 mi. W of jct. of US Hwys. 98 & 319, *Peng et al. 4345* (MO). Gadsden Co., ca. 3 mi. NW of Quincy along US Hwy. 90, *Webb & Ross 1011* (TENN). Gulf Co., between Weewahitchka & Port St. Joe, *Godfrey & Kral 54168* (DUKE, FSU, GH, NY, TEX, USF, VDB). Hamilton Co., 3 mi. E of Jasper, 1941, *West & Arnold s.n.* (FLAS). Holmes Co., 4.1 mi. W of Ponce de Leon, *McDaniel 5206* (FSU). Jackson Co., 5 mi. E of Marianna, near Rd. 90, *Hood 2593* (FLAS). Jefferson Co., W of Wacissa along Tram Rd., along St. Marks River, *Godfrey 70908* (FSU). Leon Co., 6 mi. N-NE of Chaires, *Kral 3687* (FLAS, GA, GH, NY, S, SMU, TENN, UNA, USF). Liberty Co., just S of Gadsden Co. line on Rt. 267, near jct. with Rt. 20, *Anderson 4477* (FSU, MO). Madison Co., 6.8 mi. W of Greenville on US Hwy. 90, *Raven 18625* (DS). Okaloosa Co., E of Oakgrove, near Yellow River, by FL Rt. 2, *Godfrey 75427* (FSU). Santa Rosa Co., between I-10 & Milton, *Godfrey 73798* (FSU). Wakulla Co., 6.1 mi. N of Sopchoppy along FL Hwy. 375, *Wooten 2270* (FSU). Walton Co., 3 mi. W of jct. US Hwy. 331 on US Hwy. 98, near Santa Rosa Beach, *Raven 18594* (DS, NCU). Washington Co., 3.5 mi. E of Caryville, *Kral & Godfrey 5961* (FSU, USF). GEORGIA: Appling Co., near Baxley, s.d., *s.c. 923h* (US). Atkinson Co., ca. 5 mi. S of Pierson, Coastal Plain Province, *Duncan 3015* (GA, GH, US). Baker Co., ca. Big Cypress area, 1946, *Ford & Thorne s.n.* (TENN). Brooks Co., 17 mi. N of Madison, FL on GA Hwy. 33, *Ramsey & Stripling 153* (FSU, SMU). Bryan Co., S side of Richmond Hill, *Kral 18806* (VDB). Bulloch Co., 3.5 mi. from jct. of GA Rt. 67 & GA Rt. 119, in SE part of county, near church, *Boole 1198* (NCU). Camden Co., 6.6 mi. S of Woodbine on US Hwy. 17, *Raven 18701* (DS, FLAS). Charlton Co., GA Hwy. 94, between Moniac & St. George, *Jones et al. 23027* (GA). Chatham Co., near Savannah, s.d., *s.c. 4169C* (S, US). Colquitt Co., 4.8 mi. NW of Berlin, Coastal Plain Province, *Faircloth 2676* (NCU). Cook Co., 6 mi. W of Adel at the Porter Purvis Farm, Coastal Plain Province, *Faircloth 2401* (GA, NCU). Decatur Co., 1.5 mi. E of Climax, by US Rt. 84, *Godfrey 77562* (FSU). Dooly Co., 2 mi. N of Pinehurst turnoff, by I-75, *Kral 51610* (VDB). Early Co., W central boundary of Co. in Moccasin Pond, *Duncan 4025* (GA, MO,

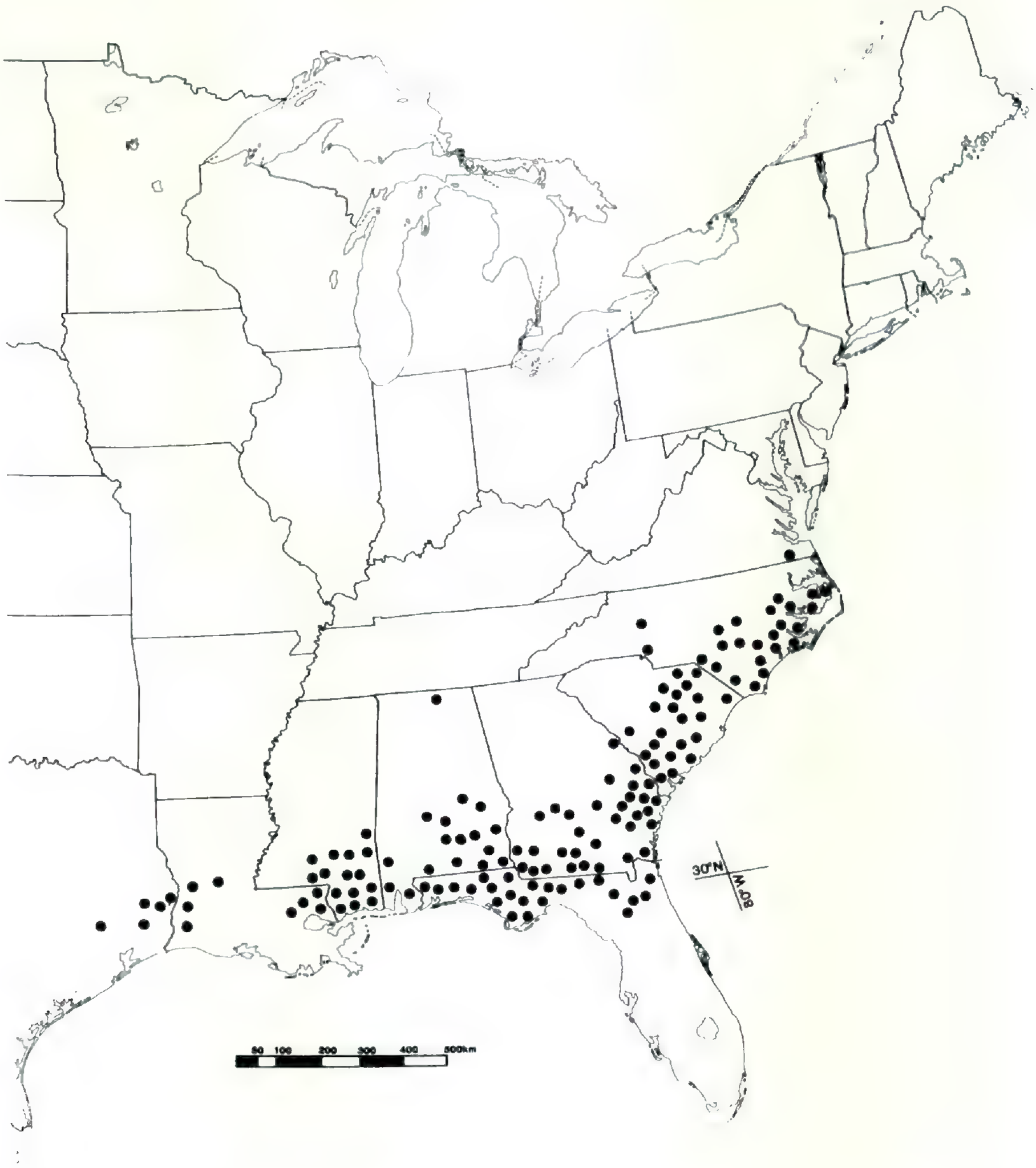

FIGURE 54. Distribution of *Ludwigia pilosa*.

SMU). Echols Co., 2.6 mi. E of Statenville, *Kral 51645* (VDB). Effingham Co., near Eden, 1875, *Curtiss s.n.* (US). Emanuel Co., 0.8 mi. S of I-16 on US 1 along the Ohoopee River, *Peng et al. 4024* (MO). Evans Co., 1 mi. S of jct. GA 169 & US 25 & 301, on US 25 & 301, *Peng et al. 4107* (MO). Grady Co., 3.5 mi. NW of Calvary on the J. R. Boyette property, *Faircloth 1510* (GA, MO, NCU). Irwin Co., 7.3 mi. SW of Irwinville at Tift–Irwin county line, *Faircloth 5408* (GA). Lanier Co., 2 mi. S of Lakeland, along GA Hwy. 31, *Thigpen et al. 226* (NCU). Liberty Co., near Hinesville, Camp Stewart, 1943, *Gumm s.n.* (C). Long Co., 4.2 mi. SE of Tattnall county line on US 301 & 25, *Peng et al. 4110* (MO). Lowndes Co., 7.3 mi. N of Valdosta, *Faircloth 2634* (GA, NCU). McIntosh Co., 2 mi. E of power line on Wesley Lake Rd., *Bozeman 2307* (GA, NCU). Richmond Co., Sanitary Dairy Pond, Augusta, 1924, *Hildebrand s.n.* (DUKE mixed with *L. pilosa* × *L. sphaerocarpa*). Screven Co., 7 mi. S of Sylvania, *Kral 22363* (VDB). Seminole Co., 1.5 mi. E of Donaldsonville, *Godfrey 63209* (FSU). Sumter Co., near Leslie, *Harper 591* (NY, US, W). Tattnall Co., 1.6 mi. N of Lane's Bridge, GA Hwy. 169, *Bozeman 5979* (NCU). Wayne Co., 5.8 mi. W-NW of Odum, *Duncan 23859* (FLAS, GA). Wheeler Co., 4.5 mi. W of Alamo, *Kral 22330* (VDB). Wilcox Co., 10.9 mi. N-NW of Abbeville, *Duncan & Hardin 14264* (GA, MISS, NCU, SMU, TENN, USF). LOUISIANA: Beauregard Parish, 6 mi. N of Singer, near Zion Church, *Thieret 28115* (FSU). Calcasieu Parish, 2.5 mi. W of Sulphur, just S of Stegall, *Thieret 20591* (DS, FSU). Livingston Parish, near Albany, *Rogers 2415-A* (NCU, SMU). Rapides Parish, near Alexandria, s.d., *Hale s.n.* (GH). St. Tammany Parish, just S of St. Tammany along Bayou Lacombe, *Thieret 21648* (DS, FSU). Tangipahoa Parish, 1 mi. W of Robert, *Correll & Correll 9288* (DUKE, FSU, ND). Vernon Parish, ca. 3.5 mi. E of Rosepine off LA 1146, *Allen & Vincent 651* (GA). Washington Parish, near Franklinton, *Demaree 46896* (MO, NO, SMU). MISSISSIPPI: Clarke Co., 1896, *Schuchert s.n.* (NY). Covington Co., S of Collins, Hwy. 49, *Jones 10908* (GA, MISS, NCU). Forrest Co., near Rayland Hills, *Rogers 4096* (MISS). George Co., near Agricola, *Demaree 32797* (DUKE, SMU, VDB). Hancock Co., 2 mi. NE of MS 603 on MS 43, *Peng et al. 4359* (MO). Harrison Co., near Handsboro, *Demaree 29713* (DUKE, NCU, SMU, TEX, VDB). Jackson Co., 2 mi. W of US 10 & MS 90, on MS 90, *Peng et al. 4354* (MO). Jones Co., 6.6 mi. NE of Moselle on MS Hwy. 11, *Raven 18568* (DS).

Lawrence Co., 2 mi. N of Monticello on Hwy. 270, *Jones 9976* (MISS). Marion Co., 0.8 mi. S of Sandy Hook on Hwy. 35, *Jones et al. 20280* (FSU, GA, MISS, VDB). Pearl River Co., 6 mi. NW of Poplarville, *Darwin et al. 729* (MO, NO). Perry Co., 5 mi. E of Runnelstown, *Jones 9599* (MISS). Stone Co., near McHenry, U. of Miss. Forest Lands, *Demaree 34056* (DS, SMU, USF). Walthall Co., N of Varnado, just over LA line on LA 21, *Kral 17394* (VDB). Wayne Co., 2.7 mi. E of county line, Hwy. 84, *Jones 9724* (MISS). NORTH CAROLINA: Beaufort Co., near Washington, *Sargent 54* (US). Brunswick Co., 0.2 mi. W of Longwood on NC 904, *Peng et al. 3886* (MO). Carteret Co., 0.25 mi. from Hwy. 70 on rd. to Harker's Island, *Blomquist 15572* (DUKE, VDB). Columbus Co., 2.7 mi. N of Wananish, *Fox & Whitford 1889* (FSU, NCSC, SMU). Craven Co., 6.3 mi. NE of Jones Co. line on county rd. 1100, *Peng et al. 3832* (MO). Cumberland Co., 1.5 mi. NE of Godwin, just E of Damat Rhode's pond, *Fox 5627* (FSU, NCSC, NY, SMU). Dare Co., just N of Manteo city limits, beside US 64, *Duke 54237* (NCU). Duplin Co., 0.7 mi. NW of Pin Hook, *Ahles 35840* (FLAS). Harnett Co., 8 mi. S-SW of Lillington on Anderson Creek at NC 210, *Beal 2702* (NSC). Hyde Co., 12 mi. W of Swan Quarter, *Oosting 30* (DUKE, FLAS). Iredell Co., near Statesville, s.d., *Hyanus s.n.* (MO). Johnston Co., E of Clayton, near jct. of NC Hwys. 96 & 42, *Radford 44388* (NCU). Jones Co., 0.4 mi. W of county rd. 1105 (Catfish Rd.), on Forest Service Rd. 172 (Mirey Branch Rd.) E-SE of Maysville off NC Rt. 58, *Peng et al. 3802* (MO). Martin Co., 1 mi. NW of Parmele, near US 64, *Radford 39337* (GH, NCU). Mecklenburg Co., near Smithsville, Oct., *s.c., s.n.* (NY). New Hanover Co., 1867, *Canby s.n.* (F, NY). Onslow Co., 5.5 mi. S of NC 41, on county rd. 1003, S of Comford, *Peng et al. 3791* (MO). Pamlico Co., 1.1 mi. W of Grantsboro, Goose Creek, *Beal 2521* (DUKE, NCSC). Pender Co., 1 mi. S of Ward's Creek on US 421, *Duke 6472* (NCU). Pitt Co., 400 yds. E of jct. of NC Hwys. 11 & 903, *Duke 54173* (NCU). Robeson Co., 2.6 mi. E of Daystrom on rd. to Philadelphus, *Ahles & Leisner 32962* (NY, VDB). Sampson Co., 0.9 mi. S of Halls Store, vicinity of Mill Pond, *Ahles & Leisner 33640* (NCU). Scotland Co., 4.7 mi. E-NE of Johns on rd. to Maxton, *Ahles 3700* (NCU). Tyrell Co., 1.5 mi. SE of Cross Landing, *Radford 42541* (NCU, USF). SOUTH CAROLINA: Aiken Co., 1969, *HWR s.n.* (US). Allendale Co., ca. 2 mi. W of Barton on County Rd. 23, *Bell 5106* (NCU). Bamberg Co., 0.7 mi. W of Olar on SC 64, then 0.8 mi. S on dirt rd. (SW of Olar), *Ahles 37683* (NCU). Beaufort Co., 5 mi. S of Hardeeville, *Eyles 4400* (GA). Berkeley Co., 10 mi. NW of Bonneau, *Godfrey & Tryon 1623* (GH, US). Charleston Co., 4.8 mi. E of SC 174 on US 17, E of Osborn, *Peng et al. 3908* (MO). Chesterfield Co., 3 mi. NW of Patrick, near SC 102, *Radford 15873* (NCU). Clarendon Co., 1 mi. S of Sandinia, Black River Swamp, *Godfrey & Tryon 1486* (F, GH, MO, NY, TENN, US). Colleton Co., 4.2 mi. E of Smoaks, *Raven 18717* (DS). Darlington Co., across lake from Hartsville, *Smith 35* (NCU). Dorchester Co., 1.5 mi. N-NE of St. George on US 15, *Ahles & Haesloop 37776* (NCU). Horry Co., on SC Hwy. 9, 3 mi. NW of jct. US Hwy. 17, *Dille & Dille 342* (MO). Jasper Co., 2.5 mi. N of SC 46 on US 17, N of Hardeeville, *Peng et al. 3973a* (MO). Richland Co., 7 mi. SE of Columbia, *Smith 860* (GH). Florence Co., forest at N limits of Scranton, *Raven 20456* (DS). Hampton Co., 1.8 mi. NW of Yemassee on SC 28, *Ahles & Bell 18351* (NCU). Horry Co., 2 mi. N of Little River, beside Hwy. 905, *Duke 54115* (NCU). Jasper Co., 2.5 mi. N of SC Hwy. 46 on US Hwy. 17, N of Hardeeville, *Peng et al. 3973-a* (MO). Kershaw Co., 4.5 mi. SE of Bethune, near Lynches River, *Radford 27737* (NCU). Lee Co., 6 mi. W of Bishopville, near SC 34, Scape Ore Swamp, *Radford 29437* (NCU). Marlboro Co., 1.5 mi. E of Wallace, near SC 90, *Radford 15626* (NCU). Orangeburg Co., *Eggleston 5025* (GH, MO, NY). Sumter Co., 15 mi. E of Mayeville, near SC 53 & Lynches River, *Radford 27561* (NCU). Williamsburg Co., 3.5 mi. S of Andrews, *Kral 19168* (VDB). TEXAS: Hardin Co., 2 mi. N of Gist, *Cory 50923* (GH, NY, SMU). Jasper Co., 20 mi. NW of Jasper, *Correll 28573* (TEX). Montgomery Co., just W of Fostoria, *Correll 33994* (GH, TEX). Newton Co., 1.5 mi. E of Kirbyville, State Forest No. 1, *Cory 49815* (DS, GH, NY, SMU, US). Tyler Co., ca. 3.5 mi. S of Warren, Hyatt Lake Estates, *Correll & Correll 36729* (TEX). VIRGINIA: Nansemond Co., S of Baines Hill School, Adams Swamp, *Fernald & Long 13705* (C, GA, GH, MO, TENN).

Ludwigia pilosa is a distinctive species in sect. *Microcarpium* characterized by being densely hirtellous throughout; reddish brown leaf midveins especially abaxially; sepals elongate-triangular, creamy, and often tinged with pink, reflexed at the tips; and capsules subglobose to somewhat oblong-obovoid, with a pair of long bracteoles attached slightly above the base. The only species that has consistently been confused with *L. pilosa* is the recently named *L. ravenii* (Peng, 1984). The similarity in these two species is in aspect and in the vestiture. They differ in many other characters, notably floral parts and breeding systems. *Ludwigia ravenii* is modally autogamous, with obscure greenish sepals, and all of its floral parts are significantly smaller than those of *L. pilosa*. Further, the seed surface cells are transversely elongate rather than subisodiametric.

The flowers of *Ludwigia pilosa*, in contrast, are unable to undergo mechanical self-pollination. Their showy sepals and copious nectar, which is produced by the nectary disc, unfailingly attract various insect visitors such as ants, wasps, bumblebees, honeybees, and moths to effect pollination. *Ludwigia pilosa* grows with diploid *L. linifolia*, *L. microcarpa*, tetraploid *L. glandulosa*, *L. lanceolata*, *L. ravenii*, *L. sphaerocarpa*, *L. suffruticosa*, and the hexaploid *L. alata*, which is closely allied to the tetraploid species group. It forms fertile hybrids with probably all tetraploid species and with *L. alata* when they grow together. Natural hybrids between *L. pilosa* and *L. ravenii* are presumably rare (*L. ravenii* is rare itself) and difficult to detect. An intersectional hybrid between *L. pilosa* and *L. arcuata* ($n = 16$; sect. *Dantia*) was found in Mobile Co., Alabama (Peng, 1988). All natural hybrids are intermediate morphologically, having vestiture similar to that of *L. pilosa* but shorter and other

features diagnostic of the other putative parents (e.g., the winged fruits of *L. lanceolata*, elongate capsules of *L. glandulosa*, and additional features). Two such hybrids have previously been named: *L. capitata β pubens* Torrey & A. Gray (= *L. pilosa* × *L. suffruticosa*) and *L. simulata* Small (= *L. pilosa* × *L. lanceolata*). Kral (1976) reported a range extension of *L. polycarpa* to Alabama, based, in fact, on a natural hybrid population of *L. pilosa* × *L. glandulosa*. The only species that hybridizes extensively with *L. pilosa* and produces many hybrid swarms or introgressed populations is *L. sphaerocarpa*. Plants of these populations exhibit a varying degree of intermediacy between the two species. They are discussed further under *L. sphaerocarpa*.

Hybrids between *Ludwigia pilosa* and the other tetraploid species or the hexaploid *L. alata* are readily synthesized in the experimental greenhouse and are quite fertile. It is generally difficult to obtain hybrids between *L. pilosa* and diploid species or the *L. curtissii* complex. Floriferous and vigorous hybrids of *L. pilosa* × *L. linifolia* and *L. pilosa* × *L. curtissii*, however, were obtained. Seed set was nonexistent or negligible in these hybrids.

11. Ludwigia ravenii Peng, Syst. Bot. 9: 129. 1984. TYPE: U.S.A. South Carolina: Berkeley Co., 0.1–0.2 mi. SW of jct. of Co. 16 and Co. 6, on Co. 16 W of Moncks Corner, scattered in roadside sedgy, sandy ditch, on loam densely covered by *Sphagnum subsecundatum* Nees, associated with *Cyperus, Xyris, Eriocaulon, Paspalum, Panicum, Hypericum, Polygonum, Rhexia, Liatris, Eupatorium, Ludwigia linearis* Walter, *L. hirtella* Raf., 9 Sep. 1982, *Ching-I Peng 4402* (holotype, MO-3041593; isotypes, B, BM, DAO, DUKE, F, FLAS, FSU, FTG, GA, GH, HAST, KYO, LE, MISS, MISSA, MO, NCSC, NCU, NY, P, PE, TAI, TAIF, TENN, TI, US, USF, VDB). Figure 55.

Plants densely hirtellous throughout. Stems erect, usually well branched and leafy, (15–)35–90 cm tall, densely hirtellous, the hairs 0.3–0.6(–0.75) mm long; aerenchyma (if any) slightly developed, in lower stems. Stolons slender, several from the base, to 18 cm long, 0.6–1.5 mm thick, glabrous or hirtellous, occasionally bearing flowers and fruits, the leaves purplish, elliptic to rotund, 10–18 mm long, 6–14 mm wide, apex rotund to acute, base attenuate into a petiole 1–3 mm long. Cauline leaves pale green on both surfaces, narrowly lance-elliptic, 13–65 mm long, 4–15 mm wide, densely hirtellous on both surfaces, the hairs 0.2–0.5 mm long, apex acute, margin entire with minute hydathodal glands, base attenuate into narrowly winged petiole 1–8 mm long. Stipules reddish purple, lanceolate to widely deltate, succulent, 0.25–0.45 mm long, 0.15–0.25 mm wide. Flowers many, in leaf axils, not congested. Sepals green on both surfaces, broadly ovate-deltate, 1.5–3 mm long, 1.4–2.1 mm wide, densely hirtellous without, glabrous within, apex acuminate, margin entire. Petals 0. Anthers 0.3–0.35 mm long, 0.4–0.5 mm wide; filaments 0.7–1.1 mm long. Pollen grains shed as tetrads. Nectary disc greenish, raised 0.3–0.4 mm on ovary apex, 1.4–2.5 mm across, 4-lobed, glabrous. Style 0.25–0.5 mm long, glabrous; stigma subglobose, 0.25–0.45 mm across. Mature capsules oblong-obovoid, obconical when young, (3–)4–5(–5.3) mm long, 2–3.5(–4) mm thick, densely hirtellous, pedicels 0.2–0.5 mm long. Bracteoles attached near capsule base, lanceolate or elliptic to very narrowly so, (1.5–)2–4.3 mm long, 0.25–0.9 mm wide, hirtellous. Seeds light brown, elliptic-oblong with slightly curved ends, 0.5–0.7 mm long, 0.25–0.35 mm thick, pluriseriate in each locule, free, the surface cells elongate transversely to the seed length. Self-compatible and modally autogamous. Gametic chromosome number, $n = 16$.

Distribution. *Ludwigia ravenii* occurs in wet, peaty habitats, such as ditches or margins of ponds, bogs, and swamps. It is found as scattered populations in coastal southeastern Virginia, eastern North Carolina, and southeastern South Carolina and with somewhat disjunct populations in northeastern Florida (Fig. 56). Flowering from July to September; fruiting from August to October.

Specimens examined are cited in full in Peng (1984).

This recently discovered species consists of scattered, morphologically very uniform populations. Owing to its densely hirtellous vestiture and relative rareness, it was previously not well understood and was confused with *Ludwigia pilosa*, the only other species of sect. *Microcarpium* that is consistently densely hirtellous; that species, however, is widespread and common. As was shown in the table comparing *L. ravenii* with related species (Peng, 1984), *L. ravenii* is very distinct from *L. pilosa*.

Ludwigia ravenii has small inconspicuous flowers with greenish sepals and short stamens and styles. Its anthers are firmly appressed to the stigma shortly after anthesis. These characteristics strongly suggest that it is modally autogamous. This was corroborated by my field study at the type

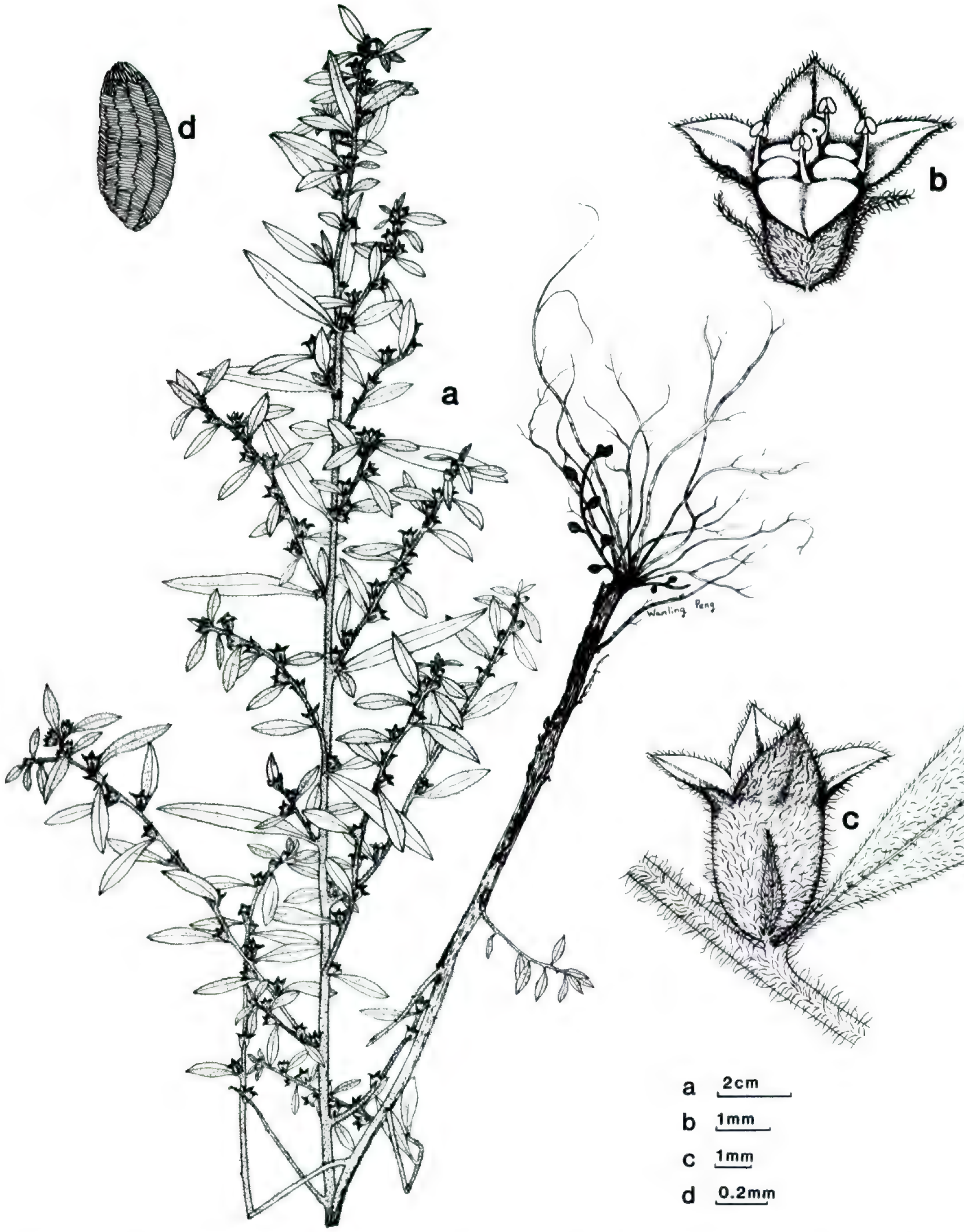

FIGURE 55. *Ludwigia ravenii* (North Carolina, Sampson Co., *Boufford & Wood 18898*, CM).—a. Habit.—b. Flower.—c. Fruit.—d. Seed. (Reprinted with permission from *Systematic Botany*.)

locality (Peng, 1984): for two hours by the ditch where *L. ravenii* grew, I did not observe any insect visitors, whereas 0.5 mi. away in the same ditch, I witnessed a swarm of honeybees visiting and hovering over flowers of a population of *L. pilosa*.

Ludwigia ravenii does not appear to grow aggressively. It starts to form stolons only late in its fruiting season (September to October). Unlike most other tetraploid members of sect. *Microcarpium*, these stolons are usually slender and short, resembling those of *L. microcarpa*. Consequently, the populations consist of scattered individuals instead of large colonies connected by stolons, as is typical in *L. pilosa* and other species.

Live plants of *Ludwigia ravenii* were not collected until after the completion of my biosystematic study of *Ludwigia* sect. *Microcarpium*, so its genetic relationships with the other tetraploid

FIGURE 56. Distribution of *Ludwigia ravenii*.

members of the section remain obscure. The extensive crossing data already available for other species clearly demonstrate, however, that pollen stainability and seed set are high in hybrids between any two tetraploid species, no matter how different morphologically they are (Peng, 1988). Circumstantial evidence thus suggests that *L. ravenii* is almost certainly interfertile with other species of the tetraploid group of sect. *Microcarpium*.

12. Ludwigia microcarpa Michaux, Fl. Bor.-Am. 1: 88. 1803. *Isnardia microcarpa* (Michaux) Poiret in Lam., Encycl. Suppl. 3: 188. 1813. LECTOTYPE: U.S.A. South Carolina: Berkeley Co., Goose Creek, wet places, 1785–1796, *A. Michaux s.n.* (lectotype, P; photograph, MO; here selected). Figure 57.

Plants glabrous, varied in habit, ranging from erect, unbranched, slender herbs to being profusely branched with somewhat woody bases. Stems erect or ascending, rarely prostrate and rooting at the nodes, 5–60 cm tall, 0.4–1.5(–4) mm thick, the leaf bases distinctly decurrent, with or without aerenchyma at stem base. Stolons pinkish, several from base, slender, 4–15(–25) cm long, 0.4–0.75 mm thick, the leaves broadly elliptic to suborbicular, 2.2–6.6 mm long, 2.2–5.2 mm wide, petioles 1.5–5 mm long. Cauline leaves obovate-spatulate or oblanceolate, sometimes narrowly oblance-elliptic, 4–17 mm long, 1.5–10 mm wide, glabrous, apex acute or mucronate, margin subentire, with prominent hydathodal glands forming minute teeth, minutely papillose-strigillose, the hairs ca. 0.05 mm long, occasionally smooth, base attenuate into winged petioles 0.5–5 mm long; main veins on each side of the midrib 3–4, obscure adaxially, conspicuous and slightly raised abaxially; branch leaves sometimes remarkably smaller than main cauline leaves. Stipules reddish purple, lanceolate-deltate, succulent, ca. 0.13–0.15 mm long, 0.1–0.13 mm wide. Flowers axillary, usually not crowd-

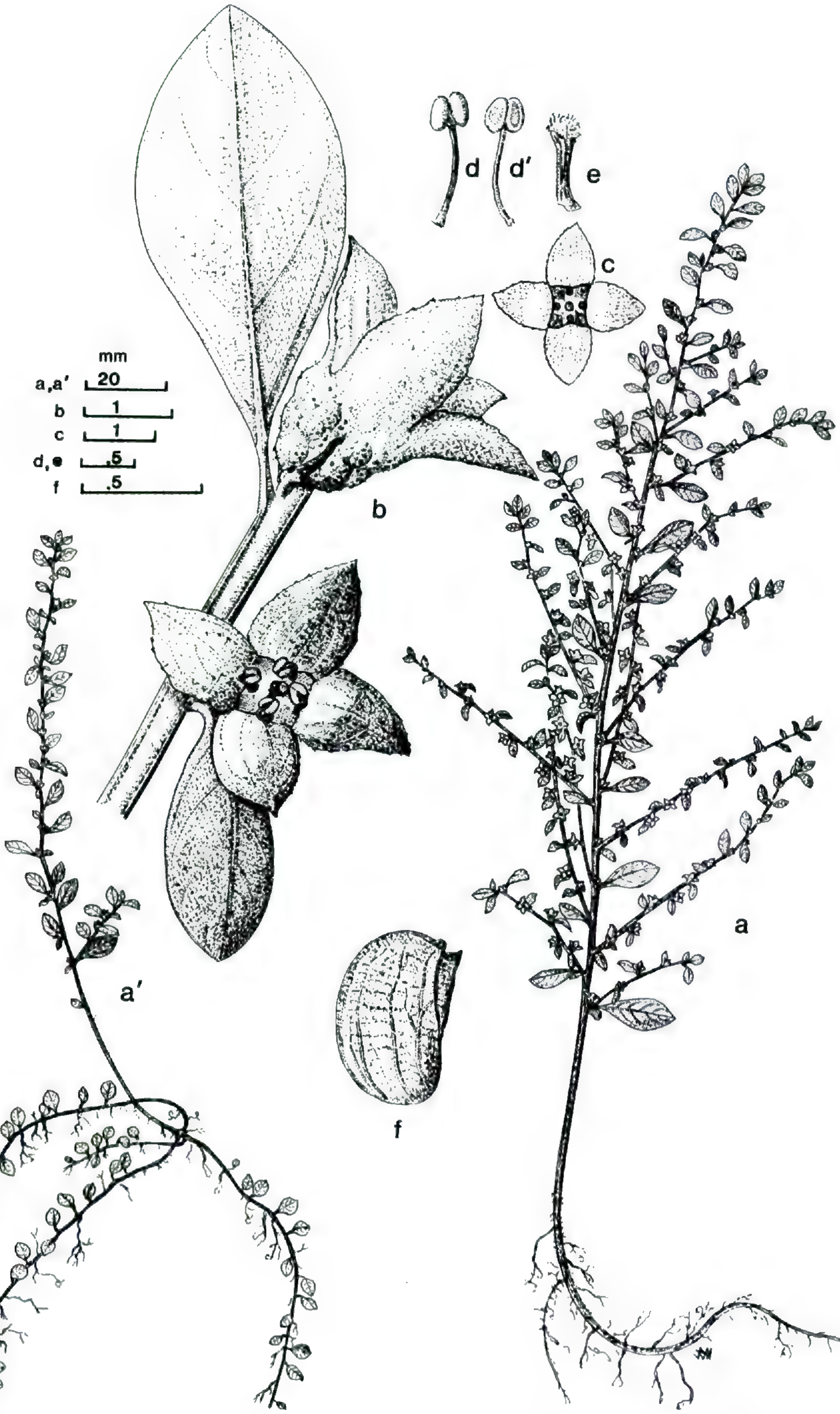

FIGURE 57. *Ludwigia microcarpa*. All but a' from Florida (Monroe Co., *Godfrey 63525*, MO); a' from North Carolina (Brunswick Co., *Leonard & Moore 7579*, MO).—a. Habit, showing erect stem.—a'. Erect plant with basal stolons.—b. Portion of branch with flower and fruit.—c. Top view of fruit.—d, d'. Adaxial and abaxial views of stamen.—e. Stigma and style with pollen on stigma.—f. Seed.

ed. Sepa is green with whitish, thickened base, ascending in flower and spreading in fruit, ovate-deltate, 0.9–2 mm long, 1–1.85 mm wide, glabrous, apex acuminate, margin remotely minutely papillose-strigillose, occasionally smooth. Petals 0. Anthers 0.1–0.2 mm long; filaments translucent, 0.4–0.55 mm long. Pollen grains shed singly. Nectary disc greenish, nearly flat on ovary apex, 0.5–1.2 mm across, 4-lobed, these represented by 4 greenish rhomboid spots, alternating with 4 smaller, rounded reddish scars of anther base on top of the mature capsule, glabrous. Style pale green, 0.25–0.4 mm long, glabrous; stigma green, subglobose, ca. 0.05–0.1 mm thick. Capsules obconical, 1–1.5 mm long, 1.4–1.9 mm thick, minutely puberulent, the hairs ca. 0.05 mm long, thin-walled, containing 6–20 seeds, these sometimes recognizable from outside as bumps, sessile or with pedicels up to 0.15 mm long. Bracteoles flanking capsule base, sublinear or narrowly oblong, 0.35–1.2(–1.5) mm long, 0.1–0.4 mm wide, usually with a swollen base, glabrous. Seeds dark reddish, ovate-oblong, 0.5–0.55 mm long, 0.3–0.4 mm thick, the surface cells transversely elongate, glabrous or sometimes densely covered by strigillose hairs (waxes?). Self-compatible and modally autogamous. Gametic chromosome number, $n = 8$.

Distribution. Plants of *Ludwigia microcarpa* grow in roadside ditches, marshes, ponds and streams at the borders, low meadows, low areas in open woods, edges of swamp forests, brackish marshes, hammocks, and solution pits of limestone on marl prairies. This species occurs along the Atlantic coast of North and South Carolina and Georgia, and throughout the Florida peninsula. It extends westward across the panhandle of Florida, southern Alabama, reaching southern Mississippi, with a single population in southwestern Louisiana. To the north, *L. microcarpa* occurs through western Georgia and central and western Alabama to southcentral Tennessee. Scattered populations are found in northcentral North Carolina and southcentral Missouri (Fig. 58). Furthermore, *L. microcarpa* occurs on several Caribbean islands, including the Bahamas, Cuba, and Jamaica. Flowering and fruiting throughout the year.

Representative specimens examined. U.S.A. ALABAMA: Baldwin Co., River Styx E of Mobile on US 90, *Kral 35805* (MSC, VDB). Bibb Co., ca. 7 mi. N Centerville by Co. 27, *Kral 47928* (VDB). Calhoun Co., 5.5 mi. W Piedmont on US 278, *Kral 37736* (VDB). Cherokee Co., US 411, 2 mi. W of Centre, *Kral 31769* (GA, NCU, SMU, VDB). Chilton Co., I-65, ca. 9 mi. N of Clanton and AL 22, *Kral 53296* (VDB). Clarke Co., on Co. 19, N of Choctaw Bluff, *Kral 35473* (NY, VDB). Conecuh Co., ca. 4 mi. NE of Lenox, *Kral 40954* (VDB). Covington Co., 2 mi. W of Opp, *Kral 20622* (VDB). Geneva Co., W side of Geneva, *Kral 32026* (FSU, SMU, VDB). Houston Co., Chattahoochee State Park, *Godfrey 75953* (FSU). Morgan Co., ca. 4 mi. S of Decatur, *Kral 33465* (C, SMU, VDB). St. Clair Co., ca. 3 mi. NW of Asheville, by US 231, *Kral 32361* (NCU, SMU, VDB). FLORIDA: Alachua Co., Gainesville, 1938, *Arnold & West s.n.* (DUKE, FLAS). Bay Co., 1 mi. N of Panama City, FL 77, *Godfrey 75318* (MO). Broward Co., S of Wiles Road, 1.4 mi. W of US 441, ca. 3 mi. N of Margate, 1964, *Will s.n.* (FLAS, FSU). Calhoun Co., banks of Chipola River, Wofaltha, *Godfrey 57758* (FSU, GH). Charlotte Co., Punta Gorda city, on US Hwy. 41, ca. 1 mi. S of jct. of US Hwys. 17 & 41, *Peng et al. 4294* (MO). Citrus Co., 5 mi. S Homosassa, *Kral 7770* (GH, US). Clay Co., 5 mi. W of Penny Farms on FL Hwy. 16, *Peng et al. 4161* (MO). Collier Co., on FL Hwy. 82, 1.2 mi. N of C-890; 5.7 mi. E of Hendry county line, *Peng et al. 4281* (MO). Columbia Co., Camp O'Leno, *Beck 243* (FLAS). Dade Co., 25 mi. W of FL Hwy. 27, on US Hwy. 41, *Peng et al. 4217b* (MO). Dixie Co., 4 mi. NW of Cross City, *Godfrey 56021* (CM, DS, DUKE, GH, LL, MO, MSU, NCU, NY, SMU, TENN). Duval Co., FL Hwy. 13, 1.1 mi. N of Interstate 295, *Peng et al. 4147* (MO). Escambia Co., Pensacola, *Godfrey 74408* (FSU, NCU, MO). Franklin Co., 41.7 mi. W of jct. (the one that is closer to Teresa Beach) of US Hwys. 98 & 319, *Peng et al. 4348* (MO). Gulf Co., 3 mi. S of Port St. Joe, *Kral & Kral 7191* (FLAS, GH, US, USF). Hendry Co., along FL 29, about 3 mi. S of La Belle, *Henderson 63-1611* (FSU). Hernando Co., 3 mi. W of Weeki Wachee Springs, *Kral & Kral 7029* (FLAS, GA, GH, NY, USF). Hillsborough Co., 2.8 mi. N of FL Hwy. 582, on E side of FL Hwy. 581, *Peng et al. 4332* (MO). Holmes Co., 1 mi. W of Wentville, *Kral & Redfearn 2885* (FSU, GH, NCU). Indian River Co., canal margins 10 mi. W of Vero Beach, *Kral 4942* (FSU, VDB). Jackson Co., Lake Seminole, N of Sneads, *Godfrey & Houk 61399* (FSU, NCU, SMU). Lake Co., 3.7 mi. S of Mascotte city limit, on county rd. 33, *Peng et al. 4166* (MO). Lee Co., 3.8 mi. S of Gladiolus Dr. (865) on San Carlos Blvd. (865), *Peng et al. 4288* (MO). Leon Co., Ochlockonee River W of Tallahassee, *Godfrey 73131* (FSU, MO, NCU, TENN). Levy Co., 0.5 mi. S of Gulf Hammock, *Kral & Kral 6963* (FLAS, GA, GH, USF). Liberty Co., 3.3 mi. E of FL 65 on FL 20, *Boufford et al. 18407* (MO). Madison Co., 2.6 mi. W of the Aucilla River on US 90, *Boufford & Ahles 9554* (CM, MO). Manatee Co., US 301 2 mi. N of Sarasota, *Raven 18657* (DS). Marion Co., Eureka, *Godfrey 60141* (FSU, MSU). Martin Co., 4.3 mi. E of Okeechobee and Martin Co. line, on FL Hwy. 710, at Brady Ranch, between RR and Hwy., *Peng et al. 4200* (MO). Monroe Co., along rd. to Watson Hammock; Big Pine Key, *Killip 44291* (DS, FLAS, GA, GH, NY). Osceola Co., N of FL 532, ca. 1.5 mi. E of Interstate 4, *Wunderlin & Shuey 5829* (USF). Palm Beach Co., NW of Loxahatchee in the Corbitt Wildlife Mgmt. area, *Kral 5634* (FSU, SMU, VDB). Pasco Co., Aripeka, *Godfrey 57244* (FSU). Pinellas Co., along FL 580, ca. 1 mi. E of its jct. with US 19, *Henderson 63-1540* (FSU, JE, TEX). Polk Co., along US 192, just inside the county line, at the edge of Davenport, *Henderson 63-1632* (FSU). Putnam Co., 2.5 mi. S of San Mateo, *Godfrey & Reinhert 61131* (FSU). St. Johns Co., 1.9 mi. N of jct. of FL Hwy. 207 & C-305, on FL Hwy. 207, *Peng et al. 4156* (MO). Sarasota Co., on FL Hwy.

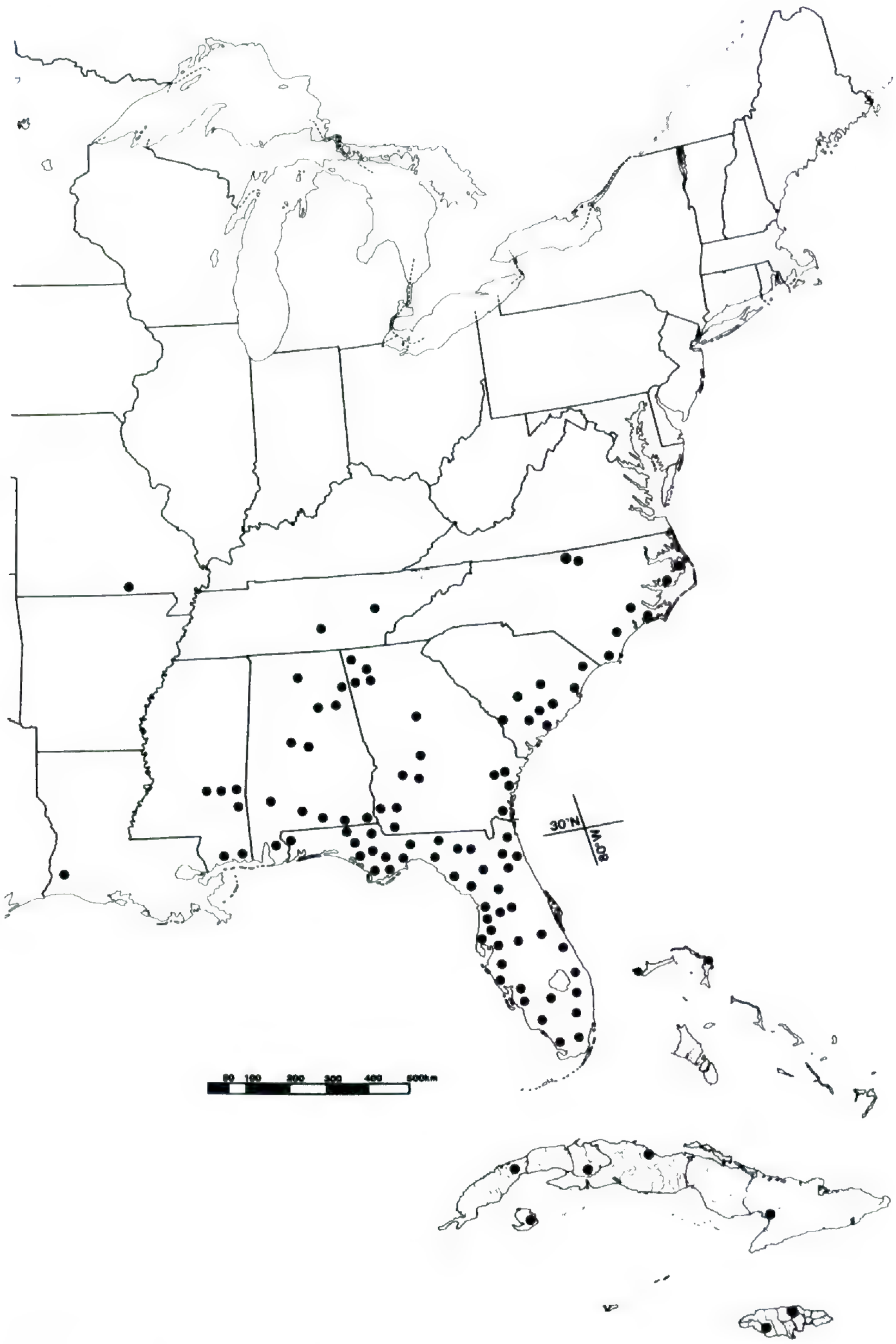

FIGURE 58. Distribution of *Ludwigia microcarpa*.

72, 0.5 mi. E of W boundary of Myakka River State Park, *Peng et al. 4313* (MO). Sumter Co., Bushnell, 14 mi. S of Rt. 301, *Sargent 6728* (SMU). Suwannee Co., Mayhaw ponds 5 mi. W of O'Brien, 1946, *West & Arnold s.n.* (FLAS). Taylor Co., on US Hwy. 98, 3.9 mi. W of jct. of US 27, 19 & 98 (Perry), *Peng et al. 336* (MO). Wakulla Co., 2 mi. N of St. Marks, *Raven 18601* (DS, NCU, USF). Washington Co., Alligator Creek, Rt. 90, W of Chipley, *Hood 2927* (FLAS). GEORGIA: Baker Co., Ivey's Mill Pond, *Eyles 7183* (DUKE, GA). Bartow Co., at edge of broad swampy runway from large spring S of Aubrey Lake, 5.6 mi., N12′ E of Cartersville, *Harris & Duncan 12797* (DUKE, FLAS, GA, GH, NCU, SMU, TENN, US, USF, VDB). Camden Co., 6.6 mi. S of Woodbine on US 17, *Raven 18703* (DS, NCU). Crisp Co., pond near Flint River, W of Cordele, *Eyles 6612* (GA). Decatur Co., along Spring Creek below dam, lots 30 and 31, District 21, *Thorne & Davidson 17267* (GA). Early Co., Cohelee Creek, 2 mi. NW of Hilton, *Duncan 6808* (GA). Floyd Co., 4.7 mi. N5′ W of Cave Springs, *Venard & Duncan 13114* (GA). Gordon Co., 1 mi. N of Fairmont, *Duncan 7219* (GA, MISS). Houston Co., 14 mi. S of Hawkinsville, *Svenson 6982* (TENN). Jasper Co., Monticello, 1846, *Porter s.n.* (GH, NY). Liberty Co., N of Liberty Co. line, S of Hinesville, *Kral 18859* (VDB). Long Co., 1.4 mi. SW of jct. of US Hwys. 301 & 25, and GA Hwy. 99, on US Hwys. 301 & 26, along Altamaha River, *Peng et al. 4127* (MO). McIntosh Co., 0.4 mi. NW of

jct. of Cox Rd. and GA Hwy. 251, on Cox Rd., *Peng et al. 4133* (MO). Sumter Co., in pine barrens, *Harper 471* (F, GH, MO, NY, US). Walker Co., Chickamauga, s.d., *s.c. 2671a* (US). LOUISIANA: Calcasieu Parish, vicinity of Lake Charles, *Mackenzie 426* (F, MO, NCU, NY). MISSOURI: Oregon Co., Hatcher's Spring in valley of Greer Spring branch, 1 mi. N of Greer, *Steyermark 27987* (F, GH). MISSISSIPPI: Clarke Co., Jackson Prairie, 1.5 mi. S-SW of Pachuta, *Jones & Jones 14614* (FSU, GA, MISS, NCU, USF, VDB). Harrison Co., ca. 4 mi. N of Biloxi, *Rogers 6780* (GH, NCU, NY). Jackson Co., 1 mi. N of Franklin Creek Church, ca. 5 mi. NE of Orange Grove, *Jones & Catchot 17421* (GA, MISS, TENN, USF). Jasper Co., 9 mi. N of Montrose, *McDaniel 2631* (NY, UNA). Smith Co., ca. 4.5 mi. W of Bay Springs, *Rogers 46028* (TENN). Wayne Co., Waynesboro, *Pollard 1215* (F, GH, MO, NY, US). NORTH CAROLINA: Brunswick Co., roadside ditch along SR 1335, 3.3 mi. SE of SR 1333, *Leonard & Moore 7579* (MO). Carteret Co., SE of Mullet Pond on Shackleford Banks, *Anderson 414* (DUKE, FSU, SMU). Dare Co., near Friscoe, *Radford 45093* (C, CM, E, FLAS, MISS, NCU, S, SMU, TENN, TEX, U, UNA, US, USCH, WCUH). Granville Co., Camp Butner, *Batson 1075* (DUKE, NY). Hyde Co., Ocracoke Isl., *Kearney 2323* (US). Jones Co., 0.4 mi. W of county rd. 1105 (Catfish Rd.), on Forest Service Rd. 172 (Mirey Branch Rd.), E-SE of Maysville of NC Hwy. 58, *Peng et al. 4800* (MO). Pender Co., 0.4 mi. N of county road 1593 and 7.3 mi. N of the New Hanover Co. line; on US Hwy. 17, N of Hampstead, *Peng et al. 4877* (MO). Person Co., Wheeley's Ch., *Batson 1074* (DUKE). SOUTH CAROLINA: Allendale Co., pond on S-3-26, 6.1 mi. S of jct. with US 301, 0.3 mi. N of jct. with S-3-41, *Radford et al. 11417* (DS, NCU). Berkeley Co., along railroad tracks, Moncks Corner, *Bradley & Blaisdell 3406* (BOON, NCU). Charleston Co., 24.5 mi. N of SC Hwy. 41 on US Hwy. 17, vicinity of Buck Hill Recreation Area, S of McClellanville, *Peng et al. 4897* (MO). Clarendon Co., Santee Reservoir, 2.8 mi. S of Jordan, *Radford 31050* (GH, NCU, NY, VDB). Colleton Co., 2.2 mi. NW of Canadys on SC 61, *Ahles & Bell 17888* (FSU, GA, NCU, USF). Dorchester Co., 2.9 mi. N of Rosinville on US 15, *Ahles & Baird 54898* (NCU). Georgetown Co., 8 mi. N of Georgetown, *Godfrey & Tryon 1043* (DUKE, F, GH, MO, NY, TENN, US). Horry Co., cart road across sand plain behind dunes, Myrtle Beach, *Godfrey & Tryon 1163* (CAS, DUKE, F, GH, MO, NY, TENN, US). Orangeburg Co., Branchville, s.d., *s.c. 2671c* (US). TENNESSEE: Coffee Co., 3.5 mi. SE of Manchester, on US 41, *Kral 26038* (FSU, VDB). Roane Co., shoreline of the Tennessee River, E of Thief Neck Isl., ca. 8 mi. SW of Kingston, *Wofford & Dennis 51043* (TENN, VDB). Union Co., stream bed of Little Barnes Creek, *Underwood 385* (TENN). BAHAMAS: Great Abaco Co., along Abaco camp road, S of Marsh Harbour, *Correll & Sauleda 50684* (IJ, MO). Great Abaco Isl., along Forest Drive, about 1.5 mi. NW of Marsh Harbour, *Correll & Meyer 44598* (F, FTG, NY, SMU, US). Grand Bahama Isl., Dead Man's Reef, 9 mi. E-SE of West End, *Lewis 7110* (FTG, NY). CUBA. HABANA PROV.: Laguna Ariguanabo, *León 8724* (GH, NY). ISLE OF PINES: San Juan, *Britton et al. 5527* (CM, F, GH, MO, NY). LAS VILLAS: Santa Clara, Caibatten, at Delores, *Ekman 16316* (S). MATANZAS: Tagüey Grande, at Babujales, *Ekman 16955* (F, G, NY, S, US). Province not known: La Magdalena, Cayamas, *Baker 4648* (POM). Cuba, *Wright 2554* (G). JAMAICA. SAINT ANN PARISH: Moneague, *Prior 902* (US); E side of the Black River Morass, ca. 1 mi. N of Mountainside, *Proctor 19694* (A, IJ, NY); Slipe District, *Proctor 33464* (IJ, RSA); *Proctor 27748* (IJ).

Ludwigia microcarpa is the only diploid species of sect. *Microcarpium* that is apetalous and has more or less spatulate leaves. It has the smallest stature, leaves, flowers, and fruits and has the fewest seeds (ca. 10–20) per capsule of any species in the section. Occasionally it may be confused with plants of the "*L. curtissii* complex" (including a hexaploid, *L. simpsonii*, and an octoploid, *L. curtissii*), which have similarly spatulate leaves and turbinate fruits. It is, however, distinguishable from the "*L. curtissii* complex" by its minute capsules (1–1.5 mm long), which are shorter than or subequal to the sepal, its nectary disc of four flat greenish spots, and its reddish seeds. For detailed comparison, see Table 6.

Ludwigia microcarpa is uniform in reproductive structures but variable in vegetative habit. The stems are, as a rule, erect and usually well branched but are sometimes single. The stems and branches are straight or slightly zigzag. In outline, the plants may appear either narrowly oblong or narrowly rhombic when the plants are single or form short, subequal, ascending branches throughout the nodes; or they are triangular or ovate when the branches are gradually shorter from lower nodes up. The stems are normally annual and herbaceous; the plants may perennate either by forming stolons or by sending new shoots up directly from the spent stem base of the previous year. Woodiness is seen in some Florida specimens, presumably as a result of a favorable climate. The following specimen from Leon County, Florida, has an exceptionally woody base about 8 mm thick: sandy alluvium bordering wet woodland, Ochlockonee River, W of Tallahassee, *Godfrey 73131* (MO).

Most plants of *Ludwigia microcarpa* start to flower when young; it is common to find plants 5–10 cm high with flowers/fruits. The apetalous flowers are very small, with a tiny, greenish nectary disc from which a small amount of nectar is produced. Mechanical self-pollination apparently predominates in this species. In the experimental greenhouse, however, it has been successfully crossed to the diploid *L. linifolia* and *L. linearis*, tetraploid *L. glandulosa*, *L. lanceolata*, *L. polycarpa*, *L. sphaerocarpa*, and hexaploid *L. alata* and *L. simpsonii*; these combinations have resulted in the production of vigorous, floriferous hybrids (Peng, 1988). None set any seed. The F_1 hybrids between *L. microcarpa* and other petaliferous dip-

TABLE 6. Comparison of *Ludwigia microcarpa* with related species.

Characters	*L. microcarpa*	*L. simpsonii*	*L. curtissii*
Chromosome number	$n = 8$	$n = 24$	$n = 32$
Habit	Erect	Erect, ascending, or decumbent, occasionally prostrate and rooting at the nodes	Usually erect
Leaf			
Phyllotaxy	Alternate	Alternate except often opposite or subopposite in seedlings or at lower nodes	Alternate
Lateral veins (abaxial)	Slightly raised, conspicuous	Not raised, usually obscure	Not raised, usually obscure
Sepal length (mm)	0.9–2	1.2–1.8	1.5–3
Petals	Absent	Absent	1–3 vestigial petals occasionally present
Anther length (mm)	0.1–0.2	0.25–0.35	0.3–0.55
Filament length (mm)	0.4–0.55	0.55–0.8	0.75–1(–1.25)
Nectary disc			
Width (mm)	0.5–1.2	0.9–1.3	0.9–1.6
Elevated or flat	Nearly flat	Elevated as conspicuous bumps	Elevated as conspicuous bumps
Capsule			
Length (mm)	1–1.5	1.5–2(–2.5)	(2–)2.5–4(–4.7)
Width (mm)	1.4–1.9	1.5–3	2–3(–3.5)
Dehiscence	Ring-dehiscent	Loculicidal-dehiscent	Loculicidal-dehiscent
Bracteole			
Length (mm)	0.35–1.2(–1.5)	0.9–1.5(–2.5)	1.5–3.5(–4)
Width (mm)	0.1–0.4	0.35–0.85	0.4–0.8
Seed			
Color	Reddish brown	Light brown	Light brown
Surface cells	Transversely elongate	Transversely elongate	Tranversely elongate
Number/capsule	Ca. 10–20	Ca. 40–80	Ca. 50–150

loids were consistently petaliferous, suggesting that petal formation is controlled by a dominant gene. In other aspects, these F_1 hybrids were intermediate between their parents. Hybrids between *L. microcarpa* and species of higher ploidy level generally resembled the latter but tended to have smaller leaves and flowers.

Ludwigia microcarpa grows with *L. alata*, *L. curtissii*, *L. glandulosa*, *L. linearis*, *L. linifolia*, *L. pilosa*, *L. simpsonii*, and *L. sphaerocarpa*. Natural hybrids have been found between *L. microcarpa* ($n = 8$) and both *L. simpsonii* ($n = 24$) and *L. curtissii* ($n = 32$), both of which resemble *L. microcarpa* morphologically and share a common genome with that species (Peng, 1988). Since *L. simpsonii* and *L. curtissii* differ only in quantitative characteristics, which often overlap, it is impossible to distinguish between *L. microcarpa* × *L. curtissii* and *L. microcarpa* × *L. simpsonii* without knowing the chromosome number, or without seeing the populations in the field. These hybrids are usually readily recognizable by their erect stems; small and oblanceolate to spatulate leaves; apetalous flowers; elevated nectary discs; and minute, obpyramidal ovaries that abort after anthesis. The corners of the ovary/capsule often appear winged to some extent, apparently as a result of the aborted ovaries, which fail to develop into seeds in the locules of such hybrid individuals.

Hybrid populations between *Ludwigia microcarpa* and *L. simpsonii* are apparently common in Florida, where the two species grow in the same

habitats, often intermixed. These plants have a modal meiotic configuration of 8 bivalents and 16 univalents (Peng, 1988).

Confirmed hybrid populations of *Ludwigia microcarpa* × *L. curtissii* were found in Martin Co., Florida, 4.3 mi. E of Okeechobee and Martin county line, on FL 710, at Brady Ranch (*Peng 4202*, MO). Here they occurred along with putative parents by a wide depression between the highway and a railroad. Plants of *L. microcarpa* grew along the swamp border, whereas plants of *L. curtissii* stood in deeper water but were not as abundant as the former. Hybrid plants were scattered between them. The hybrids formed 8 bivalents and 24 univalents at meiosis (Peng, 1988).

Intersectional hybrid populations of *Ludwigia microcarpa* with *L. palustris* (sect. *Dantia*) were found in several counties of North Carolina, Georgia, and Florida (Peng, 1988). Their leaves were small, spatulate to broadly elliptic, alternate, subopposite or opposite; their flowers were small, apetalous, with minute ovaries, and aborting after anthesis; and the stems were prostrate and rooting at the nodes to ascending, suberect, or both. The combination of alternate leaves with a more or less prostrate habit in North American *Ludwigia* is usually indicative of hybridization between plants of sect. *Microcarpium* and sect. *Dantia*.

13. Ludwigia simpsonii Chapman, Fl. South. U.S., 2nd edition, suppl. 2: 685. 1892. TYPE: U.S.A. Florida: Manatee Co., Manatee, low ground, s.d., *C. T. Simpson s.n.* (holotype, US-1384069; isotypes, GH, MO in part, US—2 sheets). Figure 59.

Ludwigia cubensis Helwig, Repert. Sp. Nov. 25: 53. 1928. TYPE: Cuba. Piñar del Río: Remates, Ciénaga La Tumba, wet places, 16 June 1920, *E. L. Ekman 11304* (holotype, B, destroyed; isotypes, S—2 sheets).

Plants glabrous, erect, ascending, decumbent, or often prostrate and rooting at the nodes. Stems 10–60(–75) cm tall, well branched, leaf base slightly decurrent. Stolons rarely seen, new shoots arising from erect stem base or nodes of the trailing main stem, ascending at first, soon erect. Leaves alternate, those on lower nodes often opposite or subopposite, shape varied: spatulate, oblanceolate to very narrowly oblanceolate, or sublinear in extreme cases, 6–15(–20) mm long, (1–)3–7(–11) mm wide, apex acute or mucronate, margin subentire, with hydathodal glands, base attenuate into narrowly winged petioles 2–10 mm long. Stipules reddish purple, narrowly ovate-deltate, succulent, 0.15–0.25 mm long, 0.1–0.15 mm wide. Flowers in leaf axils, rarely congested. Sepals green with whitish, accrescent base, ovate-deltate, ascending, 1.2–1.8 mm long, 1–2 mm wide, apex narrowly acute or acuminate, margin entire. Petals 0. Anthers 0.25–0.35 mm long; filaments nearly translucent, 0.55–0.8 mm long. Pollen grains shed singly. Nectary disc green, raised 0.3–0.35 mm on ovary apex, 0.9–1.3 mm across, distinctly 4-lobed, glabrous. Style greenish, 0.25–0.4 mm long; stigma yellowish, subglobose, 0.15–0.25 mm thick. Capsules obconical, 1.5–2.5 mm long, 1.5–3 mm thick, comprising ca. 30–70(–100) seeds, glabrous or occasionally with minute, puberulent hairs ca. 0.05 mm long, sessile or with pedicels up to 0.4 mm long. Bracteoles attached on opposite sides near the base of capsules, lance-elliptic, 0.9–1.5(–2.5) mm long, 0.35–0.85 mm wide, swollen at base. Seeds light brown or brown, ellipsoid, 0.5–0.6 mm long, 0.3–0.35 mm thick, the surface cells transversely elongate, glabrous, occasionally covered by wax (?) taking the form of minute, appressed or ascending hairs. Self-compatible. Gametic chromosome number, $n = 24$.

Distribution. *Ludwigia simpsonii* occurs in sandy, peaty ditches, open pineland swamps, edges of cypress swamps, tidal flats or nearby marshes, and limestone sinks, sometimes growing as weeds, throughout most of eastern and southern Florida, with somewhat disjunct populations in the eastern part of the Florida panhandle and southernmost Mississippi (Fig. 60). This species also occurs in Cuba and Jamaica. Flowering and fruiting all year.

Representative specimens examined. U.S.A. FLORIDA: Bradford Co., New River, 1896, *Hitchcock s.n.* (F). Brevard Co., North Merritts Island, E side of Rt. 3, N of Wilsons Corner, *Shuey M1391* (USF). Broward Co., Fort Lauderdale, *Small & Carter 1171* (FLAS, GH, NY, US). Charlotte Co., Punta Gorda, *Curtiss 6757* (E, GA, GH, NY, S, US). Collier Co., Big Cypress, 6 mi. W of Miles City, *Brass 15832* (FLAS, GH, both mixed with *L. microcarpa*). Dade Co., 4 mi. SW of Florida City, *Thorne 14899* (USF, mixed with *L. microcarpa*). Duval Co., near Jacksonville, *Curtiss 930* (GA). Highlands Co., 1 mi. E of Highlands Hammock State Park, along Rt. 364, *Popenoe 1520* (FTG). Hillsborough Co., 4 mi. E of Dale Mabry on West Waters Ave., *Raven 18650* (DS, mixed with *L. microcarpa*). Lake Co., Eustis, *Nash 2136* (E, F, FLAS, GH, MO, MSC, NCU, ND, NY, US). Lee Co., Myers, *Hitchcock 117* (F, GH, NY, US). Manatee Co., Manatee, *Tracy 7602* (CM, F, GH, MO, MSC, NY, US, W). Monroe Co., Watson Hammock, Big Pine Key, *Killip 44454* (S, mixed with *L. microcarpa*; US). Palm Beach Co., near Jupiter, *Curtiss 5545* (C, E, FLAS, GA, GH, MO, MSC, NY, US). Pinellas Co., Fort DeSoto Co. Park, S of Gulfport, Hospital Key, Gulf of Mexico, *Lakela et al. 26366* (USF). St. Johns Co., St. Augustine, 1877, *Reynolds s.n.* (F, mixed with *L. lanceolata*; GH, mixed

FIGURE 59. *Ludwigia simpsonii*. All but a′ from Florida (Collier Co., *Peng et al. 4272*, MO); a′ from Florida (Collier Co., *Peng et al. 4273*, MO).—a. Habit, erect stems.—a′. Basal ascending branches with some opposite

FIGURE 60. Distributions of *Ludwigia simpsonii* (closed circles) and *L. curtissii* (open circles).

with *L. microcarpa*; NY). Sarasota Co., 0.5 mi. E of W boundary of Myakka River State Park, on FL Hwy. 72, *Peng et al. 4313* (MO). Seminole Co., Sanford, *Nash 2278* (F, FLAS, GH, MO, NCU, ND, NY, US). Volusia Co., 6 mi. E of Geneva River on E side of St. John's River, *Kral 5171* (SMU). Wakulla Co., St. Marks, 1843, *Rugel s.n.* (NY, mixed with *L. microcarpa*). MISSISSIPPI: Harrison Co., Mississippi City, 1900, *Tracy s.n.* (MISS). CUBA. PIÑAR DEL RÍO: Remates, Ciénaga La Tumba, *Ekman 11304* (S). Cuba, *Wright 2554* (G). JAMAICA: near Black River, *Harris 9935* (BM, C, F, NY, P, RSA, US, Z). St. Elizabeth Parish, along the Broad River, 1 mi. below the Slipe Road Bridge, *Proctor 24836* (IJ).

Ludwigia simpsonii is very variable in habit and leaf shape. It, *L. curtissii* (including *L. spathulifolia*), and *L. microcarpa* form a closely knit

←

leaves.—b. Leaf.—c. Flower bud.—d. Flower.—d′. Partly dissected flower.—e, e′. Adaxial and abaxial views of stamen.—f. Capsule.—g. Dehiscent capsule.

polyploid complex, with the diploid *L. microcarpa* evidently having played a role in the formation of the other species (Peng, 1988). Its distinctiveness from the diploid *L. microcarpa* is readily perceived in capsule size, shape of nectary disc, seed color, and seed number per capsule. The characters separating *L. simpsonii* and *L. curtissii*, however, are nearly always quantitative and often overlap. Raven & Tai (1979) indicated that the diagnostic characters separating *L. curtissii* and *L. simpsonii*, such as capsule shape and size and leaf shape, are not correlated with chromosome numbers, and that the two species tend to converge in the experimental greenhouse. For reasons of this sort, these two species have frequently been merged under *L. curtissii* in the recent literature (e.g., Long & Lakela, 1976; Raven & Tai, 1979; Godfrey & Wooten, 1981; Wunderlin, 1982). By contrast, basing conclusions on abundant fieldwork and greenhouse and chromosome studies, I (1988) observed that the difference in chromosome number is correlated with mature capsule size. All plants with $n = 24$ have capsules 1.5–2(–2.5) mm long, whereas those with $n = 32$ have mature capsules (2–)2.5–4(–4.7) mm long. The morphology of plants with $n = 24$ fits closely the description of *L. simpsonii*, and the morphology of $n = 32$ plants clearly corresponds to that of *L. curtissii* (including *L. spathulifolia*). Comparison of these two species and the diploid *L. microcarpa* is in Table 6.

Although *Ludwigia simpsonii* and *L. curtissii* frequently are found in the same locality, they appear to be ecologically distinct and seldom occur side by side. *Ludwigia simpsonii* tends to grow along roadsides with other weeds in moist sandy soil. *Ludwigia curtissii* usually grows farther from roadsides, sometimes mixed with tall grasses or sedges, in black muck and often in deep standing water.

Ludwigia simpsonii sometimes grows with *L. alata*, *L. curtissii*, and *L. microcarpa*. Proven natural hybrids are known only of *L. simpsonii* × *L. microcarpa*; they occur in several scattered counties in Florida (Peng, 1988). These hybrids showed a modal meiotic configuration of 8 bivalents and 16 univalents and 4–24% stainable pollen. Their ovaries aborted after anthesis. *Ludwigia simpsonii* may form natural hybrids with *L. curtissii*, but such hybrids would be virtually impossible to pick out without studying their chromosomes and would probably be identified as one of their putative parents. Artificial hybrids between these two closely related species have been synthesized; they produced moderate numbers of seeds and had ca. 80–90% stainable pollen. They consistently showed a meiotic configuration of 24 bivalents and 8 univalents, which indicated that chromosomes of the three genomes in *L. simpsonii* pair with homologues in *L. curtissii*, leaving the eight additional chromosomes in this species unpaired. Based on morphological features and crossing relationships, the octoploid *L. curtissii* was probably derived following hybridization between a petaliferous, narrow-leaved diploid similar to *L. linearis* or *L. linifolia* and the hexaploid *L. simpsonii* (Peng, 1988).

Intersectional hybrids of *Ludwigia simpsonii* and *L. repens* ($n = 24$; sect. *Dantia*) have been found growing intermixed with both putative parents. These plants exhibited few, if any (0–1), associations of chromosomes at meiosis (Peng, 1988), which corroborated an earlier report by Schmidt (1967). The lack of chromosome pairing in hybrids strongly suggests that the three genomes of *L. simpsonii* are distinct from one another and are not homologous with any of the genomes present in *L. repens*. Judged by the fact that *L. simpsonii* often has opposite or subopposite leaves near the base of the stem or at the seedling stage, with a somewhat ascending, decumbent, or occasionally prostrate habit, it seems likely that it originated from hybridization between the diploid *L. microcarpa*, to which it is similar morphologically and with which it shares one genome, and a possibly extinct member of sect. *Dantia* with prostrate stems and opposite leaves.

Plants from the following collections are exceptionally fully prostrate and root at the nodes:

U.S.A. FLORIDA: Collier Co., 13 mi. N of U.S. 41, on U.S. 29, in vast grassy field behind roadside ditches (Big Cypress Swamp), *Peng 4268* (MO), *4273* (in part, MO).

They grow side by side with erect plants but are otherwise normal, small-fruited *L. simpsonii*, exhibiting 24 pairs of chromosomes in meiosis and setting abundant fruits with viable seeds.

Artificial hybrids between *Ludwigia simpsonii* and the diploids *L. linearis*, *L. linifolia*, *L. microcarpa*, the tetraploids *L. glandulosa*, *L. lanceolata*, the hexaploid *L. alata*, and the closely related octoploid *L. curtissii* have been synthesized, although with difficulty in some cases. Except for *L. simpsonii* × *L. curtissii*, which is highly fertile, all other combinations had 3–20% stainable pollen and produced very few, if any, seeds.

14. Ludwigia curtissii Chapman, Fl. South. U.S., 2nd edition, suppl. 621. 1883. TYPE: U.S.A. Florida: Brevard Co., ponds near Cape Malabar, July 1879, *A. H. Curtiss 922* (ho-

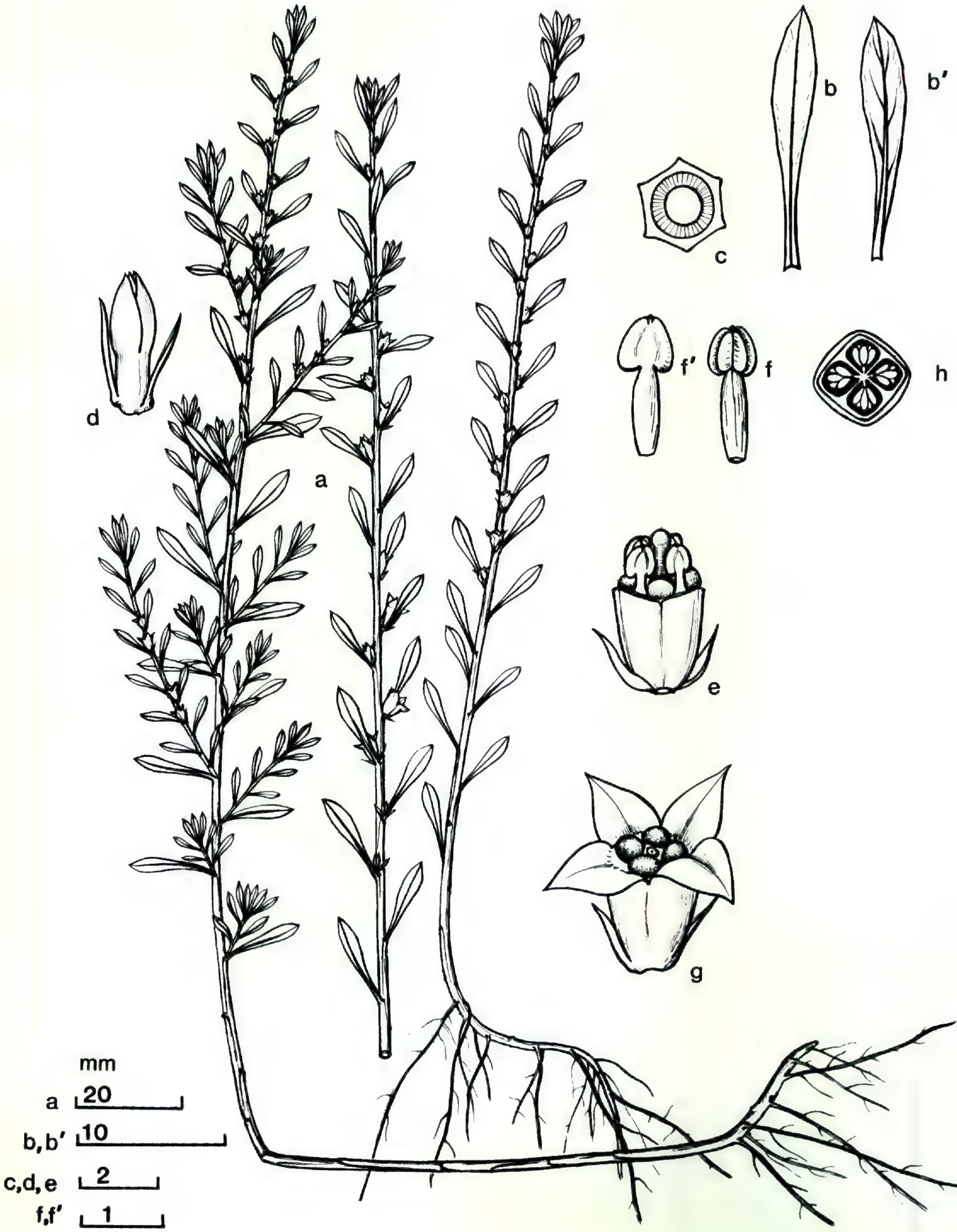

FIGURE 61. *Ludwigia curtissii* (Florida: Martin Co., *Peng et al. 4199*, MO).—a. Habit.—b. Adaxial and abaxial views of leaf.—c. Cross section of stem.—d. Flower bud.—e. Flower, partly dissected.—f, f′. Adaxial and abaxial views of stamen.—g. Capsule.—h. Cross section of capsule.

lotype, US-2630449; isotypes, BM, F, GH, M, MO—2 sheets, NY—3 sheets, PH, US). Figure 61.

Ludwigia spathulifolia Small, Man. Southeast. Fl. 943, 1506. 1933. TYPE: U.S.A. Florida: Dade Co., Everglades, northwest of Perrine, 16 Jan. 1909, *J. K. Small & J. J. Carter 2990* (holotype, NY).

Plants glabrous. Stems erect or ascending at base, very rarely creeping, 15–75 cm tall, single to well branched, the branches sometimes very slender; leaf bases slightly decurrent. Stolons not seen, new shoots ascending from base of the persistent, defoliated main stem of the previous year, very rarely prostrate and rooting at the nodes. Leaves variable in shape, most frequently oblanceolate-spatulate, sometimes spatulate or oblanceolate to very narrowly so, sublinear in extreme cases, 10–25(–30) mm long, 1.3–8 mm wide, glabrous, apex acute or mucronate, margin subentire with hydathodal glands, base attenuate into winged petioles 3–12 mm long. Stipules reddish purple, narrowly ovate, succulent, 0.2–0.3 mm long, 0.15–0.25 mm wide. Flowers in leaf axils, usually not congested. Sepals green with whitish, accrescent base, widely deltate or triangular, ascending, 1.5–3 mm long, 1.2–2 mm wide, apex narrowly acute or acuminate, margin entire. Petal usually lacking, 1–3 vestigial petals occasionally seen in some flowers, these yellow, narrowly elliptic, 1–2.5 mm long, 0.5–1 mm wide, apex obtuse, base attenuate. Anthers 0.3–0.55 mm long; filaments yellowish, 0.75–1(–1.25) mm long. Pollen grains shed singly. Nectary disc green, raised 0.3–0.4 mm on the ovary apex, 0.9–1.6 mm across, prominently 4-lobed, glabrous. Style greenish, 0.35–0.65 mm long; stigma yellowish, subglobose, 0.25–0.4 mm thick. Capsules obconical, (2–)2.5–4(–4.7) mm long, 2–3(–3.5) mm thick, glabrous, occasionally remotely minutely puberulent, the hairs 0.05–0.07 mm, pedicels 0.1–0.5 mm long. Bracteoles attached on opposite sides near base of capsule, narrowly lanceolate, lance-elliptic or oblong-linear, 1.5–3.5 (–4) mm long, 0.4–0.8 mm wide, swollen at base. Seeds light brown, ellipsoid, 0.45–0.6 mm long, 0.3–0.4 mm thick, the surface cells transversely elongate, glabrous, occasionally covered by waxes (?) that appear also like appressed or ascending hairs. Self-compatible. Gametic chromosome number, $n = 32$.

Distribution. *Ludwigia curtissii* grows in pine savannas and flatwoods, marshes, ponds, stream banks, sandy, peaty swales, limestone prairies, and in solution pits in limestone; it is restricted to the Bahamas and the peninsula of Florida (Fig. 60). Flowering and fruiting all year.

Representative specimens examined. U.S.A. FLORIDA: Brevard Co., near Eau Gallie, Indian River, *Curtiss 928* (FLAS). Charlotte Co., 3.5 mi. NW of Port Charlotte, *Godfrey 65356* (DS, DUKE, FLAS, FSU, LL, MSC, NCU, US, USF, VDB). Collier Co., Alligator Alley, picnic area ca. 5 mi. W of Miles City, *Avery 2039* (FLAS, mixed with *L. simpsonii*, FTG). Dade Co., Everglades, near Royal Palm Hammock, *Small et al. 6644* (FLAS, GH, NY, US). DeSoto Co., near Punta Gorda, *Bright 4541* (CM). Franklin Co., St. George Island, *Godfrey 71148* (FSU). Glades Co., 4.4 mi. SE of jct. of FL Hwy. 29 with US Hwy. 27, *Raven 18679* (DS, NCU). Hendry Co., 6 mi. S of La Belle, *Godfrey et al. 61009* (FSU, GH, SMU). Hernando Co., Choocochee Hammock, S of Brooksville, 1921, *Small et al. s.n.* (LL, NY). Hillsborough Co., old Memorial Highway, ca. 1.5 mi. from FL Rt. 580, NW of Tampa, *Lakela 25261* (FSU, GH, NCU, SMU, USF). Lee Co., 5 mi. N-NW of Ft. Myers, *Kral 7574* (FLAS, GH, US, USF). Manatee Co., Bradenton, *Tracy 7089* (MO, US). Martin Co., rd. between stable and exit, Jonathan Dickinson State Park, *Correll et al. 49914* (FTG, NCU). Monroe Co., 3.8 mi. W of Dade–Monroe county line, near FL Rt. 94, *Godfrey et al. 63519* (FSU, MO). Martin Co., W side of Big Pine Key, *Killip 41573* (F, NO, both mixed with *L. microcarpa*). Okeechobee Co., ca. 10 mi. N of Okeechobee, along US Hwy. 98, *Henderson 63-1621* (FSU, TEX). Palm Beach Co., NW of Loxahatchee in Corbitt Wildlife Management Area, *Kral 5636* (FSU, SMU). Pinellas Co., 4 mi. E of Clearwater, *Kral 7452* (FLAS, FSU, mixed with *L. palustris*, GA, GH, USF). Sarasota Co., 3 mi. S of Venice, *Kral 7495* (FLAS, FSU, GH, VDB). Volusia Co., 5 mi. W of New Smyrna, *Kral 18457* (VDB). BAHAMAS: South Andros, ca. 1 mi. SW of Congo Town airstrip, *Correll et al. 50247* (FTG, IJ, MO). Grand Bahama, Pelican Lake Area, *Correll & Popenoe 51315* (MO).

Ludwigia curtissii and *L. simpsonii* are both highly variable in habit and leaf shape and are often difficult to distinguish; the only consistent distinguishing character is the size of mature capsules. These two species are unique in sect. *Microcarpium* in having loculicidal capsules and in having, along with the diploid *L. microcarpa*, more or less spatulate cauline leaves. Their capsules dehisce by four longitudinally lenticular slits opposite the loculi. When dehiscence is complete, the capsule is split into four basally united parts topped with persistent but slightly shriveled sepals. This type of capsule dehiscence is highly specialized and has an anatomical basis (Peng & Tobe, 1987). *Ludwigia curtissii* and *L. simpsonii* are also distinct in that they are the only species in sect. *Microcarpium* that rarely produce true stolons. From the perennial base of the previous-year stem they form new shoots that ascend at first and soon become erect.

Some populations of *Ludwigia curtissii* from the Everglades of southern Florida and the Bahamas tend to have larger capsules (3.5–4.7 mm long) and were named *L. spathulifolia* by Small (1933). As their variation pattern closely parallels that of *L. curtissii* s. str., and they are octoploids with $n = 32$, they are here considered as variants of the slightly smaller-fruited *L. curtissii* that do not warrant taxonomic recognition, as was suggested by Long & Lakela (1976), Raven & Tai (1979), Godfrey & Wooten (1981), and Wunderlin (1982).

Ludwigia curtissii co-occurs with *L. alata*, *L. linifolia*, *L. microcarpa*, and *L. simpsonii* and hybridizes with the diploid *L. linifolia* and *L. microcarpa*, forming F_1s that form flowers but not seeds. *Ludwigia curtissii* × *L. microcarpa* exhibited 8 bivalents and 24 univalents at meiosis. The pollen stainability was 16% (Peng, 1988). As discussed above, natural hybrids between *L. curtissii* and *L. simpsonii* probably occur but would be difficult to recognize. Like *L. simpsonii*, *L. curtissii* forms intersectional hybrids with *L. repens* ($n = 24$, sect. *Dantia*) in the field. Such plants are vigorous and somewhat prostrate or suberect; they have alternate and opposite or subopposite leaves, but do not form viable seeds.

In the experimental greenhouse, artificial hybrids have been synthesized between *Ludwigia curtissii* and the diploid *L. linearis* and the tetraploids *L. glandulosa*, *L. lanceolata*, *L. pilosa*, *L. polycarpa*, *L. sphaerocarpa*, and *L. suffruticosa*. A few seeds were occasionally produced by some of the octoploid × tetraploid hybrids.

Compared with *Ludwigia simpsonii* ($n = 24$), *L. curtissii* ($n = 32$) is generally taller, more robust, more often erect, tends to have narrower and longer leaves, and nearly always has larger flowers and capsules. Further, the leaves of *L. curtissii* are nearly always alternate throughout, and the flowers occasionally have one to three vestigial petals. As these two species have three genomes in common (Peng, 1988), it is apparent that *L. curtissii* originated following hybridization between *L. simpsonii* and a diploid, petaliferous, erect species with narrow and alternate leaves, larger flowers, and longer capsules. The likely candidate for such a plant is only to be found in *L. linearis*, *L. linifolia*, the Cuban endemic *L. stricta*, or their progenitors. Indeed it is even possible that more than one of the above species hybridized with *L. simpsonii* in the past to form the present-day *L. curtissii*. If this is true, the morphological variability observed in *L. curtissii* is expected.

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TWO NEW SPECIES OF THE *LUPINUS LANATUS* COMPLEX[1]

Ana Maria Planchuelo[2] *and David B. Dunn*[3]

Abstract

The *Lupinus lanatus* complex is a group of closely related species that grow in southeastern Brazil and northeastern Argentina. They are herbaceous, perennial or occasionally biennial plants with basal leaves in the juvenile plant simple or three-foliate, stipules 3–7 cm long or longer, and large flowers 15–20 mm long having the banner glabrous and well reflexed from the wings. Two species, *L. magnistipulatus* and *L. setifolius*, are described for the first time.

This group of species appears to be closely related and can be recognized by the large stipules 3–7 cm or more long and the presence of some simple or trifoliate leaves at the base of the juvenile plants. Completely developed leaves from adult plants have five or more leaflets. They are all herbaceous perennials or short-lived perennials, or occasionally function as biennials. The flowers are commonly 15–20 mm long and glabrous, with the banner well reflexed from the wings and the sides turned back. The calyx cup tapers into the pedicel without the gibbous enlargement that is commonly present in other lupines.

We are suggesting that this group of species forms a second lineage derived from *L. paraguariensis*, which is thought to be the origin of the group, since it possesses morphological characteristics reminiscent of the group, including that the juvenile leaves and the first leaf produced on the lateral branches are simple. Planchuelo & Dunn (1984) described *L. paraguariensis* as showing a transitional stage between simple- and compound-leaved species.

Lupinus lanatus has floccose lanate indument on both sides of the leaflets (see Fig. 1A). Vegetatively it has been described as forming perennial mats up to four feet in diameter in sand dunes, with new growth developing seasonally from the tips of the stems which survive under the sand. *Lupinus magnistipulatus*, described in this paper, is similar to *L. lanatus* in the perennial condition but has less lanate hair coating (see Fig. 1B), and as its name suggests, the former develops a much larger free tip on the stipules. *Lupinus setifolius*, also described in this paper, appears to be biennial. The large free tip of the stipules and the loss of the lanate indument (see Fig. 1C) suggest the latter as a derivative from *L. magnistipulatus*.

The species *L. multiflorus*, *L. albescens*, and *L. aureonitens*, treated by Planchuelo & Dunn (1984), are relatives of this complex. They have caespitose perennial habit and a narrow free tip of the stipules like *L. lanatus* but develop a much denser indument that grades from densely short-lanate to densely sericeous, completely hiding the leaf surface.

Key to the Species of *Lupinus lanatus* Complex and Relatives

1a. Basal leaves and first leaf of each lateral branch simple, the others palmately compound ..... *L. paraguariensis* (description in Planchuelo & Dunn, 1984).

1b. All leaves of mature plants palmately compound, exceptionally with few basal simple leaves on juvenile plants.

2a. Wing tips with an upturned toothlike tip.

3a. Leaves primarily cauline; stems erect, branching above ..... *L. albescens* (description in Planchuelo & Dunn, 1984).

3b. Leaves primarily basal; stems with branches primarily basal ..... *L. aureonitens* (description in Planchuelo & Dunn, 1984).

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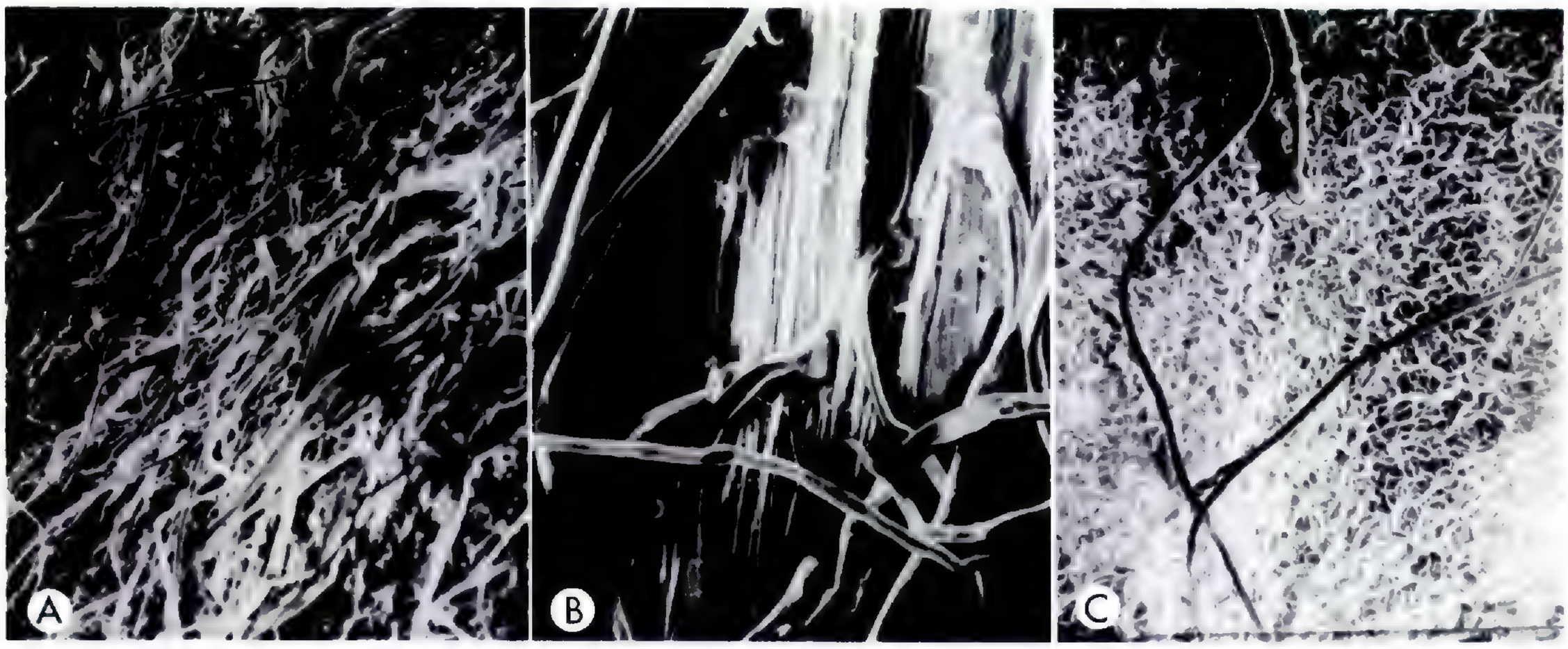

FIGURE 1. Indument of:—A. *L. lanatus*, leaflet (×100).—B. *L. magnistipulatus*, petiole (×200).—C. *L. setifolius*, leaflet (×100).

2b. Wing tips rounded, without a toothlike tip.
4a. Leaflets mostly broadly obovate or broadly oblanceolate with the tips rounded. Stipules foliaceous, with free portion ovate-lanceolate, 8–15 mm wide.
5a. Leaflets thinly floccose-lanate on both sides. Short-lived perennials ..... 2. *L. magnistipulatus*
5b. Leaflets glabrous on both sides except for setaceous hairs on the midrib, major veins, and occasionally scattered along some areas of the margins. Biennials ..... 3. *L. setifolius*
4b. Leaflets all narrowly elliptic to narrowly oblanceolate with tips acute or obtuse. Stipules not foliaceous, with free portion lance-attenuate, 2–5 mm exceptionally 6 mm wide.
6a. Leaflets abundantly floccose-lanate or thinly lanate, the larger 7–11 cm long. Stipules 3–8.5 cm long. Lower lip of the calyx often enlarging and foliaceous as fruit develops ... 1. *L. lanatus*
6b. Leaflets densely lanate to densely sericeous, the larger 4–5 cm long, rarely to 7 cm long. Stipules 1.5–2.6 cm long. Calyx not enlarging as fruit develops ..... *L. multiflorus* (description in Planchuelo & Dunn, 1984).

1. Lupinus lanatus Benth. in Mart., Fl. Brasil. 15(1): 16. 1859. TYPE: Brazil. Rio Grande do Sul: *Herb. Imp. Bras. 1511*, not seen. Figure 2.

Plants perennial, herbaceous, 25–60 cm tall, in clumps to 1.5 m wide, possibly rhizomatous or the stems arising from underground branches; *stems* fistulose, 8–12 mm diam., first internode of branches 4–9 cm long, others 1–2 cm long, covered with soft tangled lanate hairs 4–5 mm long; *stipules* 3–8.5 cm long, commonly green like the leaflets, the free portion lance-attenuate, 3–5(6) cm long, 2–5(6) mm wide, with pubescence as on stems; *petioles* 5–22 cm long, lanate as stems; *leaflets* 5–7, oblanceolate, the tips obtuse or rounded, densely or thinly lanate on both sides, thinner above, the largest 7–11 cm long, 10–20 mm wide. *Peduncles* 2.5–8 cm long, fistulose, angular and lanate as the stems; *racemes* 15–50 cm long, flowers scattered, the rachis fistulose and lanate as stems; *bracts* caducous, lance-attenuate, 12–22 mm long, lanate dorsally, glabrous ventrally; *bracteoles* 3–5 mm long, lanceolate to lance-attenuate, attached just below the lips of the lateral sinuses of the calyx; *pedicels* 1–2 mm long at anthesis, 4–6 mm long in fruit, lanate. *Calyces* lanate outside, glabrous within, the base tapering into the pedicel, lower lip 13–17 mm long, 3.2–4.5 mm wide, often enlarging and foliaceous as fruit develops, trifid, central tooth 2.5–4 mm long, lateral teeth 2–3 mm long, arching outward, upper lip 8–13 mm long, bifid, the slit 5.6–9 mm deep, the lobes 2.3–2.5 mm wide, the lips connate 3 mm; *banner* glabrous, oval-ovate, 15–17.5 mm long, including the 2–2.5-mm-long claw, 12–13.5 mm wide, appressed 4–6 mm, reflexed 12–13 mm, reflexed/appressed ratio 2.4, the angle 130°, the tip bluntly rounded; *wings* arcuate, 15.5–18.5 mm long, 6.5–7.5 mm wide, the claw 3.5 mm long, lobe above the claw 1.6–2.2 mm wide; *keel* arcuate glabrous, 4.5 mm wide in the middle, the tip arcing back in a continuous curve, no definite angle, 80–85°; *ovules* 8. *Legumes* ascending to erect, 5–9 cm long, 1–1.5 cm wide, shaggy lanate.

The floral parts, especially the calyx and the banner, are remarkably similar to those of *L. paraguariensis*. The Argentinian specimens and *Rambo 28195* from Rio Grande do Sul, Brazil, had

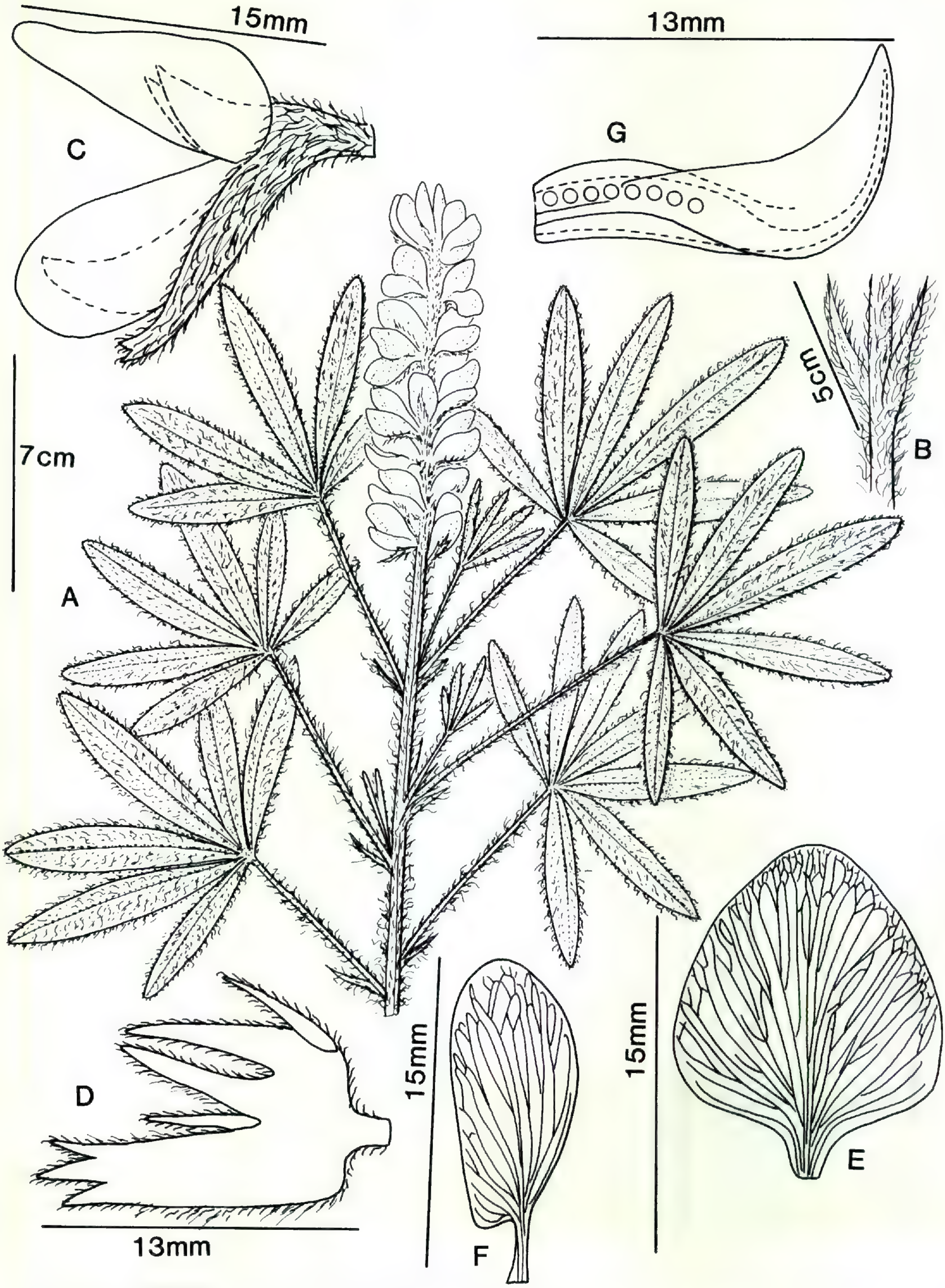

FIGURE 2. Illustration of typical structures of *Lupinus lanatus*. —A. Upper part of the plant with inflorescence. —B. Stipules detached at the node. —C. Lateral view of the left side of the flower. —D. Calyx, cut at the left lateral sinus and opened so that the inside surface shows. —E. Banner petal flattened, dorsal view. —F. Wing petal. —G. Keel petals, enclosing the staminal tube and the pistil, with the mean number of ovules drawn.

unusually large stipules, some of them 6 mm wide. All the others have most of the stipules under 5 mm wide. Although all the morphological characteristics of the large-stipuled specimens are those of the species, the enlargement of the free tip of the stipules suggests relationship with *L. magnistipulatus* and even crossing between the two species.

Lupinus lanatus occurs in the southernmost states of Brazil and in Misiones, Argentina. The plants are reported growing in open places and dunes.

Representative specimens examined. ARGENTINA. MISIONES: Campo Grande, *Bertoni 638* (LIL); Dep. Concepción, Concepción, *Schulz 6965* (LIL); Dep. San Javier, Parambí, collector's name illegible, *Inst. Miguel Lillo 188188* (LIL). BRAZIL: locality unknown, *Sello 3032* (NY, UC). RIO GRANDE DO SUL: Viera, near Rio Grande, *Archer 4303* (DS, K, NY, RB); S. Leopoldo, in dunes, *Henz 33899* (NY); Jacaré, *Rambo 38545* (MO); Apartados da Serra, próximo Capela dos Ausentes, *Pereira 6444* (NY); Nonvaí, Municipio de Sarandi, at flumen Alto Uruguaí, *Rambo 28195* (LIL); Pareci Velho p. Cai, *Rambo 43841* (LIL, US).

2. Lupinus magnistipulatus Planchuelo & Dunn, sp. nov. TYPE: Brazil. Santa Catarina: Campos dos Padres, 1,900 m, *R. Reitz 2377* (holotype, SI; isotype, RB; photo, UMO). Figure 3.

Plantae perennes, 17–35 cm altae; *caules* erecti, fistulosi, pagina multis pilis patentibus, 4–7 mm longis ornata; *stipulae* virides foliaceae, 4–7 cm longae, parte adnata 1.2–2 cm longa, parte libera divergenti et ascendenti, 2–5 cm longa, 8–15 mm lata, lanata; petiolis 4–8.5(11) cm longi, lanati; *folia* (3)5–9-palmata, foliolis lanatis, oblanceolatis, apice rotundatis, 5–7 cm longis, 15–20 mm latis, complanatis; *racemus* major 20–30 cm longus, floribus diffusis; *bractae* foliolaceae, lanceolatae, apice acuminatae, 12–23 mm longae, 2.5–4 mm latae, in dorso lanatae; bracteolae 3.5–6 mm longae, 0.5–1.2 mm latae; *flores calycibus* in dorso lanatis, ventraliter glabris, labio inferiore triangulare, 10–16.6 mm longo, 3.5–4 mm lato, tridentato, dentibus 1.7–4.5 mm longis, lateralibus brevibus, labium superiore 7–10.6 mm longo, bifido, incisura 5–7.8 mm profunda, lobis 2.5–3 mm latis; *vexilum* glabrum, ovatum, 15.5–20.6 mm longum, 9.7–15.6 mm latum, ungue 3.4–4.5 mm longo, parte reflexa 9–13.5 mm; *alae* 13–21 mm longae, 6.4–11 mm latae, ungue 3.3–4.5 mm longo; *carina* glabra, 3.4–5.5 mm lata; *ovula* 4–8; *legumina* lanata, immatura, 5 cm longa, 7 mm lata; *semina* non visa.

Plants short-lived perennials, 17–35 cm tall; *stem* erect, simple or with some basal branches, more often branching from the upper nodes after the first inflorescence, hollow, angular, to somewhat fistulose, covered with soft, spreading, tangled hairs 4–7 mm long; *stipules* 4–7 cm long, membranaceous, encircling ca. 40% of the stem circumference, 1.2–2 cm fused to the petioles, the free portion green, foliaceous, ovate-lanceolate, diverging away and ascending, 2–5 cm long, 8–15 mm wide, thinly lanate on both sides; *petioles* 4–8.5(11) cm long, lanate as the stems; basal juvenile leaves simple, the rest compound; *leaflets* (3)5–9, broadly oblanceolate, the tips generally rounded, lanate on both sides, the largest 5–7 cm long, 15–20 mm wide, mostly complanate at maturity. *Peduncles* 4–6 cm long on the primary inflorescence; *racemes* all immature on the primary inflorescences, 20–30 cm long, flowers scattered to subverticillate, the rachis lanate; *bracts* green, foliaceous, caducous, lanceolate, the tips acuminate, largest below, smaller above, 12–23 mm long, 2.5–4 mm wide, lanate dorsally; *bracteoles* lanceolate, 3.5–6 mm long, 0.5–1.2 mm wide, attached near or slightly below the lips of the lateral sinuses of the calyx; *pedicels* 2.6–5 mm long, ascending lanate. *Calyces* lanate outside, glabrous within, the lower lip triangular, 10–16.6 mm long, 3.5–4 mm wide, the tip trifid, the teeth 1.7–4.5 mm long, the laterals only slightly shorter, the upper lip 7–10.6 mm long, deeply bifid, the notch 5–7.8 mm deep, the lobes 2.5–3 mm wide, the lips connate 2.8–4.5 mm laterally; *banners* glabrous, ovate, 15.5–20.6 mm long, including the 3.4–4.5-mm-long claw, 9.7–15.6 mm wide, reflexed 9–13.5 mm, appressed 5.8–9.5 mm, reflexed/appressed ratio 1.45–1.6, the angle 127–144°; *wings* 13–21 mm long, 6.4–11 mm wide, the claw 3.3–4.5 mm long; *keels* glabrous, 3.4–5.5 mm wide in the middle, the angle 96–103°; *ovules* 4–8. *Legumes* shaggy lanate, immature, 5 cm long, 7 mm wide; *seeds* not seen.

The name *Lupinus magnistipulatus* was suggested several years ago by Prof. A. Burkart on herbarium specimens. Some of the specimens cited here were labeled by Burkart as a new species, *L. reitzii*. Our interpretation of the material is that these specimens are juvenile plants and do not differ otherwise from the others. Therefore we have not recognized *L. reitzii*.

The new species apparently grows only in southeastern Brazil in the states of Santa Catarina and Paraná at altitudes from 700 to 1,650 m. Flowering occurs from late October to late January.

Representative specimens examined. BRAZIL. PARANÁ: Mun. Guarapuana, Guara, *Hatchback & Guimaraes 20492* (NY, US). SANTA CATARINA: Mun. Bom. Retiro, Campo dos Padres, *Smith, Reitz & Klein 7703* (NY, US); *Smith & Reitz 10326* (US); Campo dos Padres, 1,900 m, *R. Reitz 2377* (holotype, SI; isotype, RB; photo, UMO); Mun. Joaqaba, Campo de Palmas, 52 km W of Caqador, *Smith & Reitz 9155* (SI, US); Mun.

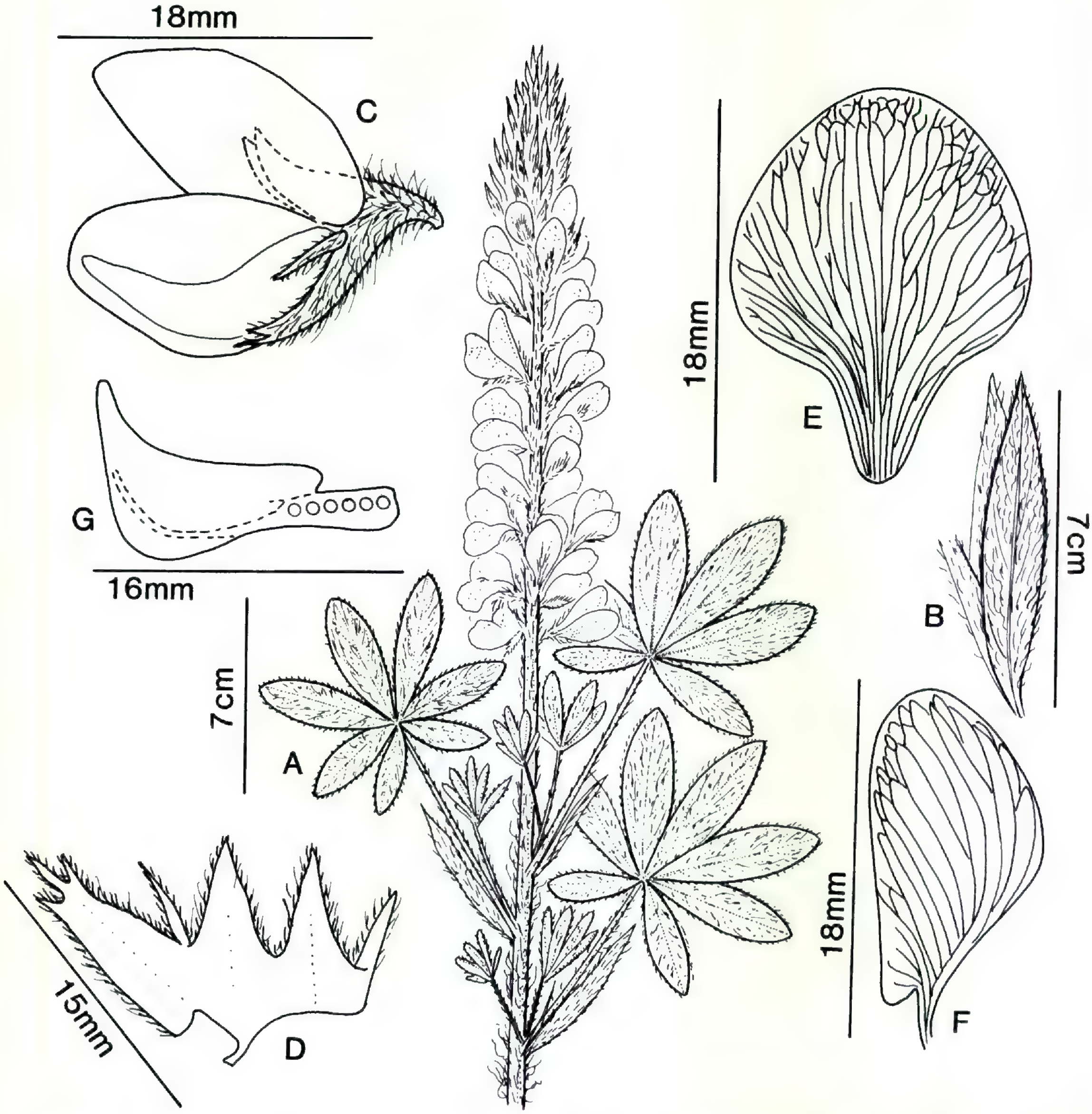

FIGURE 3. Illustration of typical structures of *Lupinus magnistipulatus*.—A. Upper part of the plant with inflorescence.—B. Stipules detached at the node.—C. Lateral view of the left side of the flower.—D. Calyx, cut at the left lateral sinus and opened so that the inside surface shows.—E. Banner petal flattened, dorsal view.—F. Wing petal.—G. Keel petals, enclosing the staminal tube and the pistil, with the mean number of ovules drawn.

Ponte Serrada, by road to Xanxere, 700–900 m, ruderal, *Smith & Klein 13054* (US, SI, fragments); Mun. São Joaquin, Serra do Oratorio, *Reitz & Klein 7417* (SI, US); *Smith & Reitz 10135* (US).

3. Lupinus setifolius Planchuelo & Dunn, sp. nov. TYPE: Brazil. Rio Grande do Sul: locality unknown, *Rambo 36208* (holotype, SI; photos, NY, UMO, US). Figure 4.

Plantae probabiliter biennes, 25–30 cm altae; *caules* erecti, fistulosi, pilis paucis patentibus ornatis; *stipulae* virides, foliaceae, 5–6 cm longae, parte adnata, 1.5–2 cm longa, parte libera lanceolato-ovata, glabrata, 2.5–4 cm longa, 10–15 mm lata; *petioli* 6–7.5 cm longi; *folia* 5–7-palmata, folia juvenalia basi plantae locata et folia prima ramorum lateralium foliolis tribus notata, eis late oblanceolatis; *foliola* 6–7 cm longa, 20–25 mm lata, apice rotundatis ubique glabris praeter marginem et costam infra pilis patulis setaceis ornatis; *racemus* densus, floribus diffusis; *bractae* 13–20 mm longae, 3–5 mm latae, margine setaceo; bracteolae 3.7–4.8 mm longae, 0.8–1 mm latae; *flores calycibus* in dorso laxe subsericeis, ventraliter glabris, labio inferiore 10–11.3 mm longo, 3–4 mm lato, tridentato, dentibus 2.3–3 mm longis, 0.5–0.8 mm latis, labio superiore 7.5–8 mm longo, bifido, incisura 4.5–5 mm profunda, lobis 1.2–1.5 mm latis, *vexillum* glabrum, ovatum, 15.5–16.5 mm longum, 11.5–12.5 mm latum, ungue 3–3.5 mm longo, parte reflexa

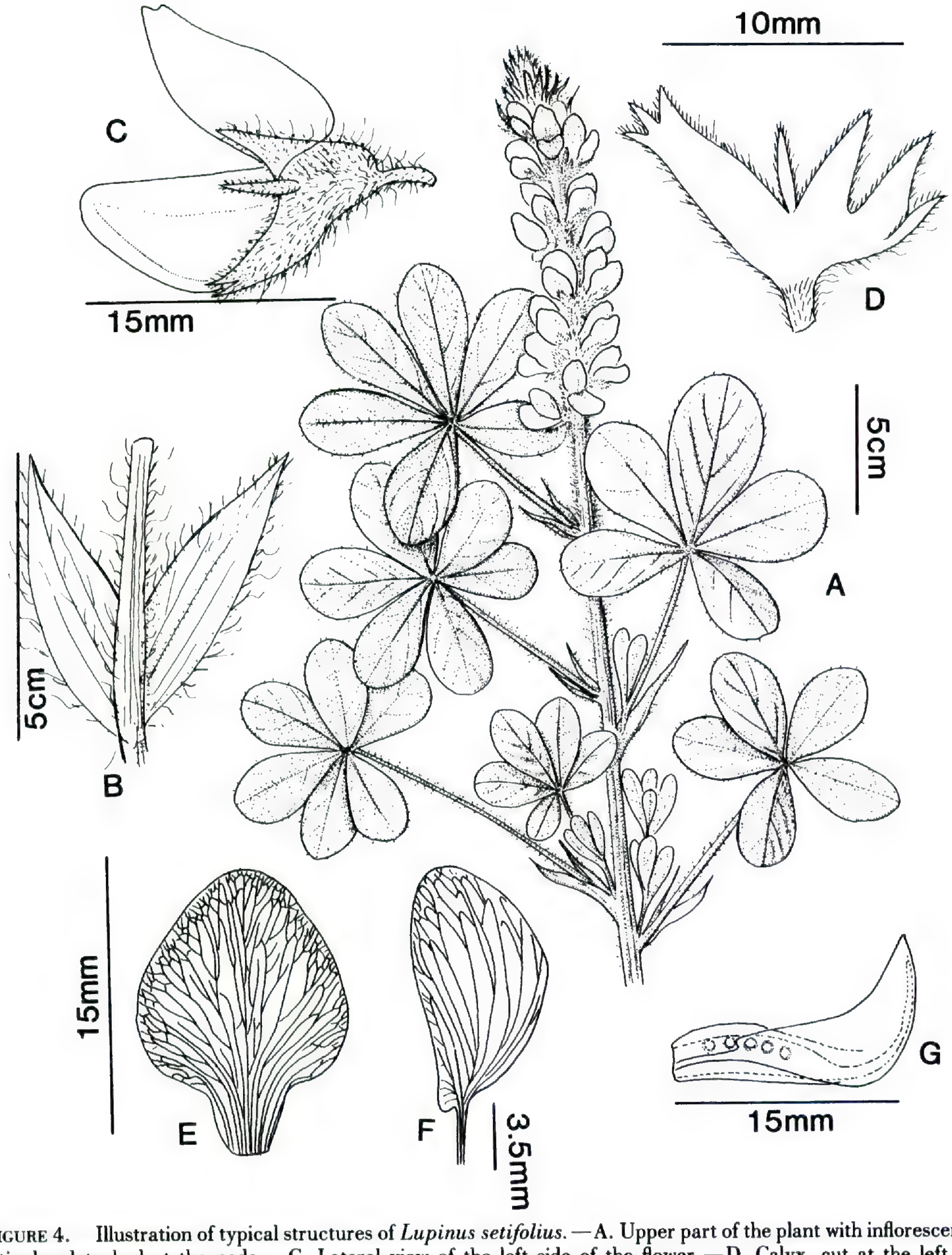

FIGURE 4. Illustration of typical structures of *Lupinus setifolius*. —A. Upper part of the plant with inflorescence.—B. Stipules detached at the node.—C. Lateral view of the left side of the flower.—D. Calyx, cut at the left lateral sinus and opened so that the inside surface shows.—E. Banner petal flattened, dorsal view.—F. Wing petal.—G. Keel petals, enclosing the staminal tube and the pistil, with the mean number of ovules drawn.

11–12 mm; *alae* 16–16.5 mm longae, 5.8–6.5 mm latae; *carina* glabra, 3.5–4.5 mm lata; *ovula* 5–6; legumina non visa.

Plants probably biennial, ca. 25–30 cm tall; *stems* erect, fistulose, 6–7 mm diam., angular from the ridges by veins from the petioles, with scattered spreading hairs 3–4 mm long, these more numerous above; *stipules* foliaceous, 5–6 cm long, the adnate portion 1.5–2 cm long, the free portion ovate-lanceolate, the tip acute or obtuse, 2.5–4 cm long, 10–15 mm wide, glabrous on both sides except a few hairs on the veins and margins; *petioles* of larger leaves 6–7.5 cm long; juvenile *leaves* at the base of the plant and first leaves of lateral branches with 3 leaflets, the upper leaves with 5–7 leaflets, these broadly oblanceolate, the tips

rounded, glabrous on both sides, except a few spreading hairs on the veins below or on the margin, the largest 6–7 cm long, 20–25 mm wide, mostly complanate. *Peduncle* 5 cm long, with more numerous spreading hairs than the stem; *raceme* (immature) dense, the flowers scattered; *rachis* with denser spreading hairs; *bracts* lanceolate, the tips acuminate, 13–20 mm long, 3–5 mm wide, dorsally pubescent on the veins, glabrous ventrally on the lower half; bracteoles 3.7–4.8 mm long, 0.8–1 mm wide, glabrous with margin setaceous, narrowly lanceolate, attached just below the lips of the lateral sinuses of the calyx; *pedicels* 3 mm long at anthesis, spreading pilose. *Calyces* covered with long soft hairs outside, glabrous within, the base tapering but slightly gibbous above, lower lip 10–11.3 mm long, 3–4 mm wide, the tip trifid, all teeth 2.3–3 mm long, 0.5–0.8 mm wide, upper lip 7.5–8 mm long, 4 mm wide, bifid, the notch 4.5–5 mm deep, the lobes 1.2–1.5 mm wide; *banner* glabrous, ovate, the base tapering into a claw, 15.5–16.5 mm long including the 3–3.5-mm-long claw, 11.5–12.5 mm wide, reflexed 11–12 mm, appressed 4–5 mm, reflexed/appressed ratio 2.2–3, the angle double, the lower 132–146°; *wings* 16–16.5 mm long, 5.8–6.5 mm wide, the tip rounded, the claw 3.5–3.8 mm long; *keel* glabrous, 3.5–4.5 mm wide in the middle, the angle 92–109°, the tip not curled back; *ovules* 5–6. *Legumes* not seen.

The description was based solely on the holotype. The taxon appears to be closely related to *L. magnistipulatus*. The flowers are smaller and the base of the calyx has a ridge above and below at the pedicel, while that of *L. magnistipulatus* tapers more gradually into the pedicel.

Representative specimen examined. BRAZIL. RIO GRANDE DO SUL: locality unknown, *Rambo 36208* (holotype, SI; photos, NY, UMO, US).

CONCLUSIONS

The three species, *L. paraguariensis*, *L. albescens*, and *L. aureonitens*, not treated in this paper are included in the key to facilitate identification of presumably closely related species. In seedlings of *L. albescens* grown from an herbarium specimen, the first leaf of the plant was simple and the second three-foliate. This particular characteristic should be common to the group of species treated in the key, although it is difficult to find in herbarium specimens. Considering the taxonomic studies of the genus *Lupinus* for South America (Planchuelo-Ravelo, 1984), this complex and its related species are representatives of the lupines of the "Atlantic Region" and are the only group of perennial plants with large compound leaves growing in the area.

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AUGUSTUS FENDLER'S VENEZUELAN PLANT COLLECTIONS[1]

Carol A. Todzia[2]

ABSTRACT

Between 1854 and 1858, Augustus Fendler resided in Colonia Tovar, a German village in the Coastal Cordillera of Venezuela, where he assembled one of the finest collections of plant specimens for his time. Fendler's life in Colonia Tovar is described from his correspondence with Daniel C. Eaton, Asa Gray, George Engelmann, and Joseph Henry. Because of his devotion to plant collecting and his acute powers of observation, Fendler's 2,630 flowering plant specimens from Venezuela are extremely valuable; 223 (8.5% of his total collections) have been designated as types. Although most specimens were labeled as having been collected in Colonia Tovar, state of Aragua, Venezuela, Fendler's field notebooks cite many different localities in the states of Carabobo and Aragua, and in the Distrito Federal. A map and list of Fendler's collecting localities are provided. An annotated list including collection data extracted from his notebook is given for the angiosperm types that he collected.

In the mid nineteenth century South America was poorly known botanically compared with most other parts of the world. At this time, plants generally were collected by people who traveled through one or several countries, making plant specimens along their way (e.g., Ruíz & Pavón; Humboldt & Bonpland). Few collectors lived in an area long enough to sample a region thoroughly and collect the relatively rare species. Augustus Fendler was a notable exception. He resided four years in Colonia Tovar,[3] a small German colony 35 miles west of Caracas, Venezuela (Rasmussen, 1943), and collected over 3,000 ferns and flowering plants. These collections are noteworthy, not only for their excellence, but also because a great number of new species were based on his material. To this day, new species are being described from Fendler's Venezuelan specimens (e.g., Croat & Lambert, 1986).

Although his Venezuelan collections are extremely important, Augustus Fendler is perhaps best known for his collections of New Mexican plants between 1846 and 1847. Gray (1849) published an annotated list of Fendler's New Mexican plants, which Shaw (1982) discussed more recently. Fendler's other collecting trips to Panama, Venezuela, and Trinidad are not as well known as those he took in the United States. In Panama, Fendler (Fig. 1) collected near the Chagres River for four months in 1849 and 1850. He resided in Trinidad from 1877 until his death in 1883. His most valuable collections were made in Venezuela between January 1854, and September 1858.

This paper is an account of Fendler's life in Venezuela constructed from his letters to D. C. Eaton, G. Engelmann, and A. Gray in the Yale University Library, Missouri Botanical Garden, and Gray Herbarium archives, respectively. This correspondence provides insight not only into Fendler, but also into the difficulties of life as a plant collector in the 1800s. Fendler corresponded with Engelmann in German and with Eaton and Gray in English. These lucid and detailed letters are a chronicle of plant collecting in South America in the mid nineteenth century and are even more remarkable since German was Fendler's native language.

According to various biographical notes (Canby,

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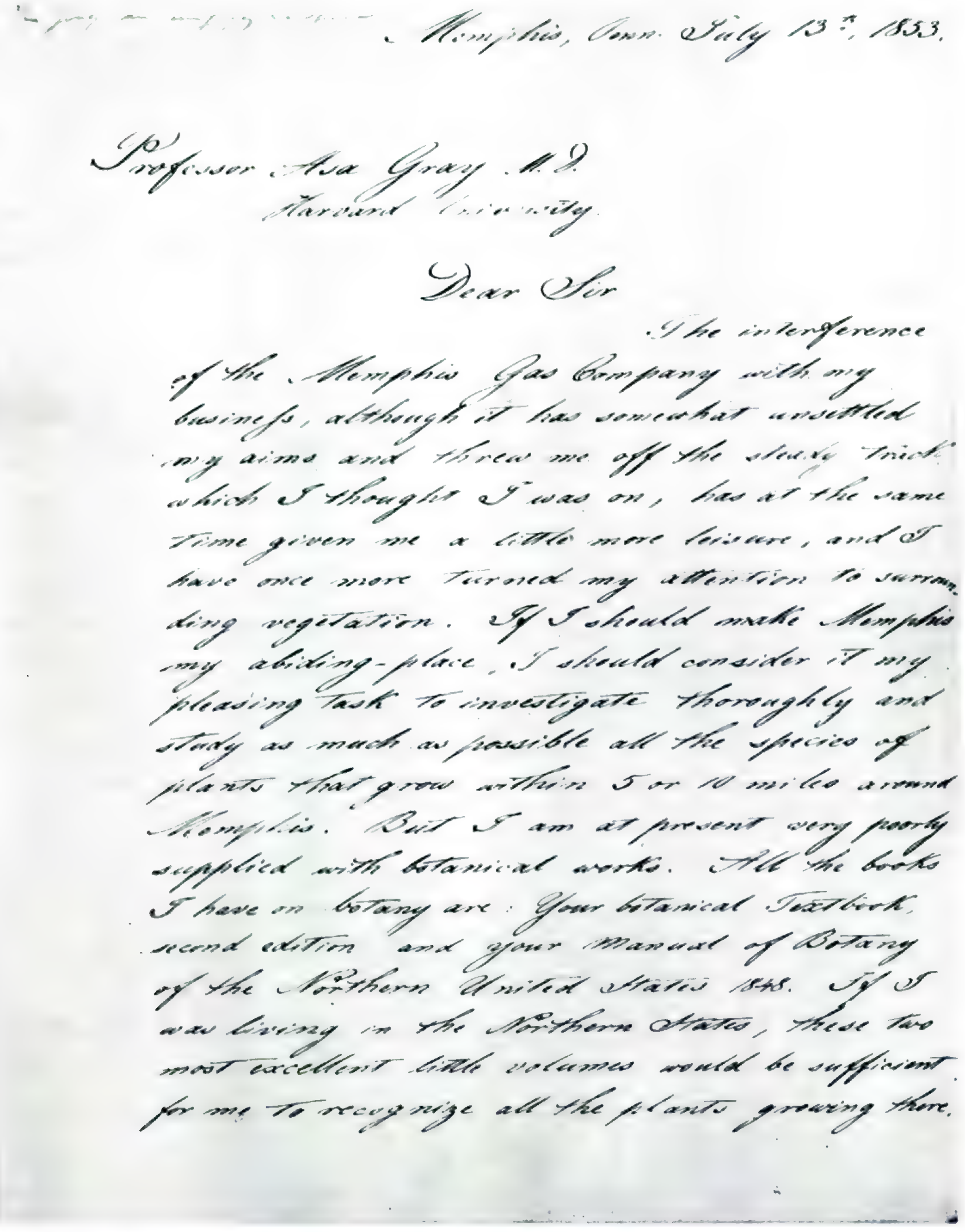
[3] Colonia Tovar is located in the state of Aragua and is not to be confused with Tovar in the state of Mérida, in the western part of Venezuela (Steyermark, 1981).

FIGURE 1. Photograph of Augustus Fendler probably taken in St. Louis, ca. 1860.

1885; Gray, 1885; Rohl, 1944), Fendler was born in Gumbinnen, eastern Prussia, in January 1813. At the age of 12 he was sent to a preparatory school where he mastered the fine penmanship that was as delightful to his correspondents as it is to his present-day historians (Fig. 2). Fascinated with traveling, Fendler sailed from Bremen to Baltimore in 1836 and within two years moved to St. Louis. During a visit to Europe in 1844, Fendler met Professor Ernst Meyer of the University at Koenigsberg in Prussia, who encouraged him to collect plants in the western United States and send them to him for sale. On his return to St. Louis, Fendler brought his specimens for identification to George Engelmann, the botanist who advised Henry Shaw, founder of the Missouri Botanical Garden (Stieber & Lange, 1986). Fendler and Engelmann struck up a friendship that spanned nearly 40 years. Engelmann later introduced Fendler to Asa Gray, who described Fendler as "a close, accurate observer, a capital collector and specimen-maker" (J. L. Gray, 1893: 341).

After a year of plant collecting in New Mexico, a failed attempt to collect plants near the Great Salt Lake, and two sojourns in Arkansas and Louisiana, Fendler settled in Memphis, Tennessee in



Memphis, Tenn. July 13th 1853.

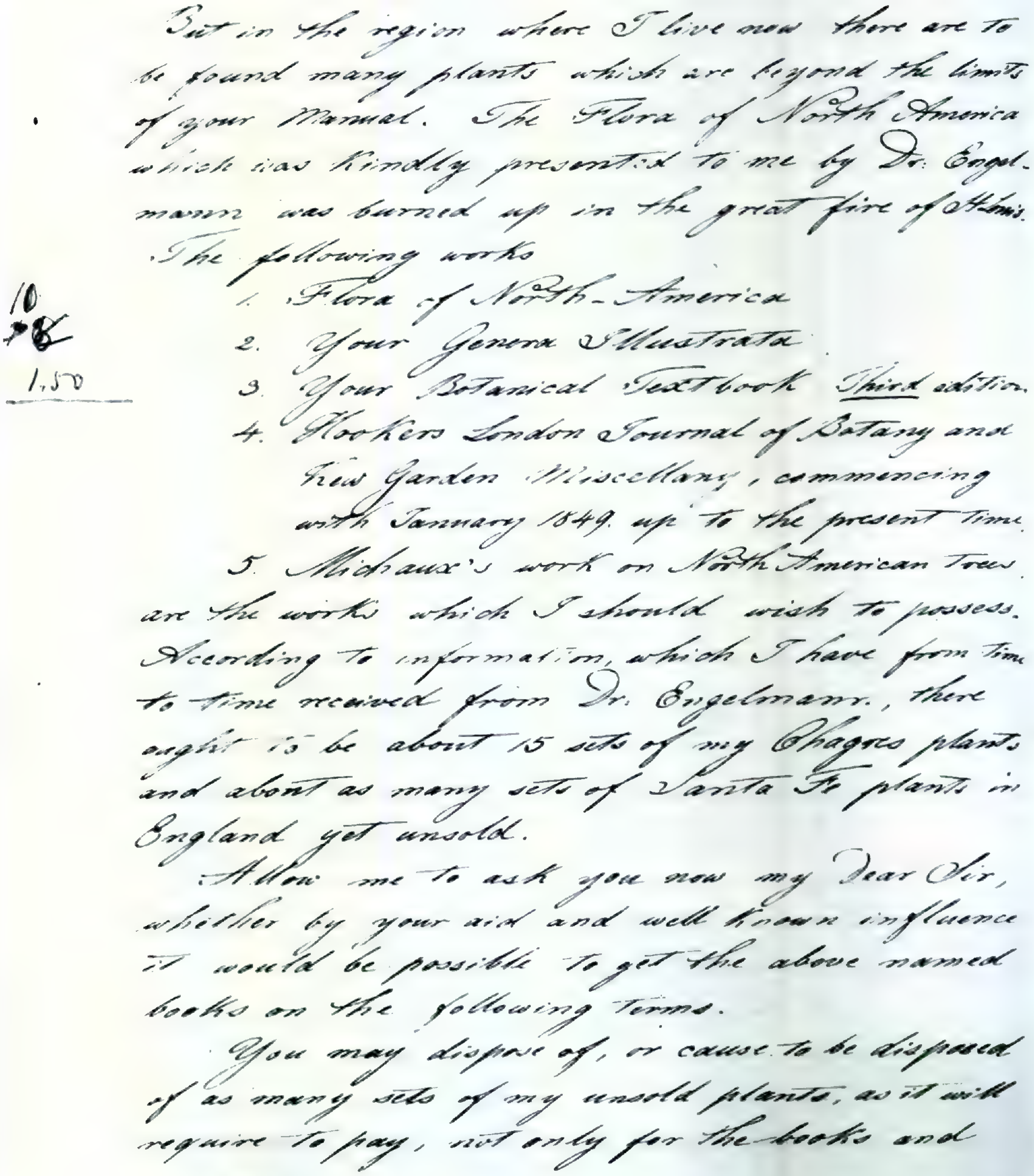
Professor Asa Gray M.D.
Harvard University.

Dear Sir

The interference of the Memphis Gas Company with my business, although it has somewhat unsettled my aims and thrown me off the steady track which I thought I was on, has at the same time given me a little more leisure, and I have once more turned my attention to surrounding vegitation. If I should make Memphis my abiding-place, I should consider it my pleasing task to investigate thoroughly and study as much as possible all the species of plants that grow within 5 or 10 miles around Memphis. But I am at present very poorly supplied with botanical works. All the books I have on botany are: Your botanical Textbook, second edition and your Manual of Botany of the Northern United States 1848. If I was living in the Northern States, these two most excellent little volumes would be sufficient for me to recognize all the plants growing there.

FIGURE 2. Letter by Augustus Fendler to Asa Gray (Memphis, Tennessee, July 13, 1853). Missouri Botanical Garden archives.

1850, and prospered there for four years in the gas-lamp business (Stieber & Lange, 1986). In 1853, when the lamp-lighting business in Memphis faltered, he was eager for a change of pace and wanted to resume collecting plants. He wrote to Gray on 11 August 1853 about his collecting plans: "My principal object in going to Caracas is: to go into a business again, by which I can support myself. But I hope I shall have plenty of leisure to make botanical collections besides. If I collect again I shall aim to make the sets as large and complete as possible. Do you think 15 sets, each containing from 1,000–1,500 species of plants collected about Caracas could meet with a ready sale?" On 15 August 1853, he wrote Engelmann that he wished to move to a town near Caracas because "In a city with a population of 70,000 I believe to be able to find more security than here,



But in the region where I live now there are to be found many plants which are beyond the limits of your Manual. The Flora of North America which was kindly presented to me by Dr. Engelmann was burned up in the great fire of St. Louis. The following works

1. Flora of North-America
2. Your Genera Illustrata
3. Your Botanical Textbook Third edition.
4. Hookers London Journal of Botany and Kew Garden Miscellany, commencing with January 1849 up to the present time.

5. Michaux's work on North American Trees.

are the works which I should wish to possess. According to information, which I have from time to time received from Dr. Engelmann., there ought is be about 15 sets of my Chagres plants and about as many sets of Santa Fe plants in England yet unsold.

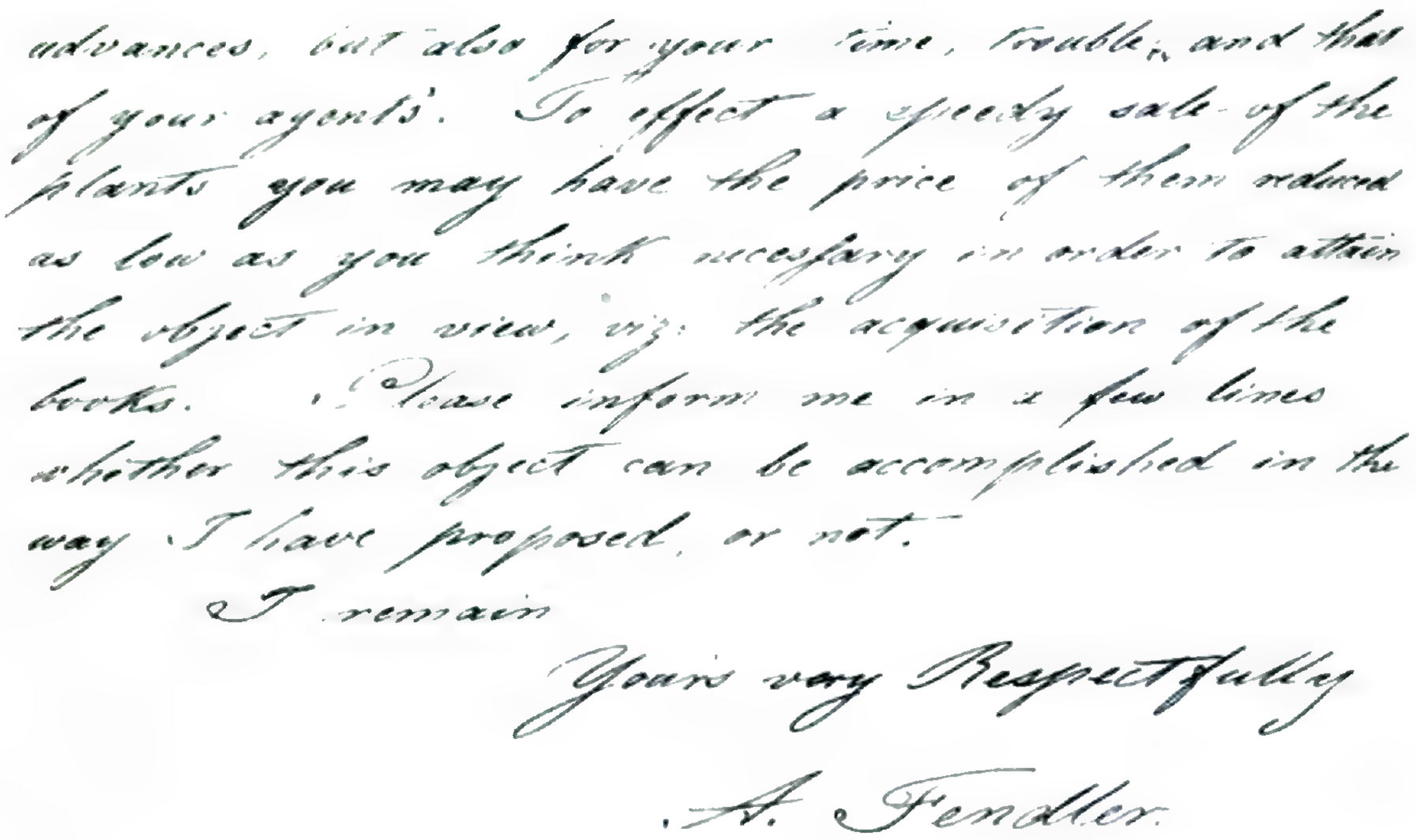
Allow me to ask you now my Dear Sir, whether by your aid and well known influence it would be possible to get the above named books on the following terms.

You may dispose of, or cause to be disposed of as many sets of my unsold plants, as it will require to pay, not only for the books and

FIGURE 2. Continued.

and secondly, because I believe I shall have a better climate there. Then also, the wish to live again in a mountain valley and to be in the vicinity of a rich mountain flora! without having the difficulties of long and difficult communication as I found in Santa Fe."

On the 24th of December 1853, Fendler sailed for Venezuela from New York harbor, accompanied by his chronically ill brother. They arrived in La Guaira, Venezuela, on 21 January 1854. In his day, it took five hours to reach Caracas from the coast. Upon arriving, he commenced collecting plants in the vicinity. Prompted by the high cost of living in Caracas, he went up to Colonia Tovar after only six weeks. After reaching the settlement, he wrote to Gray on 16 December 1854: "The base of the valley is 5,600 ft. above the sea, and some of the surrounding mountains about 2,000



advances, but also for your time, trouble, and that of your agents'. To effect a speedy sale of the plants you may have the price of them reduced as low as you think necessary in order to attain the object in view, viz: the acquisition of the books. Please inform me in a few lines whether this object can be accomplished in the way I have proposed, or not.

I remain

Yours very Respectfully

A. Fendler.

FIGURE 2. Continued.

feet higher . . . . The road from Caracas leads at first along a small river, which is very rapid and has to be crossed 42 times. The valley in which this river flows becomes at last very narrow and the road turns off to the left ascending a high mountain, from the tip of which it leads on in a westerly course along the very summit of the principal mountain range, through the deep shades of the primitive forest and down the valley of the Colony."

While at Colonia Tovar, Fendler also corresponded with Joseph Henry of the Smithsonian Institution, who published Fendler's letters and meteorological observations in the *Annual Report of the Board of Regents of the Smithsonian Institution*. Fendler was an ardent amateur meteorologist and in Venezuela traveled with a barometer, rain gauge, and thermometer. From his correspondence with Gray, Fendler provided a very rich description of Colonia Tovar (Fendler, 1857): "The valley in which Colonia Tovar is situated was, so late as December, 1841, a perfect wilderness, covered with primitive forest. Not even the existence of this valley was known fifteen years ago, neither to the government nor to its owner, although it is only thirty-five miles west of Caracas, the capital of Venezuela, and in a straight line cannot be more than twelve miles from the sea. And when an attempt was made to explore this region not even a guide could be found for the small exploring party of fifteen men, headed by Colonel Codazzi, a skillful officer and compiler of the new map of Venezuela. When this party at last succeeded in crossing this region and reaching the sea-shore, they thought they had achieved a most extraordinary thing, (to cross a distance of twelve miles in six days;) and after they had returned to their homes none of them had a desire to do the feat over again. This was a party of natives. And when, at a later period, after the establishment of the colony, another skillful engineer found, with a party of colonists, his way to the opposite port of the sea-shore, the party did not venture to go back the same route, but rather chose the way by sea to Laguayra, from there to Caracas and back to the colony, a very circuitous route certainly. Such is the nature of this mountain region, with its precipices, waterfalls, deep ravines, and its dense, almost impenetrable primeval forests."

Shortly after arriving in Colonia Tovar, Fendler bought a small farm in 1854 for 47 dollars. He described his new home in his letter to Gray of 16 December 1854: "My cottage stands on a small hill which is projecting from the sloping side of a mountain overlooking the greater part of the Colony. On the slopes of this little hill we have made terraces planted with *Musa sapientum*, with apple trees, Palms (*Oenocarpus utilis*), and stately tree ferns 14 feet high. Near the brown polished stem of the Palm the clear arch of a fountain (9 feet high) glitters in the tropical sun sending unceasingly its sparkling little stream to the top of the young

Palm. This fountain I made in a few days without outlay of money. Two pieces of the trunk of *Ceroxylon andicola* served as pipes." Fendler clearly enjoyed Colonia Tovar: "A visitor who never before lived in a valley like this finds here many peculiarities of vegetation, surface and climate which make him feel that he is not far off the land of perpetual peace; for he has entered the happy region of the ferns, the 'tierra templada de los helechos.' There is no scorching summer's heat, no fearful winter's cold, neither tornados to devastate the country nor gales to blind the inhabitants with sand and dust or penetrate their clothes and flesh with piercing frost" [Fendler to Gray, 16 December 1854]. His years in the village were the most enjoyable time of his life, and later letters indicate that he very much would have liked to return there [Fendler to Engelmann, 20 July 1882, Trinidad].

During his first year at Colonia Tovar, Fendler devoted much of his time to plant collecting. He wrote to Professor Henry: "In collecting botanical specimens, I have penetrated, without companion, the wilderness around in different directions, also that on the other side of the principal mountain range towards the sea, and can testify to the difficulties and hardships which are met with in exploring such a country . . . . In these woods, where the rays of the sun never touch the ground, there it is where moisture and a cool temperature reign forever. The trunk of every tree and its branches are covered with Ferns, Lycopodiaceae, Mosses, Hepaticae, Lichens, Orchids, Bromeliads, Araceae and besides Piperacae with many exogenous plants too numerous to mention" (Fendler, 1857).

Fendler wrote in detail to Gray, who had offered to enlist subscribers for his sets of plants. "I have already 8 boxes full of dried plants. The most attention I have hitherto paid to ferns of which I have 255 species, most of them complete; other plants I have not yet enumerated. For the last four or five weeks I have been employed with arranging my collections but have not yet finished. The fine dry weather which is now approaching urges me again to renewed activity in the field. The woods here are very dense and impenetrable without a sabre. The neighboring country is much diversified" [Fendler to Gray, 16 December 1854].

"Of Palms I have collected 6 species, of which 5 grow in the colony. Tree ferns 9 or 10 species. Cruciferae and Umbelliferae are represented only by 2 or 3 species. I do not intend to send plants until I can send something complete, and until I can ascertain the safest way to forward them" [Fendler to Gray, 16 December 1854]. Less than a year later, Fendler wrote: "Of flowering plants I have about 1,850 species, although my search after these may be called but a superficial one. I think from 800–1,000 more species might be collected and of ferns perhaps from 80–100 more" [Fendler to Gray, 25 November 1855]. In addition to ferns and angiosperms, Fendler collected fungi for M. A. Curtis, a mycologist in the Carolinas, lichens for Professor E. Tuckerman, a lichenologist at Amherst College, and mosses for William Starling Sullivant, a distinguished American bryologist in Ohio.

In 1857, after collecting in Colonia Tovar for over two years, Fendler found it increasingly difficult to find novel species. "In coming to a new country it is at first comparatively easy to make a living by collecting plants; for the collector can make use of all the different species that meet his eye, and can carry them home without the aid of other hired persons or beasts of burden. But after he has explored the neighborhood and is obliged to make extensive excursions of from 8–14 days or 3 weeks, the case is different, and he soon finds that his earnings do not come up to his expenses" [Fendler to Gray, 1 July 1857].

After collecting thoroughly around Colonia Tovar, Fendler took longer excursions crossing "the principal mountain chain in three different places. One from Maracai to Columbia [Puerto Colombia] to the very margin of the sea; the other from Valencia to San Estevan within 3 miles of Puerto Cabello; the third from Petaquire to within a few miles of the sea-shore. The two first regions are West, the third one East of Colonia Tovar. Besides these I have made a number of minor excursions into the neighboring valleys" [Fendler to Gray, 1 July 1857]. During these long excursions he reflected: "The more I attempt to explore these regions the more am I convinced, that a great deal remains yet to be done with regard to discovering and making known the plants of this country. These extensive ranges of mountains with their innumerable recesses and deep ravines, covered with the densest growth of primeval forest uninterrupted for more than 150 miles from East to West, have been in most places never been traversed by civilized men. When standing on some high mountain-peak and looking over a part of this territory, it needs no great power of imagination to be filled with a longing and an ardent desire to embark in enterprises even of the most perilous kinds, in order to penetrate the unknown abysses and to bring to light the hidden treasures of vegetation. And when in such moments I compare my strength and my fast waning pecuniary means, which forbid to hire

a companion to help me carry the burden, then I feel somewhat akin to depression of mind which prompts me to leave the spot and retrace my steps homewards."

Because Fendler viewed plant collecting as a business, he was very concerned with the marketability of his specimens, which were valued according to their origin, rarity, and completeness of identifications. Thus Fendler wished to have his plant collections be as rare as possible, as well as to have them determined. He was concerned that Karl Moritz, who had been living in Colonia Tovar for over ten years, would begin again to collect plants in his territory. "The present letter is chiefly written to make you acquainted with my intentions of sending the collections as soon as possible, that you may be enabled to correspond or to publish something to that account and secure me from 10–13 subscribers in time, because Mr. Moritz, who is still here has sometime ago commenced again to collect ferns, which he intends to send at an early date to Germany (I think to Berlin). I have seen Moritz's own set of his former collections when he used to travel about the greater part of Venezuela viz: the Orinoco, the mountains of Merida, Cumana, Caripe and a great many other regions; but the number of all his species of ferns will hardly exceed 250 or 260, while I have already 314, of which at least 290 are collected at the Colony or from 4–8 miles around it. There are several regions not far-off, where I never yet have been and which promise a very rich harvest of new species. I think I could augment the number of species considerably and discover many more new ones if I am sure that they find a market on which I may rely. I am therefore anxious to secure subscribers for them; so that I need not fear competition and then I shall go at it with renewed vigour; and if my life and health be spared I think of bringing together a rather complete representation of the vegetation of this and other parts of Venezuela. When I came here, Moritz seemed rather surprised that I should go at collecting plants in a place which he thought of being thoroughly ransacked, and he said that it would be a hard matter to find any new species. He seems however to have altered his opinion in this respect, after I had been in the field for some time; for I showed him many a plant which was new to him" [Fendler to Gray, 25 November 1855]. Fendler's Venezuelan collections surpass Moritz's in quantity and quality (J. A. Steyermark, pers. comm.; A. R. Smith, pers. comm.).

Plant collecting, however, was not profitable enough for Fendler to support himself and his invalid brother. "Whenever I was engaged in scientific pursuits for any length of time I was soon obliged to go to work at some other more profitable business, although that business might not be in accordance with my inclinations. And now I find again that the little capital, which I had earned at Memphis during three years by distilling camphene, is rapidly vanishing, notwithstanding the most frugal mode of living. I am therefore under necessity to try my hand for a while at something else beside collecting plants, and have already commenced to make experiments in brewing beer and making brandy; and shall be obliged (with regret do I say it), to spend most of my time behind the still . . . . By no means do I wish by the preceeding lines to convey to you the idea, that I am discouraged or that I have given up collecting plants. As long as strength and life and a few spare dollars remain with me I shall continue to do all I can for my favorite pursuit; and even now, whenever time and circumstances allow me to do so, I shall do it with the same zeal as I have done heretofore" [Fendler to Gray, 1 July 1857].

Fendler's Collections

In Venezuela Fendler collected under two number series, one for the ferns beginning at no. 1 and ending at no. 500, and one for flowering plants, numbers 1–2,630. Sets of Fendler's Venezuela plants were purchased by the following people and institutions (the number before the name indicates which set went to that recipient). (2) Hooker (K), (3) Grisebach (GOET), (4) A. Gray (GH), (5) Engelmann (MO), (6) Short (PH), (7) Charles Wyville Thomson (E), (8) Boissier (G), (9) De Candolle (G), (10) Oxford herbarium (OXF), (11) Harvey (TCD), (12) Delessert (G), (13) Martius (BR), (17) Eaton (YU), (18) Miss Elizabeth Morriss (?PHA), (21) Eaton (YU). It is not known whether sets 14–16 were sold at a later date, or whether they remained at GH. Sets 2–13 included ferns and phanerogams; sets 17–23 consisted only of ferns. The first and most complete set was retained by Fendler at first. Later he sold this first set of angiosperms to Gray. "My full set of Venezuelan plants contained over twice as many species as set No. 4, and therefore I hope that by the addition of those plants your herbarium would gain something. I would rather see them incorporated with your herbarium than with that of anyone else. The naming of the price of the lot I leave to you as you can judge best of their value, and I know that I am in good hands when I am in yours" [Fendler to Gray, 28 October

FIGURE 3. Map of the localities in northern Venezuela where A. Fendler collected in 1854–1858.

1863, St. Louis]. Ten cents per sheet was the usual asking price, although it was slightly higher for the orchids since they were often unicates.

At times Fendler felt he was not justly compensated for his specimens. For example, Lindley thought the price too high. "If Dr. Lindley was advised to pay but £2 per 100 for my Orchidae, then I will ask nothing more, and he shall be very welcome to them if he finds them to be worth that much. But if on the contrary he finds that the greater part of them, from being common things, are of no use to him, which I am inclined to infer from his letter, then I should be very sorry indeed that I ever offered them to him. To me that would be at least objects of remembrance of the amount of labor, bestowed upon, and perhaps of an over-animated enthusiasm in searching for them" [Fendler to Gray, 27 March 1859, St. Louis].

FENDLER'S FIELD NOTEBOOK

In 1859, Fendler sent Gray the field notes for his Venezuelan plants, retaining the information only on his personal set of specimens (set No. 1) [Fendler to Gray, 15 December 1859, St. Louis]. The field notes contain all dates and localities from which a particular species was collected, as well as elevation and notes about habit. Fendler numbered his plant collections according to the classification schemes presented in Gray's *Botany of the Northern United States* and Lindley's *Vegetable Kingdom* rather than the order in which they were collected, as is usually done today.

To obtain more complete sets of specimens, which could then be sold at a higher price, Fendler often applied the same number to specimens he believed to be the same species but were from widely distant localities. Fendler also attributed to the same collection number specimens collected on as many as five different dates. This was a common practice among professional plant collectors, particularly those working with Gray (Ewan, 1969), and a source of problems for plant systematists. The *International Code of Botanical Nomenclature* (Burdet et al., 1983) states that an "isotype is any duplicate (part of a single gathering made by a collector at one time) of the holotype." Since Fendler did not indicate on his specimens what specific date a particular sheet was collected, technically no isotypes can be designated. Of the 225 names in this list, 66 were collected on more than one date. Few taxonomists have previously been aware of this problem with the Fendler Venezuelan collections.

LOCALITIES

Almost all of Fendler's Venezuelan specimens bear blue labels imprinted at the top with "Plantae Venezuelanae" and "Prope coloniam Tovar legit

TABLE 1. Localities used in Fendler's angiosperm list.

	State	Latitude	Longitude	Approximate Elevation in Meters
Agua Blanca = Quebrada Agua Blanca	Aragua	9°54′N	69°22′W	
Biscaina	Aragua	10°20′N	67°15′W	1,000
Campanero	Carabobo	10°26′N	68°01′W	150
Caracas	D.F.	10°30′N	66°55′W	914
Cariaca = Carayaca	D.F.	10°32′N	67°07′W	800
Chichiribichi = Chichiriviche	D.F.	10°33′N	67°14′W	0
Choroni	Aragua	10°29′N	67°37′W	0
Colombia = Puerto Colombia	Aragua	10°30′N	67°36′W	0
Colonia Tovar	Aragua	10°25′N	67°17′W	2,400
Consejo = El Consejo	Aragua	10°14′N	67°16′W	200
Cumbote = Cumboto	Aragua	10°24′N	66°26′W	70
Esmeralda	Aragua	10°25′N	67°36′W	200
Guacara	Carabobo	10°14′N	67°53′W	438
Güigüe	Carabobo	10°05′N	67°47′W	420
Hacienda Curisal (not located)				
La Guayra = La Guaira	D.F.	10°36′N	66°56′W	0
Lagunassa = Lagunazo	D.F.	10°25′N	67°10′W	2,000
Las Aguntas = Las Adjuntas	D.F.	10°26′N	67°01′W	900
La Victoria	Aragua	10°14′N	67°20′W	585
Macarao	D.F.	10°26′N	67°02′W	1,400
Maracai = Maracay	Aragua	10°15′N	67°36′W	445
Maya, Punta	Aragua	10°32′N	67°24′W	1,400
Petaquire	D.F.	10°32′N	67°05′W	1,600
Piedernales = Pedernales	Carabobo	10°03′N	67°43′W	500
Puerto Cabello	Carabobo	10°28′N	68°01′W	0
San Carlos River	Aragua	10°19′N	67°19′W	
San Estévan = San Esteban	Carabobo	10°26′N	68°01′W	200
San Joaquin	Carabobo	10°16′N	67°47′W	450
Turmero	Aragua	10°14′N	67°29′W	466
Tuy River	Aragua, Miranda			
Urvina = La Urbina	D.F.	10°27′N	67°14′W	1,400
Valencia	Carabobo	10°11′N	72°12′W	478

A. Fendler 1845–5" at the bottom. The collection number is usually on the label, although it occasionally is on a slip of paper attached to the plant. Apparently Gray had these labels printed as he did for Wright's Cuban collections. Only the first set of Fendler's specimens, now at GH, has any collection data on them. Although the labels indicate that the sets were collected near Colonia Tovar in the state of Aragua, they were in fact also collected in the state of Carabobo and in the Distrito Federal. Figure 3 maps the Fendler localities in northern Venezuela, and Table 1 presents a list of these localities.

TYPE LIST

Of Fendler's 2,630 Venezuelan angiosperm collections, this study located records of 225 that have been designated as types. Since only the first of the 20 sets has collection data, full localities from the notebook are given for these types. In the following annotated list of angiosperm types based on Fendler Venezuelan collections, the number in the parentheses refers to the number of dates listed in the notebook. The orchids, numbers 1,359–1,489 and 2,124–2,155, were not included in the notebook.

The species names listed in Appendix I were gleaned mostly from the *Flora de Venezuela* and the *Catálogo de La Flora Venezolana* (Pittier et al., 1945–1947), as well as with the help of several specialists (see Appendix I). The current accepted names are given when known to me. Herbaria data were gathered from the original descriptions, the TROPICOS data base at MO, the specialists listed in Appendix I, and the author's search through the

MO herbarium. Unfortunately, there is no record of the number of duplicates made of each collection number (although the number may be on the labels of set No. 1 at GH, as with the ferns (Smith & Todzia, 1989), and therefore there is no way to ascertain which specific specimens are at any one herbarium. Since GH received Fendler's first set of angiosperms, excluding the orchids which went to Lindley, there are probably specimens for all numbers there. However, only herbaria where a specimen is confirmed to be deposited are included in the list. Overall, Fendler's Venezuelan specimens are widely distributed in the United States and Europe. The following 18 herbaria are known to have some Fendler Venezuelan collections (Lanjouw & Stafleu, 1957; pers. obs.): AMES, BR, BUF, C, CM, F, G, G-DC, GH, GOET, K, MO, NY, OXF, P, PH, S, and US.

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Appendix I

List of species with type specimens collected by A. Fendler in Venezuela (1854–1858). The collection dates listed by Fendler in his notebook are indicated in square brackets. If duplicates of a given collection number were made on a single date only, the exact date is given and is expressed as day/month/year; the year is between 1854 and 1858. All collection localities for a given collection number are furnished. Information enclosed in brackets comes directly from Fendler's notebook. The location of specimen(s), if known, is cited. In many cases, however, information from the literature did not record the place of deposition of the specimen seen, although in some cases it can be inferred. Specimens were searched for at MO and if not found in the herbarium were not cited. I thank the following people for help with specific plant groups: E. A. Christenson (Orchidaceae), T. B. Croat (Araceae), W. G. D'Arcy (Solanaceae), G. Davidse (Cyperaceae, Poaceae), B. Hammel (Cyclanthaceae), J. Kuijt (Loranthaceae), C. Luer (Orchidaceae), J. Steyermark (Rubiaceae), H. van der Werff (Lauraceae), J. Wurdack (Melastomataceae, Polygalaceae), and J. Zarucchi (Apocynaceae, Fabaceae).

ANNONACEAE

Rollinia fendleri R. E. Fries, Acta Horti Berg. 12: 152, tab. 15. 1934.
[Biscaina, 3,000 ft., 5/6/55], *Fendler 196* (holotype, K).

APIACEAE

Hydrocotyle venezuelensis Rose ex Mathias, Brittonia 2: 226. 1936.
[Colonia Tovar, 6,000 ft., 13/4/54], *Fendler 524* (holotype, M; isotypes, G, K).

APOCYNACEAE

Amblyanthera fendleri Muell. Arg., Linnaea 30: 417. 1859–1860.
[A few mi. SE of Colonia Tovar, 5,000 ft., 12/4/54, 6/7/54, 4/9/54], *Fendler 1032* (G-DC, photo at B, BR, F, K, MO).
= *Mandevilla fendleri* (Muell. Arg.) Woodson

Dipladenia fendleri Muell. Arg., Linnaea 30: 417. 1859–1860.
[A few mi. W of Colonia Tovar, 7,000 ft., 12/5/54], *Fendler 1030* (holotype, G-DC, photo at F; isotypes, B, BR, F, K, MO).

ARACEAE

Anthurium bredemeyeri Schott var. **elongata** Engl., Fl. Bras. 3: 80. 1878.
[Colonia Tovar, 6,000–7,000 ft., 25/5/54, 15/9/54, 15/10/54], *Fendler 1346* (lectotype, MO; isolectotype, K).
= *Anthurium bredemeyeri* Schott

Anthurium fendleri Schott, Prodr. Syst. Aroid. 468. 1860.
[Biscaina, 3,000 ft., 10/5/54], *Fendler 1343* (holotype, K; isotype, GH).

Anthurium nymphaeifolium K. Koch & C. Bouché var. **ovatum** Engl., Monogr. Phan. 2: 177. 1879.
[6–8 mi. SE of Colonia Tovar, 5,000–6,000 ft., 12/5/54, 28/7/54, 15/10/54], *Fendler 1336* (syntype, K).
= *Anthurium ornatum* Schott

Philodendron deviatum Schott, Bonplandia 7: 29. 1859.
[Biscaina, 3,000 ft., 10/5/55], *Fendler 1329* (holotype, K).

Philodendron effusilobum Croat, Aroideana 9: 99. 1986.
[Near San Estevan, 1,000 ft., 9/3/57], *Fendler 2573* (holotype, GH).

Philodendron fraternum Schott, Bonplandia 7: 29. 1859.
[Colonia Tovar, 6,000–6,500 ft., 16/8/54, 19/6/55, 3/7/55], *Fendler 1327* (holotype, K; isotypes, GH, US).

ARALIACEAE

Dendropanax fendleri Seemann, J. Bot. 2: 301. 1914.
[A few mi. S of Colonia Tovar, 16/4/55], *Fendler 529* (MO).

ASCLEPIADACEAE

Philibertia fendleri A. Gray, Proc. Amer. Acad. Arts 21: 395. 1886.
[La Victoria, 20/11/56], *Fendler 2119* (GH, MO).
= *Sarcostemma bilobum* Hook. & Arn. subsp. *lindeniana* (Decne.) Holm

ASTERACEAE

Clibadium parviceps S. F. Blake, Contr. U.S. Natl. Herb. 22: 598. 1924.
[Between Maracai and Choroni, 4,000 ft., 12/12/56; also between Petaquire and Cariaca, 4,000 ft., 12/2/58], *Fendler 1967* (holotype, GH; isotype, US).

Eupatorium neriifolium B. L. Robinson, Contr. Gray Herb. 65: 49. 1922.
[Colonia Tovar, 6,500 ft., 23/6/55], *Fendler 634* (GH, photo at F).

Eupatorium steetzii B. L. Robinson, Proc. Amer. Acad. Arts 55: 36. 1919.
[Colonia Tovar, 6,500 ft., 27/8/54], *Fendler 647* (holotype, GH).

Eupatorium tovarense B. L. Robinson, Proc. Amer. Acad. Arts 54: 259. 1918.
[Between Petaquire and the sea, 4,000 ft., 22/4/58], *Fendler 1947* (holotype, GH; isotype, MO).
= *Ayapana tovarensis* (B. L. Robinson) R. King & H. Robinson

Eupatorium xestolepis B. L. Robinson var. **xestolepis,** Proc. Amer. Acad. Arts 54: 261. 1918.
[Between Caracas and La Guayra; also a few mi. SE of Colonia Tovar, 7/5/55, 10/5/55, 16/8/55], *Fendler 638* (holotype, GH).

Hieracium tovarense Fries, Epicris. Hierac. 152. 1862.
[Around Colonia Tovar, 6,000–7,500 ft., 26/7/54, 7/5/55, 28/6/55, 23/8/55, 17/7/56], *Fendler 718* (G, photo at F).
= *Hieracium avilae* H.B.K.

Mikania gracilipes B. L. Robinson, Contr. Gray Herb. 61: 15. 1920.
[Between Valencia and Campanero, 5,000 ft., 27/2/57], *Fendler 2348* (holotype, GH; isotypes, MO, G, photo at F).

Mikania hexagona B. L. Robinson, Proc. Amer. Acad. Arts 47: 196. 1911.
[Tuy River below Colonia, 4,000 ft., 21/10/54], *Fendler 626* (holotype, GH, photo at F).

Mikania racemulosa Klatt, Abh. Naturf. Ges. Halle 15: 325. 1882.
[Colonia Tovar, 6,000–7,000 ft., 31/3/54, 28/6/55], *Fendler 625* (GH, MO, photo at F) syntype with *Schomburgk 480* (G).

Mikania vitrea B. L. Robinson, Contr. Gray Herb. 61: 22. 1920.
[Colonia Tovar, 6,500 ft., 24/5/57], *Fendler 2349* (holotype, GH; isotype, G, photo at F).
= *Mikania hookeriana* DC. var. *crassicaulis* Steyerm.

Piptocarpha sprucei Baker, Fl. Bras. 6(2): 129. 1873.
[Between Maracai and Choroni, 2,500 ft., 28/1/57], *Fendler 1957* (syntype).

Senecio cucullatus Klatt, Abh. Naturf. Ges. Halle 15: 331. 1882.
[Colonia Tovar, 6,500 ft., 24/8/55], *Fendler 702* (P, MO, photo at F).

Trichogonia rhadinocarpa B. L. Robinson, Proc. Amer. Acad. Arts 42: 36. 1906.
[Biscaina, 3,200 ft., 5/6/55], *Fendler 651* (GH).

BEGONIACEAE

Begonia fagopyroides Kunth & Bouché var. **fendleriana** A. DC., Prodr. 15(1): 289. 1864.
[A few mi. SE of Colonia Tovar, in ravines, 3,500 ft., 9/3/55, 7/5/55], *Fendler 513* (G-DC, K).

BROMELIACEAE

Aechmea cymoso-paniculata Baker, J. Bot. 17: 165. 1879.
[Between Petaquire and the sea, 3,000 ft., 9/2/57], *Fendler 2453* (holotype, K; isotype, MO).

Aechmea fendleri André ex Mez, Bromel. Andreanae 13. 1889.
[Between Petaquire and Colonia Tovar, 7,000 ft., 11/2/57], *Fendler 2454* (holotype, K; isotype, GH).

Bilbergia filicaulis Griseb., Nachr. Königl. Ges. Wis. Georg-Augusts-Univ. 1864: 13. 1865.
[Between Valencia and Campanero, 500 ft., 7/3/57], *Fendler 2452* (holotype, GOET, photo US).
= *Aechmea filicaulis* (Griseb.) Mez

Caraguata coriostachya Griseb., Nachr. Königl. Ges. Wis. Georg-Augusts-Univ. 1864: 21. 1865.
[Between Maracai and Choroni, 4,000 ft., 13/12/56], *Fendler 2167.*
= *Guzmania coriostachya* (Griseb.) Mez

Nidularium albo-roseum Griseb., Nachr. Königl. Ges. Wis. Georg-Augusts-Univ. 1864: 12. 1865.
[High mountains E of Colonia Tovar, 24/6/55], *Fendler 1521* (holotype, GOET; isotype, GH).
= *Greigia albo-rosea* (Griseb.) Mez

Pitcairnia fendleri Mez, Monogr. Phan. 9: 387. 1896.
[Between Caracas and La Guayra, 1,500 ft., 16/8/55], *Fendler 1550* (holotype, GOET, photo US).

Tillandsia acorifolia Griseb., Nachr. Königl. Ges. Wis. Georg-Augusts-Univ. 1864: 19. 1865.
[Seaside of mountains N of Colonia Tovar, 6,000 ft.,

22/1/56], *Fendler 1771* (holotype, GOET).
= *Guzmania acorifolia* (Griseb.) Mez

Tillandsia aurantiaca Griseb., Nachr. Königl. Ges. Wis. Georg-Augusts-Univ. 1864: 16. 1865.
[Between Petaquire and Cariaca, 4,500 ft., 12/2/58], *Fendler 2575* (holotype, GOET, photo US).
= *Tillandsia tetrantha* Ruíz Lopez & Pavón var. *aurantiaca* (Griseb.) Lyman B. Smith

Tillandsia caribaea Lyman B. Smith, Proc. Amer. Acad. Arts 70: 155. 1935.
[High mountains near Colonia Tovar, 6,000 ft., 14/2/55, 17/6/55], *Fendler 1523* (holotype, GOET, photo US).

Tillandsia compacta Griseb., Nachr. Königl. Ges. Wis. Georg-Augusts-Univ. 1864: 18. 1865.
[A few mi. SE of Colonia Tovar, 6,000 ft., 25/5/54, 21/6/54], *Fendler 1508* (holotype, GOET; isotype, K).
= *Tillandsia compacta* Griseb. var. *compacta*

Tillandsia excelsa Griseb. var. **latifolia** Griseb., Nachr. Königl. Ges. Wis. Georg-Augusts-Univ. 1864: 17. 1865.
[A few mi. SE of Colonia Tovar, 6,000 ft., 7/5/55], *Fendler 1516* (GH, GOET).
= *Tillandsia fendleri* Griseb. var. *fendleri*

Tillandsia fendleri Griseb., Nachr. Königl. Ges. Wis. Georg-Augusts-Univ. 1864: 17. 1865.
[Between Caracas and Colonia Tovar, 6,000 ft., 7/5/55], *Fendler 1515* (holotype, GOET, photo US).
= *Tillandsia fendleri* Griseb. var. *fendleri*

Tillandsia grisebachiana Baker, J. Bot. 26: 143. 1888.
[Colonia Tovar, 6,500 ft., 25/5/54, 21/6/54], *Fendler 1509* (GH).

Tillandsia incurva Griseb., Nachr. Königl. Ges. Wis. Georg-Augusts-Univ. 1864: 15. 1865.
[6 mi. SE of Colonia Tovar, 6,000 ft., 28/8/54, 7/5/55], *Fendler 1524* (holotype, GOET; isotype, GH).
= *Vriesea incurva* (Griseb.) Read

Tillandsia laxa Griseb., Nachr. Königl. Ges. Wis. Georg-Augusts-Univ. 1864: 18. 1865.
[Between Maracai and Choroni, 3,000 ft., 29/1/57], *Fendler 2166* p.p. (holotype, GOET, photo US).
= *Vriesia laxa* (Griseb.) Mez

Tillandsia lineatifolia Mez, Monogr. Phan. 9: 686. 1896.
[Between Petaquire and the sea, 3,500 ft., 2/9/57], *Fendler 2447* (GOET, photo GH).
= *Tillandsia anceps* G. Lodd.

Tillandsia longibracteata Baker, J. Bot. 26: 81. 1888.
[Between Petaquire and the sea, 5,000 ft., 9/2/57], *Fendler 2449* (syntype).
= *Vriesea splendens* (Brongn.) Lemaire var. *formosa* Sur. ex Witte

Tillandsia longifolia Baker, Handb. Bromel. 185. 1889.
[A few mi. SE of Colonia Tovar, between rocks, 6,000–6,700 m, 7/5/55, 14/5/55], *Fendler 1522.*

Tillandsia mucronata Griseb., Nachr. Königl. Ges. Wis. Georg-Augusts-Univ. 1864: 20. 1865.
[Between Maracai and Choroni, 6,500 ft., 29/1/57], *Fendler 2159* (holotype, GOET, photo US; isotype, K).
= *Guzmania mucronata* (Griseb.) Mez

Tillandsia myriantha Baker, J. Bot. 25: 242. 1887.
[7 mi. SE of Colonia Tovar, 5,000 ft., 14/5/55], *Fendler 1530* (holotype, K; isotype, GOET).

Tillandsia pleiosticha Griseb., Nachr. Königl. Ges. Wis. Georg-Augusts-Univ. 1864: 19. 1865.
[High mountains E of Colonia Tovar, 7,000 ft., 11/7/54, 19/3/55], *Fendler 1514* (holotype, GOET, photo US; isotype, K).
= *Guzmania pleiosticha* (Griseb.) Mez

Tillandsia robusta Griseb., Nachr. Königl. Ges. Wis. Georg-Augusts-Univ. 1864: 15. 1865.
[Maya, 4,000 ft., 23/6/55], *Fendler 1525.*
= *Vriesea robusta* (Griseb.) Lyman B. Smith

Tillandsia tovarensis Mez, Monogr. Phan. 9: 769. 1896.
[Between Petaquire and Colonia Tovar, 26/10/57], *Fendler 2446* (holotype, GOET, photo US).

Tillandsia ventricosa Griseb., Nachr. Königl. Ges. Wis. Georg-Augusts-Univ. 1864: 19. 1865.
[High mountains E of Colonia Tovar, 7,000 ft., 7/5/55], *Fendler 1517* (holotype, GOET; isotypes, GH, K).
= *Guzmania ventricosa* (Griseb.) Mez

BURSERACEAE

Protium laxiflorum Engl. var. **fendleri** Engl., Monogr. Phan. 4: 67. 1883.
[Large tree yielding a resin called "Taca mahac," flowers green. Colonia Tovar, 6,400 ft., 22/4/54, 19/9/55], *Fendler 177* (holotype, G, photo F).

CAPPARACEAE

Cleome moritziana Klotzsch ex Eichler, Fl. Bras. 13(1): 250. 1841.
[A few mi. S of Colonia Tovar, 4,000 ft., 18/5/55], *Fendler 27* (lectotype, F?).

CELASTRACEAE

Maytenus fendleri Briq., Annuaire Conserv. Jard. Bot. Genève 20: 360. 1919.
[A few mi. SW of Colonia Tovar, 6,500 ft., 28/6/55], *Fendler 215* (F, G).

CHLORANTHACEAE

Hedyosmum pseudoandromeda Solms-Laub., Prodr. 16(1): 481. 1869.
[Colonia Tovar, 6,500 ft., 26/7/56, 21/8/56, 4/9/56], *Fendler 1127* (lectotype G, photos GH, MO, NY; isolectotypes, BR, G, GH, MO, NY, S, US).

COMMELINACEAE

Phaeosphaerion efoveolatum C. B. Clarke, Monogr. Phan. 3: 136. 1881.
[Between Caracas and Colonia Tovar, 6,000 ft., 23/8/55], *Fendler 1555* (holotype, G).

CONVOLVULACEAE

Ipomoea alatipes Hook., Bot. Mag. pl. 5330. 1862.
[Between Biscaina and La Victoria, 2,000 ft., 8/9/56], *Fendler 2084* (syntype, K).
= *Operculina alatipes* (Hook.) House

Ipomoea fendleriana Kuntze, Rev. Gen. Pl. 2: 444. 1891.
[La Victoria, 2,000 ft., 21/11/56], *Fendler 2083.*
= *Ipomoea calantha* Griseb.

Ipomoea fruticosa Kuntze, Revis. Gen. Pl. 2: 444. 1891.
[A few mi. W of Colonia Tovar, 7,000 ft., 17/4/55, 3/2/58], *Fendler 941.*

[Between Turmero and Agua Blanca, 1,800 ft., 30/1/57, 30/1/58], *Fendler 2082.*

CUCURBITACEAE

Echinocystis polycarpa Cogn., Mém. Couronnés Autres Mém. Acad. Roy. Sci. Belgique 28: 90. 1878.
[Caracas, 3,000 ft., 23/2/54], *Fendler 503* (G, photo at F).

Edmondia spectabilis Cogn., Monogr. Phan. 3: 420. 1881.
[Colonia Tovar, 6,500 ft., 5/5/54, 6/3/55], *Fendler 489* (G, photo at F).

Gurania wagneriana Cogn., Mém. Couronnés Autres Mém. Acad. Roy. Sci. Belgique 28: 25. 1877.
[A few mi. S of Colonia Tovar, 3,000–4,000 ft., no date], *Fendler 490* (G, photo at F).

Sicyos macrocarpus Cogn., Monogr. Phan. 3: 893. 1881.
[Near Güigüe, 2,000 ft., 25/1/55], *Fendler 502* (syntype, K).
= *Anomalosicyos macrocarpus* (Cogn.) H. Gentry

CYCLANTHACEAE

Asplundia fendleri Harling, Acta Horti Berg. 18: 221. 1958.
[In and near Colonia Tovar, 6,000–6,500 ft., 7/7/54, 23/8/56], *Fendler 1348* (holotype, K; isotype, GH).

Evodianthus funifer (Poit.) Lindman subsp. **fendlerianus** Harling, Acta Horti Berg. 18: 274. 1958.
[Between Petaquire and the sea, 3,500 ft., 22/4/58], *Fendler 2617* (holotype, K; isotypes, GH, GOET).

CYPERACEAE

Rhynchospora rudis C. B. Clarke, Kew Bull. 8: 39. 1908.
[A few mi. W of Colonia Tovar, 7,000 ft., 28/8/54, 19/9/55, 19/7/56], *Fendler 1591* (holotype, K).

DIOSCOREACEAE

Dioscorea fendleri R. Knuth, Pflanzenr. 4, Fam. 43: 65. 1924.
No information in notebook. *Fendler 2171.*

ELAEOCARPACEAE

Sloanea fendleriana Benth., J. Linn. Soc. Bot. 5, suppl. 2: 70. 1861.
[Seaside of mountains between Maracai and Choroni, 3,000–4,000 ft., 26/10/56, 12/12/56], *Fendler 2489* (holotype, K).

EUPHORBIACEAE

Acalypha villosa Jacq. var. **intermedia** Muell. Arg., Linnaea 34: 8. 1865.
[La Victoria, 2,000 ft., 21/12/56], *Fendler 1825* (syntype, G-DC; isotype, MO).
[Near La Victoria, 2,500 ft., 14/11/56], *Fendler 2408* (syntype, G-DC).
= *Ricinocarpus villosus* (Jacq.) Kuntze var. *intermedius* (Muell. Arg.) Kuntze

Alchornea grandiflora Muell. Arg., Linnaea 34: 170. 1865.
[Colonia Tovar, 6,500 ft., 7/4/54, 13/4/54, *Fendler 1272* (G-DC, MO, photo F).
= *Ricinocarpus villosus* (Jacq.) Kuntze var. *intermedius* (Muell. Arg.) Kuntze

Euphorbia tovarensis Boiss., Prodr. 15(2): 59. 1862.
[Maya, 3,000 ft., 12/12/54], *Fendler 1191* (holotype, G; isotype, MO).

Excoecaria obtusiloba Muell. Arg., Linnaea 32: 125. 1865.
[Biscaina, 3,000 ft., 5/6/55], *Fendler 1230* (G-DC, photo F).

Mabea rubrivenium Poeppig & Endl.
[Colonia Tovar, 6,500 ft., 7/5/54, 16/6/55], *Fendler 1232.*

Pedilanthus fendleri Boiss., Prodr. 15(2): 5. 1862.
[Between Caracas and La Guayra, 1,000 ft., 16/8/55], *Fendler 1202* (G-DC, photo F).

Plukenetia penninervia Muell. Arg., Linnaea 34: 158. 1865.
[Near Biscaina, 3,000 ft., 1/2/57], *Fendler 2412* (holotype, G-DC, photo F).

Tragia fendleri Muell. Arg., Linnaea 34: 179. 1865–1866.
[Biscaina, 3,000 ft., 5/6/55], *Fendler 1208* (holotype, G-DC, photo F).

FABACEAE

Calliandra laxa var. **parvifolia** Benth., Trans. Linn. Soc. London 30(3): 551. 1875.
[Between La Victoria and Biscaina, 2,500 ft., 1/2/57], *Fendler 2255* (K).

Canavalia fendleri Piper, Contr. U.S. Natl. Herb. 20(14): 570. 1875.
[Biscaina, 7/9/55], *Fendler 248* (holotype, K; isotype, MO).

Cassia viciifolia Benth., Trans. Linn. Soc. London 27: 544. 1871.
[Between Turmero and La Victoria, 2,000 ft., 14/3/57], *Fendler 2230* (lectotype, K).
= *Senna viciifolia* (Benth.) Irwin & Barneby

Inga fendleriana Benth., Trans. Linn. Soc. London 30(3): 630. 1875.
[Valley of Macarao, 3,500 ft., 18/1/57], *Fendler 2259* (K).

Machaerium moritzianum Benth., J. Proc. Linn. Soc., Bot. 4(suppl.): 58. 1860.
[Valley of Macarao, 4,000 ft., 4/7/56], *Fendler 1750* (syntype, K).
[Near La Victoria, 2,200 ft., 21/11/56], *Fendler 1866* (syntype, K).

Machaerium tovarense Pittier, Contr. U.S. Natl. Herb. 20(3): 121. 1917.
[La Victoria, 2,000 ft., 14/11/56], *Fendler 1865* (holotype, GH; isotype, MO).

Mimosa tovarensis Benth., Trans. Linn. Soc. London 30(3): 407. 1875.
[Caracas, 3,500 ft., 13/2/54], *Fendler 344* (holotype, K; isotype, MO).

Moldenhawera mollis Benth., Fl. Bras. 15(2): 77. 1870.
[La Victoria, 2,000 ft., 21/11/56], *Fendler 1864* (K).

GENTIANACEAE

Symbolanthus magnificus Gilg, Engl. Bot. 22: 343. 1896.
[10 mi. SE of Colonia Tovar, 5,000–6,000 ft., 8/4/54, 19/6/54, 4/9/54], *Fendler 830* (B, MO, photo F).

= *Symbolanthus calygonus* (Ruíz Lopez & Pavón) Griseb.

GESNERIACEAE

Columnea fendleri Sprague, Kew Bull. 1912: 41. 1912.
[Between Petaquire and the sea, 5,000 ft., 9/2/57], *Fendler 2031* (probably K).
= *Columnea scandens* L. var. *fendleri* (Sprague) Wiehler

Monopyle leucantha Moritz ex Benth., Icon. Pl. 12: 87. 1876.
[Colonia Tovar, 5,800–6,200 ft., 31/2/54, 27/3/54, 10/5/55, 17/6/54, 29/8/54], *Fendler 794* (MO).

LAMIACEAE

Salvia tovariensis Briq., Annuaire Conserv. Jard. Bot. Genève 2: 130. 1898.
[Between Caracas and Maya, 3,200 ft., 12/2/54, 12/5/54], *Fendler 876* (G).

Stachys fendleri Briq., Annuaire Conserv. Jard. Bot. Genève 2: 115. 1898.
[Near Colonia Tovar, 6,500 ft., 31/2/54, 19/12/54, 20/6/55, 21/9/55], *Fendler 879* (G, MO, photo F).

LAURACEAE

Gymnobalanus fendleri Meissn., Prodr. 15(1): 142. 1864.
[Between Valencia and Campanero, 5,500 ft., 7/3/57], *Fendler 2395* (holotype, G-DC).
= *Ocotea fendleri* (Meissn.) Rohwer

Gymnobalanus latifolia Meissn., Prodr. 15(1): 141. 1864.
[Between Colonia Tovar and Petaquire, 5,000 ft., 19/2/55], *Fendler 1095* (G-DC, photo F).

Mespilodaphne vaginans Meissn., Prodr. 15(1): 104. 1864.
[Colonia Tovar, 6,000 ft., 21/6/54, 21/3/57], *Fendler 1098* (types, G-DC, photo F, G, K, MO, NY, US).
= *Ocotea vaginans* (Meissn.) Mez

Nectandra leucantha Nees & Martius var. **attenuata** Meissn., Prodr. 15(1): 151. 1864.
[La Victoria, 2,000 ft., 14/10/56], *Fendler 2393* (syntypes G, K, MO).

LECYTHIDACEAE

Eschweilera fendleriana Miers, Trans. Linn. Soc. 30: 250, t. 60, fig. 6. 1874. *Fendler s.n.* (K).
= *Lecythis fendleriana* (Miers) Kunth

LILIACEAE

Smilax scabriuscula H.B.K. var. **fendleri** A. DC., Monogr. Phan. 1: 143. 1878.
[Near Colonia Tovar, 6,000–7,000 ft., 19/6/54, 3/12/54, 16/9/55], *Fendler 1546* (G, MO, photo at F).

LOGANIACEAE

Strychnos fendleri Sprague & Sandw., Kew Bull. 1927: 129. 1927.
[La Victoria, 2,500 ft., 21/11/56], *Fendler 2314* (K).

LORANTHACEAE

Dendrophthora basiandra Kuijt, Wentia 6: 32. 1961.
[Colonia Tovar, 6,800 ft., 10/8/54], *Fendler 1104* (holotype, GH; isotypes, GH, K).

Dendropthora eichleriana Urban, Ber. Deutsch. Bot. Ges. 14: 287. 1896.
[Colonia Tovar, 6,800 ft., 14/2/55], *Fendler 1101* (holotype, K; isotypes, GH, K, MO, PH).

Phoradendron bilineatum Urban, Bot. Jahrb. Syst. 23, Beibl. 57: 5. 1897.
[La Victoria, 2,000 ft., 21/1/56], *Fendler 1811.*

Phoradendron cuneifolium Urban, Bot. Jahrb. Syst. 23, Beibl. 57: 5. 1897.
[Biscaina, 3,200 ft., 5/6/55], *Fendler 1115.*

Phoradendron fendlerianum Eichler, Fl. Bras. 5(2): 129. 1868.
[Colonia Tovar, 8/4/54, 10/5/54, 9/3/55], *Fendler 1102* (MO).

Phoradendron longipetiolatum Urban, Bot. Jahrb. Syst. 23, Beibl. 57: 6. 1897.
[Colonia Tovar, 6,500 ft., 10/7/56], *Fendler 1762.*

Phoradendron ovalifolium Urban, Bot. Jahrb. Syst. 23, Beibl. 57: 6. 1897.
[Biscaina, 3,500 ft., 10/5/55], *Fendler 1108.*

Phoradendron rigidum Urban, Bot. Jahrb. Syst. 23, Beibl. 57: 7. 1897.
[Colonia Tovar, 6,500 ft., 1/6/55], *Fendler 1105.*

Phoradendron tovarense Urban, Bot. Jahrb. Syst. 23, Beibl. 57: 8. 1897.
[A few mi. SE of Colonia Tovar, 6,000 ft., 26/7/56], *Fendler 1761.*
= *Phoradendron dipterum* Eichler

Phoradendron tubulosum Urban, Eng. Bot. Jahrb. 23, Beibl. 57: 5. 1897.
[Biscaina, 3,200 ft., 7/9/55], *Fendler 1106* (syntype).

Phoradendron venezuelense Trel., Genus Phoradendron, 111. 1916.
[La Victoria, 2,000 ft., 21/11/56], *Fendler 1810* (holotype, K; isotype, GH).
= *Phoradendron quandrangulare* (H.B.K.) Krug & Urban

Stachyphyllum fendleri van Tiegh., Bull. Soc. France 42: 565. 1895.
[Colonia Tovar, 6,500 ft., 15/8/54, 24/10/55, 8/11/56], *Fendler 1125* (holotype, P; isotypes, GH, MO).
= *Antidaphne viscoidea* Poeppig & Endl.

MELASTOMATACEAE

Arthrostemma alatum Triana, Trans. Linn. Soc. London 28: 35. 1871.
[Near La Victoria, 2,000 ft., 21/11/56], *Fendler 1832* (G, MO, photo F).

Blakea grisebachii Cogn., Monogr. Phan. 7: 1071. 1891.
[Seaside of mountains, N of Agua Blanca, 4,000 ft., 30/1/58], *Fendler 2547* (syntypes, GH, GOET).

Blakea longibracteata Cogn., Monogr. Phan. 7: 1074. 1891.
[Between Petaquire and the seashore, 5,500 ft., 22/4/58], *Fendler 2593* (holotype, GOET).

Calophysa ? flexuosa Triana, Trans. Linn. Soc. London 28: 141. 1871.
[Between Petaquire and the sea, 4,000 ft., 9/2/57], *Fendler 2261.*
= *Clidemia flexuosa* (Triana) Cogn.

Clidemia ampla Cogn., Monogr. Phan. 7: 1023. 1891.
[Between Petaquire and the seashore, 5,500 ft., 22/4/58, *Fendler 2594* (syntypes, F, G, GH, GOET, K, MO).

Clidemia ciliata D. Don var. **grandifolia** Cogn., Monogr. Phan. 7: 1020. 1891.
[Between Maracai and Choroni, 3,000 ft., 24/1/57], *Fendler 436.*
= *Clidemia ciliata* D. Don var. *ciliata*

Clidemia fendleri Cogn., Monogr. Phan. 7: 1016. 1891.
[Mountains near Caracas, a few mi. SE of Colonia Tovar, 17/2/54, 7/5/55, 19/6/55, 3/7/55], *Fendler 438* (G, MO, photo F).

Clidemia grandifolia Cogn., Monogr. Phan. 7: 1018. 1891.
[Between Maracai and Choroni, 4,000 ft., 28/1/57], *Fendler 2263* (syntypes, G, MO).

Henriettella tovarensis Cogn., Monogr. Phan. 7: 1044. 1891.
[Near Colonia Tovar, 5,600 ft., 6/4/54, 22/9/55, 3/10/55], *Fendler 444* p.p. (G, photo F, MO).

Henriettella tovarensis Cogn. var. **angustifolia** Cogn., Monogr. Phan. 7: 1044. 1891.
[Near Colonia Tovar, 5,600 ft., 6/4/54, 22/9/55, 3/10/55], *Fendler 444* p.p. (syntype, G, photo F).

Heterotrichum glandulosum Cogn., Monogr. Phan. 7: 955. 1891.
[A few mi. SE of Colonia Tovar, 5,100 ft., 4/9/54, 3/7/55], *Fendler 432* (G, photo F).
= *Micronia araguensis* Wurdack

Heterotrichum lucidum Triana, Trans. Linn. Soc. London 28: 134. 1871.
[Colonia Tovar, 6,500 ft., 2/9/56], *Fendler 1845* (MO).

Leandra fendleri Cogn., Monogr. Phan. 7: 653. 1891.
[Near Colonia Tovar, 7,000 ft., 12/6/54, 3/12/54, 12/5/55, 27/8/55], *Fendler 439* (G, MO, photo F).
= *Leandra lindeniana* (Naud.) Cogn.

Meriania subumbellata Cogn., Monogr. Phan. 7: 430. 1891.
[Between Maracai and Choroni, 4,000 ft., 12/12/56, 29/1/57], *Fendler 1830.*

Miconia fendleriana Cogn., Monogr. Phan. 7: 822. 1891.
[Between Maracai and Choroni, 4,000 ft., 12/12/56], *Fendler 1835* (syntype, GOET).
[Between Maracai and Choroni, 6,000 ft., 12/12/56], *Fendler 1836* (syntype, GOET).

Miconia multinervulosa Cogn., Monogr. Phan. 7: 926. 1891.
[Near Colonia Tovar, 6,500 ft., 15/5/55, 23/8/56], *Fendler 415* (syntypes, G, photo F).
= *Miconia theaezans* (Bonpl.) Cogn.

Miconia resimoides Cogn., Monogr. Phan. 7: 926. 1891.
[Near Colonia Tovar, 6,500 ft., 15/5/55, 23/8/56], *Fendler 414* (G, MO, photo F).

Miconia rubens Naudin var. **latifolia** Cogn., Monogr. Phan. 7: 921. 1891.
[Between Maracai and Choroni, 4,000 ft., 12/12/56], *Fendler 1834.*

Miconia tovarensis Cogn., Monogr. Phan. 7: 917. 1891.
[Colonia Tovar, 6,500 ft., 29/4/54], *Fendler 419* (G, photo F, MO).
= *Miconia rubens* Naudin var. *rubens*

Tibouchina moritziana Cogn., Monogr. Phan. 7: 259. 1891. *Fendler 404* p.p. (MO).
= *T. geitneriana* (Schltr.) Cogn.

MELIACEAE

Trichilia montana H.B.K. var. **fendleriana** C. DC., Monogr. Phan. 1: 654. 1878.
[Colonia Tovar, 6,300 ft., 17/5/54, 21/6/55, 24/10/55], *Fendler 139* (G, photo F).
= *Trichilia pallida* Sw.

MONIMIACEAE

Siparuna venezuelensis Perkins, Bot. Jahrb. Syst. 28: 679. 1901.
[Between Valencia and Campanero, 7/4/57], *Fendler 2358.*

MYRSINACEAE

Ardisia robinsonii Mez, Pflanzenr. 4, Fam. 236: 77. 1902.
[Between Caracas and Colonia Tovar, 6,000 ft., 30/4/57], *Fendler 2357* (GH, photo F).

Conomorpha caracasana Mez, Pflanzenr. 4, Fam. 236: 260. 1902.
[Colonia Tovar, 6,500 ft.], *Fendler 751* (MO, photo F).

Conomorpha glabra Mez, Pflanzenr. 4, Fam. 236: 254. 1902.
[High mountains around Colonia Tovar, 7,000 ft., 19/3/55, 23/6/55], *Fendler 752* (paratype, MO, photo F).

Conomorpha laurifolia Mez, Pflanzenr. 4, Fam. 236: 254. 1902.
[Crest of mountains near Colonia Tovar, 7,000 ft., 9/11/54, 14/2/55], *Fendler 756* (G, MO, photo F).

Cybianthus fendleri Mez, Pflanzenr. 4, Fam. 236: 218. 1902.
[Between Petaquire and Colonia Tovar, 6,800 ft., 11/2/57], *Fendler 2015* (G, GH, MO, photo F).

Cybianthus klotzschii Mez, Pflanzenr. 4, Fam. 236: 180. 1902.
[Colonia Tovar, 7,000 ft., 31/8/54, 1/9/54], *Fendler 757* (GH, 3 sheeets, MO).

Parathesis moritziana Mez, Pflanzenr. 4, Fam. 236: 180. 1902.
[Colonia Tovar, 6,500 ft., 6/4/54], *Fendler 754* (holotype, MO).

ORCHIDACEAE

Cranichis fendleri Schltr., Repert. Spec. Nov. Regni Veg. Beih. 6: 30. 1919.
No information in notebook. *Fendler 2135.*

Gomphichis psilosepala Renz, Candollea 11: 245. 1948.
No information in notebook. *Fendler 1402* (isotype, MO).

Liparis fendleri Schltr., Repert. Spec. Nov. Regni Veg. Beih. 6: 32. 1919.
No information in notebook. *Fendler 1422* (MO).
= *Liparis brachystalix* Reichb. f.

Physurus brachyrrhynchus Reichb. f., Xenia Orch. 2: 184. 1873.
Fendler s.n.
= *Aspidogne brachyrrhyncha* (Reichb. f.) Garay

Physurus hyphaematicus Reichb. f., Xenia Orch. 2: 184. 1873.
Fendler s.n.
= *Aspidogne hyphaematica* (Reichb. f.) Garay

Physurus xystophyllus Reichb. f., Xenia Orch. 2: 183. 1873.
Fendler s.n.

Pleurothallis apiculata Lindley, Fol. Orch. Pleuroth. 17. 1859.
No information in notebook. *Fendler 2155* (K).

Pleurothallis clandestina Lindley, Fol. Orch. Pleuroth. 43. 1859.
No information in notebook. *Fendler 2148* (K).

Pleurothallis exasperata Lindley, Fol. Orch. Pleuroth. 15. 1859.
No information in notebook. *Fendler 1490* (K).
= *Myoxanthus exasperatus* (Lindley) Luer

Pleurothallis viridula Lindley, Fol. Orch. Pleuroth. 19. 1859.
No information in notebook. *Fendler 1486* (K).
= *Restrepiopsis viridula* (Lindley) Luer

Stelis alata Lindley, Fol. Orch. Stelis, 18. 1858.
No information in notebook. *Fendler 2154* (K).

Stelis coriifolia Lindley, Fol. Orch. Stelis, 18. 1858.
No information in notebook. *Fendler 2444* (K).

Stelis fendleri Lindley, Fol. Orch. Stelis, 18. 1858.
No information in notebook. *Fendler 1470* (K, MO).

Stelis humulis Lindley, Fol. Orch. Stelis, 10. 1858.
No information in notebook. *Fendler 1467* (K).

Stelis lutea Lindley, Fol. Orch. Stelis, 7. 1858.
No information in notebook. *Fendler 1461* (K).

Stelis muscifera Lindley, Fol. Orch. Stelis, 2. 1858.
No information in notebook. *Fendler 1460* (K).

Stelis muscosa Lindley, Fol. Orch. Stelis, 7. 1858.
No information in notebook. *Fendler 1468* (K).

Stelis tenuilabris Lindley, Fol. Orch. Stelis, 18: 1858.
No information in notebook. *Fendler 1469* (K).
No information in notebook. *Fendler 1471* (K, MO).

PASSIFLORACEAE

Passiflora velata Mast., Fl. Bras. 13(1): 560. 1872.
[Between Turmero and La Victoria, 2,000 ft., 14/3/57], *Fendler 2329* (lectotype, designated by Killip, 1938, K).
= *Passiflora serrulata* Jacq.

PIPERACEAE

Peperomia adscendens C. DC., J. Bot. 4: 140. 1866.
[Colonia Tovar, 6,500 ft., 1/4/54, 20/5/54, 3/6/55], *Fendler 1153* (holotype, G-DC; isotypes, GH, K, MO, NY, PH; also the type of *Peperomia glabra* C. DC.).

Peperomia blanda H.B.K. var. **dissimilis** C. DC., Prodr. 16(1): 459. 1869.
[A few mi. W of Colonia Tovar, 7,000 ft., 28/6/55], *Fendler 1170* (GH, MO, NY).

Peperomia carlosiana C. DC., J. Bot. 4: 140. 1866.
[Valley of San Carlos River, 3,500 ft., 25/10/54], *Fendler 1148* (holotype, G, photo F).
= *Peperomia lanceolata-peltata* var. *carlosiana* (C. DC.) Trelease & Yuncker

Peperomia choroniana C. DC., J. Bot. 4: 141. 1866.
[Between Maracai and Choroni, 3,000 ft., 12/12/57], *Fendler 2402* (holotype, G, photo F).

Peperomia decurrens C. DC., J. Bot. 4: 143. 1866.
[High mountains E of Colonia Tovar, 7,000 ft., 28/9/55], *Fendler 1169* (G, photo F).

Peperomia diffusa C. DC., J. Bot. 4: 133. 1866.
[A few mi. S of Colonia Tovar; Biscaina, 3,000–4,000 ft., 18/5/55, 5/6/55], *Fendler 1178* (holotype, G-DC; isotypes, GH, K, MO, NY, PH).

Peperomia ellipticifolia C. DC., Prodr. 16(1): 463. 1866.
[Colonia Tovar, 6,500 ft., 10/5/54, 14/5/55], *Fendler 1171* (holotype, G-DC; isotype, GH).
= *Peperomia blanda* (Jacq.) H.B.K.

Peperomia ernstiana C. DC., Prodr. 16(1): 397. 1869.
[Near the River Tuy, 5,000–5,500 ft., 2/6/54, 29/7/54, 20/6/55, 3/7/55], *Fendler 1163* (holotype, G-DC; isotypes, GH, MO, NY, PH).
= *Peperomia venezueliana* C. DC.

Peperomia fendleriana C. DC., Prodr. 16(1): 460. 1869.
[Colonia Tovar, 6,500–7,000 ft., 20/5/54, 16/6/54], *Fendler 1174* (syntype, G-DC; isotypes, GH, MO, NY, PH).

Peperomia fragrans C. DC., J. Bot. 4: 140. 1866.
[Maya, banks of River Tuy, 3,000 ft., 20/6/55], *Fendler 1156* (holotype, G-DC; isotypes, GH, K).

Peperomia glabra C. DC., J. Bot. 4: 143. 1866.
[Colonia Tovar, 6,500–7,000 ft., 25/5/54], *Fendler 1153* (holotype, K; isotype, GH; also the type collection of *Peperomia adscendens* C. DC.
= *Peperomia adscendens* C. DC.

Peperomia laevis C. DC., J. Bot. 4: 139. 1866.
[6 mi. SE of Colonia Tovar, 6,000 ft., 7/5/55], *Fendler 1164* (G, photo F; isotype, GH).
= *Peperomia alata* Ruíz Lopez & Pavón

Peperomia lanceolata-peltata C. DC., J. Bot. 4: 136. 1866.
[Biscaina, 3,000 ft., 13/8/55], *Fendler 1149* (syntype (at G-DC) with *Hoffmann 414* (at B); isosyntypes, GH, K, MO, PH).

Peperomia linearis C. DC., J. Bot. 4: 145. 1866.
[Colonia Tovar, 6,500–7,000 ft., 17/6/54, 3/11/56], *Fendler 1176* (syntype with *Jameson s.n.*, both G-DC; isosyntypes, GH, MO, NY, PH).
= *Peperomia swartziana* Miq.

Peperomia magnoliifolia A. Dietr. var. **emarginulata** C. DC., Prodr. 16(1): 427. 1869.
[Near Colonia Tovar, 6,500–7,000 ft., 25/5/54], *Fendler 1152* (also cited as a type of *Peperomia decurrens*) (lectotype, G-DC (per Trel. & Yuncker, Piperac. No. S. Amer. 685. 1950), isolectotypes, GH, MO, NY, PH).
= *Peperomia obtusifolia* (L.) A. Dietr. var. *emarginata* (C. DC.) Trel. & Yuncker

Peperomia patula C. DC., J. Bot. 4: 133. 1866.
[Near Colonia Tovar, 6,500 ft., 16/5/54, 26/11/56], *Fendler 1166* (holotype, G, photo F).

Peperomia pseudodependens C. DC., J. Bot. 4: 137. 1866.
[La Victoria, 2,000 ft., 20/11/56], *Fendler 1817* (holotype, G, photo F; isotype, GH).

Peperomia pseudopeltoidea C. DC., Prodr. 16(1): 434. 1869.
[Colonia Tovar, 6,500 ft., 6/6/54, 16/5/55], *Fendler 1150b* (G, photo F).

Peperomia purpurella C. DC., Prodr. 16(1): 414. 1869.
[River Tuy below Colonia Tovar, 5,000 ft., 29/8/54], *Fendler 1161* (G, photo F).
= *Peperomia patula* C. DC.

Peperomia reflexa (L.) A. Dietr. var. *coriacea* C. DC., Prodr. 16(1): 452. 1869.

[Colonia Tovar, 6,500 ft., 3/4/54, 2/5/54, 5/8/54], *Fendler 1183* (holotype, G-DC, isotypes, GH, MO, NY, PH).
= *Peperomia reflexa* (L.) A. Dietr.

Peperomia san-carlosiana C. DC., J. Bot. 4: 138. 1866.
[San Carlos River valley, 3,500 ft., 7/9/54], *Fendler 1151* (holotype, G, photo F).

Peperomia succulenta C. DC., J. Bot. 4: 142. 1866.
[10 mi. S of Colonia Tovar, 3,500 ft., 10 mi. S of Colonia Tovar, 18/5/55], *Fendler 1157* (holotype, G, photo F; isotype, K).

Peperomia tenella A. Dietr. var. **glabra** C. DC., Prodr. 16(1): 397. 1869.
[Between Maracai and Choroni, 3,000 ft., 12/12/56], *Fendler 1818* (holotype, G-DC; isotypes, GH, K, MO, PH p.p.).

Peperomia tovariana C. DC., Prodr. 16(1): 404. 1869.
[Between Colonia Tovar and Petaquire, 19/4/55], *Fendler 1168* (syntype at G-DC with *Moritz 1941* (at BM); isosyntypes, GH, MO, NY, PH).

Peperomia trinervula C. DC., Prodr. 16(1): 420. 1869.
[High mountains E of Colonia Tovar, 7,000 ft., 28/9/55], *Fendler 1167* (lectotype, G-DC; isolectotype, GH).

Peperomia venezueliana C. DC., J. Bot. (Hooker) 4: 139. 1866.
[Between Colonia Tovar and Petaquire, 6,500 ft., 22/4/58], *Fendler 2618* (holotype, G, photo F).

Piper caracasanum Bredem. ex Link var. **firmius** C. DC., Prodr. 16(1): 306. 1869.
[Colonia Tovar, 6,000 ft., 28/4/54, 7/4/54], *Fendler 1143* (syntype at G-DC with *Bredemeyer 679* (at B-Willd.); 2 sheets at GH; isotype, GH).
= *Piper caracasanum* Bredem. ex Link

Piper cumbotianum C. DC., Prodr. 16(1): 268. 1869.
[Between Agua Blanca and Cumbote, 5,000 ft., 30/1/58], *Fendler 2571* (G, photo F).

Piper fendlerianum C. DC., J. Bot. 4: 213. 1866.
[10 mi. E of Colonia Tovar, 7,500 ft., 26/5/55, 17/6/55], *Fendler 1140* (G, photo F; isotypes, GH, K, MO, NY, PH).

Piper glanduligerum C. DC., J. Bot. 4: 215. 1866.
[Colonia Tovar, 6,500 ft., 6/4/54, 27/6/56], *Fendler 1137* (syntype, G, photo F; isosyntypes, GH, MO, NY, US).

Piper nobile C. DC., Prodr. 16(1): 289. 1869.
[Colonia Tovar, 6,500 ft., 16/6/55], *Fendler 1144* (holotype, G-DC; isotypes, GH, MO, NY, PH).

Piper ovale C. DC., J. Bot. 4: 166. 1866.
[A few mi. SE of Colonia Tovar, 4,000 ft., 27/2/57], *Fendler 2398* (syntype, G-DC; isosyntype, GH).
= *Piper crassinervium* H.B.K.

Piper tovarense Trel. & Yuncker, Piperac. N. South Amer. 1: 27, fig. 17. 1950.
[10 mi. E of Colonia Tovar, 7,000 ft., 17/6/55], *Fendler 1145* (holotype, GH).

Piper tristemon C. DC., Prodr. 16(1): 328. 1869.
[10 mi. E of Colonia Tovar, 7,500 ft., 26/5/55, 17/6/55], *Fendler 1141* (holotype, G-DC, photo F; isotypes, GH, MO).

Piper venezuelense C. DC., J. Bot. 4: 216. 1866.
[Between Agua Blanca and Cumbote, 5,000 ft., 30/1/58], *Fendler 2572* (holotype, G-DC, photo F; isotypes, GH, MO, PH).
= *Piper glabrescens* (Miq.) C. DC. var. *venezuelense* (C. DC.) Trel. & Yuncker

Piper victorianum C. DC., J. Bot. 4: 218. 1866.
[La Victoria, 2,000 ft., 21/11/56], *Fendler 1139* (holotype, G-DC, photo F; isotypes, GH, K, MO, PH).
= *Piper amalgo* var. *medium* (Jacq.) Yuncker

POACEAE

Chusquea fendleri Munro, Trans. Linn. Soc. 26: 61. 1868.
[In and about Colonia Tovar, common, 6,000–7,900 ft., 17/4/55], *Fendler 1627* (holotype, K; isotype, MO).

PODOCARPACEAE

Podocarpus harmsianus Pilger, Pflanzenr. IV. 5(Heft 18): 69. 1903.
[Colonia Tovar, 6,500 ft., 6/4/54], *Fendler 1289.*
= *Prumnopitys harmsiana* (Pilger) Laubenf.

POLYGALACEAE

Polygala fendleri Chodat, Mém. Soc. Phys. Genève 31, pt. 2, no. 2: 167. 1893.
[A few mi. SW of Colonia Tovar, 5,000 ft., 13/9/55, 8/9/56], *Fendler 238* (G).

Polygala tovarensis Chodat, Mém. Soc. Phys. Genève 31, pt. 2, no. 2: 32. 1893.
[Caracas; also a few mi. W of Colonia Tovar, 500–6,500 ft., 31/1/54, 13/9/55, 19/7/56], *Fendler 240* (G).

Securidacea fendleri Chodat, Bull. Herb. Boissier 3: 545. 1895.
Fendler s.n.

RUBIACEAE

Cephaelis aneurophylla Standley, Publ. Field Columbian Mus., Bot. Ser. 8: 63. 1930.
[Between Maracai and Choroni, 5,000 ft., 12/12/56], *Fendler 1979* (holotype, GH; isotype, K).
= *Psychotria aneurophylla* (Standl.) Steyerm.

Cephaelis macrocarpa Standley, Publ. Field Columbian Mus., Bot. Ser. 8: 64. 1930.
[Between Maracai and Choroni, 5,000 ft., 12/12/56], *Fendler 1990* (holotype, GH; isotype, K).
= *Psychotria costanensis* Steyerm. subsp. *costanensis*

Elaeagia karstenii Standley, Field Columbian Mus., Bot. Ser. 8: 50. 1930.
[Colonia Tovar, 13/8/54], *Fendler 594* (holotype, GH; isotypes, F, MO).

Malanea fendleri Standley, Publ. Field Columbian Mus., Bot. Ser. 8: 61. 1930.
[Between Petaquire and Cariaca, 6,000 ft., 12/2/58], *Fendler 2555* (holotype, GH).

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Manettia schumanniana Sprague, Bull. Herb. Boiss. 2(5): 834. 1905.
[A few mi. E of Colonia Tovar, 7,500 ft., 5/1/57], *Fendler 589.*

Palicourea fendleri Standley, Publ. Field Columbian Mus., Bot. Ser. 8: 65. 1930.
[Between Maracai and Choroni, 5,000 ft., 29/1/57], *Fendler 1983* (holotype, GH, photo F; isotype, K).

Rudgea apodantha Standley, Publ. Field Columbian Mus., Bot. Ser. 8: 72. 1930.
[Between Petaquire and the sea, 4,000 ft., 9/2/57], *Fendler 1993* (holotype, GH, photo F; isotype, K).

SAPINDACEAE

Matayba longipes Radlkofer, Sitzungsber. Math-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9: 626. 1879.
[Colonia Tovar, 6,500 ft., 28/6/56], *Fendler 1748* (holotype, G, photo F; isotype, MO).

SAPOTACEAE

Crepindodendron crotonoides Pierre, Not. Bot. Sap. 28. 1890.
[Seashore near Colombia, 100 ft., 26/1/57], *Fendler 749* (holotype, P).
= *Pouteria crotonoides* (Purre) Baehni

SOLANACEAE

Cestrum laetum Francey, Candollea 6: 378. 1935.
[Colonia Tovar, 6,500 ft., 13/4/54, 7/5/54], *Fendler 955* (holotype, NY).

Cestrum tovarense Francey, Candollea 6: 388. 1935.
[Colonia Tovar, 6,000 ft., 31/8/55], *Fendler 962* (holotype, NY; isotype, MO).

Saracha nitida Bitter, Repert. Spec. Nov. Regni Veg. 19: 265. 1924.
[10 mi. E of Colonia Tovar, 17/6/55, 21/9/55], *Fendler 1007* (G, photo F).

Solanum tovarense Bitter, Repert. Spec. Nov. Regni Veg. 18: 65. 1922.
[Colonia Tovar, 6,000 ft., 27/4/54, 16/8/55, 22/9/55], *Fendler 980* (G, photo F).

STYRACACEAE

Styrax macrotrichus Perkins, Repert. Spec. Nov. Regni Veg. 2: 23. 1906.
[A few mi. SE of Colonia Tovar, 4,500 ft., 9/3/55], *Fendler 746* (G, MO, photo F).

TURNERACEAE

Piriqueta tovarensis Urban, Jahrb. Königl. Bot. Gart. Berlin 2: 69. 1883.
[Savannahs S of Colonia Tovar, 4,000 ft., 13/9/55], *Fendler 115.*

URTICACEAE

Hemistylis macrostachya Wedd., Ann. Sci. Nat. (Paris) 4(1): 208. 1854.
[Between Caracas and La Guayra, 1,000 ft., 16/8/55], *Fendler 1259* (G, photo F).

Hemistylis odontophylla Wedd., Prodr. 16(1): 235. 1869.
[La Victoria, 2,000 ft., 21/11/56], *Fendler 1827* (G, photo F).

Phenax uliginosus Wedd., Ann. Sci. Nat. (Paris) 4(1): 192. 1854.
[Colonia Tovar, 31/4/54, 21/8/55], *Fendler 1268* (G, MO, photo F).

Pilea dauciodora Wedd., Ann. Sci. Nat. (Paris) ser. 3. 18: 223. 1852.
[High mountains around Colonia Tovar, 7,000 ft., 10/5/54, 24/6/55], *Fendler 1246* (G, MO, photo F).

Pilea mollis Wedd., Arch. Mus. Hist. Nat. 8: 251. 1855.
[River Tuy below Colonia Tovar, 4,000–5,500 ft., 2/7/54, 29/8/54, 22/4/58], *Fendler 1241* (G, MO, photo F).

Pilea urticella Wedd., Prodr. 16(1): 157. 1869.
[Between Valencia and Campanero, 4,000 ft., 7/3/57], *Fendler 2429* (G, MO, photo F).

Pouzolzia acalyphioides Wedd., Prodr. 16(1): 234. 1869.
[Biscaina, 3,000 ft., 10/5/55], *Fendler 1264* (G, photo F).

VERBENACEAE

Aegiphila fendleri Moldenke, Repert. Spec. Nov. Regni Veg. 33: 121. 1933.
[Between Agua Blanca and Cumbote, 4,000 ft., 30/1/58], *Fendler 2032* (holotype, GH; isotypes, G, K).

Aegiphila floribunda Moritz & Moldenke, Repert. Spec. Nov. Regni Veg. 33: 122. 1933.
[Colonia Tovar, 6,000 ft., 13/6/55, 16/6/55], *Fendler 845* (MO, W, photo F).

Aegiphila lewisiana Moldenke, Repert. Spec. Nov. Regni Veg. 33: 131. 1933.
[Between Caracas and La Guayra, 2,000 ft., 16/8/55], *Fendler 844.*

Citharexylum venezuelense Moldenke, Repert. Spec. Nov. Regni Veg. 37: 237. 1934.
[Between Caracas and La Guayra, 1,000 ft., 16/8/55], *Fendler 1298.*

Appendix II

List of Fendler Venezuelan collections cited in Appendix I by number and their basionyms.

27 *Cleome moritziana* Klotzsch ex Eichler (Capparaceae)
115 *Piriqueta tovarensis* Urban (Turneraceae)
139 *Trichilia montana* H.B.K. var. *fendleriana* C. DC. (Meliaceae)
177 *Protium laxiflorum* Engl. var. *fendleri* Engl. (Burseraceae)
196 *Rollinia fendleri* R. E. Fries (Annonaceae)
215 *Maytenus fendleri* Briq. (Celastraceae)
238 *Polygala fendleri* Chodat (Polygalaceae)
240 *Polygala tovarensis* Chodat (Polygalaceae)
248 *Canavalia fendleri* Piper (Fabaceae)
344 *Mimosa tovarensis* Benth. (Fabaceae)
404 *Tibouchina moritziana* Cogn. (Melastomataceae)
404 *Henriettella tovarensis* Cogn. var. *angustifolia* Cogn. (Melastomataceae)
414 *Miconia resimoides* Cogn. (Melastomataceae)
415 *Miconia multinervulosa* Cogn. (Melastomataceae)
419 *Miconia tovarensis* Cogn. (Melastomataceae)
432 *Heterotrichum glandulosum* Cogn. (Melastomataceae)
436 *Clidemia ciliata* D. Don var. *grandifolia* Cogn. (Melastomataceae)
438 *Clidemia fendleri* Cogn. (Melastomataceae)
439 *Leandra fendleri* Cogn. (Melastomataceae)
444 *Henriettella tovarensis* Cogn. (Melastomataceae)
444 *Henriettella tovarensis* Cogn. var. *angustifolia* Cogn. (Melastomataceae)
489 *Edmondia spectabilis* Cogn. (Cucurbitaceae)

490 *Gurania wagneriana* Cogn. (Cucurbitaceae)
502 *Sicyos macrocarpus* Cogn. (Cucurbitaceae)
503 *Echinocystis polycarpa* Cogn. (Cucurbitaceae)
513 *Begonia fagopyroides* Kunth & Bouché var. *fendleriana* A. DC. (Begoniaceae)
524 *Hydrocotyle venezuelensis* Rose ex Mathias (Apiaceae)
529 *Dendropanax fendleri* Seemann (Araliaceae)
569 *Malanea hirsuta* Standley (Rubiaceae)
589 *Manettia schumanniana* Sprague (Rubiaceae)
594 *Elaeagia karstenii* Standley (Rubiaceae)
625 *Mikania racemulosa* Klatt (Asteraceae)
626 *Mikania hexagona* B. L. Robinson (Asteraceae)
634 *Eupatorium neriifolium* B. L. Robinson (Asteraceae)
638 *Eupatorium xestolepis* B. L. Robinson var. *xestolepis* (Asteraceae)
647 *Eupatorium steetzii* B. L. Robinson (Asteraceae)
651 *Trichogonia rhadinocarpa* B. L. Robinson (Asteraceae)
702 *Senecio cucullatus* Klatt (Asteraceae)
718 *Hieracium tovarense* Fries (Asteraceae)
746 *Styrax macrotrichus* Perkins (Styracaceae)
749 *Crepindodendron crotonoides* Pierre (Sapotaceae)
751 *Conomorpha caracasana* Mez (Myrsinaceae)
754 *Parathesis moritziana* Mez (Myrsinaceae)
756 *Conomorpha laurifolia* Mez (Myrsinaceae)
757 *Cybianthus klotzschii* Mez (Myrsinaceae)
794 *Monopyle leucantha* Moritz ex Benth. (Gesneriaceae)
830 *Symbolanthus magnificus* Gilg (Gentianaceae)
844 *Aegiphila lewisiana* Moldenke (Verbenaceae)
845 *Aegiphila floribunda* Moritz & Moldenke (Verbenaceae)
876 *Salvia tovariensis* Briq. (Lamiaceae)
879 *Stachys fendleri* Briq. (Lamiaceae)
941 *Ipomoea fruticosa* Kuntze (Convolvulaceae)
955 *Cestrum laetum* Francey (Solanaceae)
962 *Cestrum tovarense* Francey (Solanaceae)
980 *Solanum tovarense* Bitter (Solanaceae)
1007 *Saracha nitida* Bitter (Solanaceae)
1030 *Dipladenia fendleri* Muell. Arg. (Apocynaceae)
1032 *Amblyanthera fendleri* Muell. Arg. (Apocynaceae)
1095 *Gymnobalanus latifolia* Meissn. (Lauraceae)
1098 *Mespilodaphne vaginans* Meissn. (Lauraceae)
1101 *Dendrophthora eichleriana* Urban (Loranthaceae)
1102 *Phoradendron fendlerianum* Eichler (Loranthaceae)
1104 *Dendrophthora basiandra* Kuijt (Loranthaceae)
1105 *Phoradendron rigidum* Urban (Loranthaceae)
1106 *Phoradendron tubulosum* Urban (Loranthaceae)
1108 *Phoradendron ovalifolium* Urban (Loranthaceae)
1115 *Phoradendron cuneifolium* Urban (Loranthaceae)
1125 *Stachyphyllum fendleri* van Tiegh. (Loranthaceae)
1127 *Hedyosmum pseudoandromeda* Solms-Laub. (Chloranthaceae)
1137 *Piper glanduligerum* C. DC. (Piperaceae)
1139 *Piper victorianum* C. DC. (Piperaceae)
1140 *Piper fendlerianum* C. DC. (Piperaceae)
1141 *Piper tristemon* C. DC. (Piperaceae)
1143 *Piper caracasanum* Bredem. ex Link var. *firmius* C. DC. (Piperaceae)
1144 *Piper nobile* C. DC. (Piperaceae)
1145 *Piper tovarense* Trel. (Piperaceae)
1148 *Peperomia carlosiana* C. DC. (Piperaceae)
1149 *Peperomia lanceolata-peltata* C. DC. (Piperaceae)
1150b *Peperomia pseudopeltoidea* C. DC. (Piperaceae)
1151 *Peperomia san-carlosiana* C. DC. (Piperaceae)
1152 *Peperomia magnoliifolia* A. Dietr. var. *emarginulata* C. DC. (Piperaceae)
1153 *Peperomia adscendens* C. DC. (Piperaceae)
1153 *Peperomia glabra* C. DC. (Piperaceae)
1156 *Peperomia fragrans* C. DC. (Piperaceae)
1157 *Peperomia succulenta* C. DC. (Piperaceae)
1161 *Peperomia purpurella* C. DC. (Piperaceae)
1163 *Peperomia ernstiana* C. DC. (Piperaceae)
1164 *Peperomia laevis* C. DC. (Piperaceae)
1166 *Peperomia patula* C. DC. (Piperaceae)
1167 *Peperomia trinervula* C. DC. (Piperaceae)
1168 *Peperomia tovariana* C. DC. (Piperaceae)
1169 *Peperomia decurrens* C. DC. (Piperaceae)
1170 *Peperomia blanda* H.B.K. var. *dissimilis* C. DC. (Piperaceae)
1171 *Peperomia ellipticifolia* C. DC. (Piperaceae)
1174 *Peperomia fendleriana* C. DC. (Piperaceae)
1176 *Peperomia linearis* C. DC. (Piperaceae)
1178 *Peperomia diffusa* C. DC. (Piperaceae)
1183 *Peperomia reflexa* A. Dietr. var. *coriacea* C. DC. (Piperaceae)
1191 *Euphorbia tovarensis* Boiss. (Euphorbiaceae)
1202 *Pedilanthus fendleri* Boiss. (Euphorbiaceae)
1208 *Tragia fendleri* Muell. Arg. (Euphorbiaceae)
1230 *Excoecaria obtusiloba* Muell. Arg. (Euphorbiaceae)
1241 *Pilea mollis* Wedd. (Urticaceae)
1246 *Pilea dauciodora* Wedd. (Urticaceae)
1259 *Hemistylis macrostachya* Wedd. (Urticaceae)
1264 *Pouzolzia acalyphioides* Wedd. (Urticaceae)
1272 *Alchornea grandiflora* Muell. Arg. (Euphorbiaceae)
1289 *Podocarpus harmsianum* Pilger (Podocarpaceae)
1298 *Citharexylum venezuelense* Moldenke (Verbenaceae)
1327 *Philodendron fraternum* Schott (Araceae)
1329 *Philodendron deviatum* Schott (Araceae)
1336 *Anthurium nymphaeifolium* K. Koch & C. Bouché var. *ovatum* Engl. (Araceae)
1343 *Anthurium fendleri* Schott (Araceae)
1346 *Anthurium bredemeyeri* Schott var. *elongata* Engl. (Araceae)
1348 *Asplundia fendleri* Harling (Cyclanthaceae)
1422 *Liparis fendleri* Schltr. (Orchidaceae)
1460 *Stelis muscifera* Lindley (Orchidaceae)
1461 *Stelis lutea* Lindley (Orchidaceae)
1467 *Stelis humulis* Lindley (Orchidaceae)
1468 *Stelis muscosa* Lindley (Orchidaceae)
1469 *Stelis tenuilabris* Lindley (Orchidaceae)
1470 *Stelis fendleri* Lindley (Orchidaceae)
1471 *Stelis tenuilabris* Lindley (Orchidaceae)
1486 *Pleurothallis viridula* Lindley (Orchidaceae)
1490 *Pleurothallis exasperata* Lindley (Orchidaceae)
1508 *Tillandsia compacta* Griseb. (Bromeliaceae)
1509 *Tillandsia grisebachiana* Baker (Bromeliaceae)
1514 *Tillandsia pleiosticha* Griseb. (Bromeliaceae)
1515 *Tillandsia fendleri* Griseb. (Bromeliaceae)
1516 *Tillandsia excelsa* Griseb. var. *latifolia* Griseb. (Bromeliaceae)
1517 *Tillandsia ventricosa* Griseb. (Bromeliaceae)

1521 *Nidularium albo-roseum* Griseb. (Bromeliaceae)
1523 *Tillandsia caribaea* Lyman B. Smith (Bromeliaceae)
1524 *Tillandsia incurva* Griseb. (Bromeliaceae)
1525 *Tillandsia robusta* Griseb. (Bromeliaceae)
1530 *Tillandsia myriantha* Baker (Bromeliaceae)
1546 *Smilax scabriuscula* Humb. & Bonpl. ex Willd. var. *fendleri* A. DC. (Liliaceae)
1550 *Pitcairnia fendleri* Mez (Bromeliaceae)
1552 *Tillandsia longifolia* Baker (Bromeliaceae)
1555 *Phaeosphaerion efoveolatum* C. B. Clarke (Commelinaceae)
1591 *Rhynchospora rudis* C. B. Clarke (Cyperaceae)
1627 *Chusquea fendleri* Munro (Poaceae)
1748 *Matayba longipes* Radlkofer (Sapindaceae)
1750 *Machaerium moritzianum* Benth. (Fabaceae)
1761 *Phoradendron tovarense* Urban (Loranthaceae)
1762 *Phoradendron longipetiolatum* Urban (Loranthaceae)
1771 *Tillandsia acorifolia* Griseb. (Bromeliaceae)
1810 *Phoradendron venezuelense* Trel. (Loranthaceae)
1811 *Phoradendron bilineatum* Urban (Loranthaceae)
1817 *Peperomia pseudodependens* C. DC. (Piperaceae)
1818 *Peperomia tenella* A. Dietr. var. *glabra* C. DC. (Piperaceae)
1825 *Acalypha villosa* Jacq. var. *intermedia* Muell. Arg. (Euphorbiaceae)
1827 *Hemistylis odontophylla* Wedd. (Urticaceae)
1830 *Meriania subumbellata* Cogn. (Melastomataceae)
1832 *Arthrostemma alatum* Triana (Melastomataceae)
1834 *Miconia rubens* Naudin var. *latifolia* Cogn. (Melastomataceae)
1835 *Miconia fendleriana* Cogn. (Melastomataceae)
1836 *Miconia fendleriana* Cogn. (Melastomataceae)
1845 *Heterotrichum lucidum* Triana (Melastomataceae)
1865 *Machaerium tovarense* Pittier (Fabaceae)
1866 *Machaerium mortizianum* Benth. (Fabaceae)
1947 *Eupatorium tovarense* B. L. Robinson (Asteraceae)
1957 *Piptocarpha sprucei* Baker (Asteraceae)
1967 *Clibadium parviceps* S. F. Blake (Asteraceae)
1979 *Cephaelis aneurophylla* Standley (Rubiaceae)
1983 *Palicourea fendleri* Standley (Rubiaceae)
1990 *Cephaelis macrocarpa* Standley (Rubiaceae)
1993 *Rudgea apodantha* Standley (Rubiaceae)
2015 *Cybianthus fendleri* Mez (Myrsinaceae)
2031 *Columnea fendleri* Sprague (Gesneriaceae)
2032 *Aegiphila fendleri* Moldenke (Verbenaceae)
2082 *Ipomoea fruticosa* Kuntze (Convolvulaceae)
2083 *Ipomoea fendleriana* Kuntze (Convolvulaceae)
2084 *Ipomoea alatipes* Hook. (Convolvulaceae)
2119 *Philibertia fendleri* A. Gray (Asclepiadaceae)
2135 *Cranichis fendleri* Schltr. (Orchidaceae)
2148 *Pleurothallis clandestina* Lindley (Orchidaceae)
2154 *Stelis alata* Lindley (Orchidaceae)
2155 *Pleurothallis apiculata* Lindley (Orchidaceae)
2159 *Tillandsia mucronata* Griseb. (Bromeliaceae)
2166 *Tillandsia laxa* Griseb. (Bromeliaceae)
2167 *Caraguata coriostachya* Griseb. (Bromeliaceae)
2171 *Dioscorea fendleri* R. Kunth (Dioscoreaceae)
2230 *Cassia viciifolia* Benth. (Fabaceae)
2255 *Calliandra laxa* Benth. var. *parvifolia* Benth. (Fabaceae)
2259 *Inga fendleriana* Benth. (Fabaceae)
2261 *Calophysa flexuosa* Triana (Melastomataceae)
2263 *Clidemia grandifolia* Cogn. (Melastomataceae)
2314 *Strychnos fendleri* Sprague & Sandw. (Loganiaceae)
2329 *Passiflora velata* Mast. (Passifloraceae)
2348 *Mikania gracilipes* B. L. Robinson (Asteraceae)
2349 *Mikania vitrea* B. L. Robinson (Asteraceae)
2357 *Ardisia robinsonii* Mez (Myrsinaceae)
2358 *Siparuna venezuelensis* Perkins (Monimiaceae)
2393 *Nectandra leucantha* Nees & Martius var. *attenuata* Meissn. (Lauraceae)
2395 *Gynobalanus fendleri* Meissn. (Lauraceae)
2398 *Piper ovale* C. DC. (Piperaceae)
2402 *Peperomia choroniana* C. DC. (Piperaceae)
2408 *Acalypha villosa* Jacq. var. *intermedia* Muell. Arg.
2412 *Plukenetia penninervia* Muell. Arg. (Euphorbiaceae)
2429 *Pilea urticella* Wedd. (Urticaceae)
2444 *Stelis coriifolia* Lindley (Orchidaceae)
2446 *Tillandsia tovarensis* Mez (Bromeliaceae)
2449 *Tillandsia longibracteata* Baker (Bromeliaceae)
2452 *Bilbergia filicaulis* Griseb. (Bromeliaceae)
2453 *Aechmea cymoso-paniculata* Baker (Bromeliaceae)
2454 *Aechmea fendleri* André ex Mez (Bromeliaceae)
2489 *Sloanea fendleriana* Benth. (Elaeocarpaceae)
2547 *Blakea grisebachii* Cogn. (Melastomataceae)
2555 *Malanea fendleri* Standley (Rubiaceae)
2571 *Piper cumbotianum* C. DC. (Piperaceae)
2572 *Piper venezuelense* C. DC. (Piperaceae)
2573 *Philodendron effusilobum* Croat (Araceae)
2575 *Tillandsia aurantiaca* Griseb. (Bromeliaceae)
2593 *Blakea longibracteata* Cogn. (Melastomataceae)
2594 *Clidemia ampla* Cogn. (Melastomataceae)
2617 *Evodianthus funifer* (Poit.) Lindman subsp. *fendlerianum* Harling (Cyclanthaceae)
2618 *Peperomia venezueliana* C. DC. (Piperaceae)

AUGUSTUS FENDLER'S VENEZUELAN COLLECTIONS OF FERNS AND FERN ALLIES[1]

Alan R. Smith[2] *and Carol A. Todzia*[3]

ABSTRACT

Augustus Fendler collected over 500 collection numbers of pteridophytes in Venezuela between 1854 and 1858. These collections are noteworthy because of the large number of dispersed duplicates, rarities, and types (44 collection numbers thus far identified) among them. This paper presents an annotated list of Fendler's Venezuelan pteridophyte collections and a historical account of the collections, including a portrayal of Fendler's fascination with ferns.

Augustus Fendler collected in northern Venezuela between 1854 and 1858, where he amassed important collections of angiosperms, ferns, fern allies, lichens, mosses, liverworts, and fungi. Although a general account of his Venezuelan collecting is given in the previous paper (Todzia, 1989), this article deals specifically with his fern collections. Fendler's pteridophyte collections are noteworthy because they represent the first intensive gathering of ferns and fern allies from the Coastal Cordillera of Venezuela, and because they are widely distributed. Consequently, they have become type specimens of a great many fern species. The following account has been assembled with the aid of Fendler's correspondence with Daniel C. Eaton and Asa Gray, at the YU and GH archives, respectively.

Fendler's Venezuelan fern collections as well as his sets of flowering plants were distributed by Asa Gray. As with the angiosperms, Fendler initially retained the first set for himself. In 1859 he received a request from Thomas Moore of the Chelsea Botanic Garden for a set, but since Moore had access to William Hooker's herbarium containing set 2, Fendler decided to sell his first set to Daniel C. Eaton, who was then a student of Gray. He did this because Eaton agreed to publish a list of these collections, and because the collections would then remain in the United States, where Fendler would have easy access to them. In a letter to Eaton, Fendler stated, "The only set remaining with me is set No. 1 which I used for comparison and in which I felt a pride and a pleasure to lay up not only the most complete but also the finest specimens selected from the rest. There was a time when I thought I could never part with these plants. In bringing them up from their hidden places I have neither shun danger nor travelling expenses, and it was chiefly the search after *Ferns*, which induced me to cross the principal chain of the cordillera of the coast upon four different tracks. I therefore need not say how dear they are to me, and I never would have sold them to anyone except to a Botanist, who is able to make the proper use of them" [Fendler to Eaton, 24 January 1859, St. Louis]. Fendler went on to say, "For my part I have neither the necessary books, time, nor herbarium to do it. Great resources undoubtedly are necessary to determine, which of the species are new and which are not; for I have reason to believe that in works on Ferns, with many species, a critical and patient overhauling is very desirable, in order to disperse the existing confusion. I remember to have seen in one herbarium the same species under four different names, one of these specimens was even disposed of under a new genus" [Fendler to Eaton, 24 January 1859, St. Louis]. In total, Fendler sent Eaton close to 500 collection numbers

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with about 564 sheets. Eaton paid 10 cents a sheet for a total cost of $56.40.

In 1860, Eaton was awarded a Bachelor of Science degree from Harvard University for his dissertation enumerating Fendler's Venezuelan fern collections along with those collected by Wright in Cuba, and a few collections of Schott and Hayes from Panama and Colombia. A year later, Eaton's dissertation was published (Eaton, 1861). Fendler, however, was not pleased with this work. In the following long passage, we can see what a keen observer Fendler was. "In regard to Mr. Eaton's Filices I am sorry to say that I was very much disappointed. Being in possession of the names of Dr. Engelmann's set of ferns as determined by Prof. Mettenius,[4] I was able to compare them with those given by Eaton and find that the names of 146 sp. agree with those determined by Mettenius, while the names of 101 spec. disagree. I am not able to say who is in the right, but should be inclined to depend more upon the one that has the longest experience in the matter [Mettenius]. Such differences of different authors are most discouraging to the student of botany and a severe drawback in the acquisition of knowledge. But what concerns me more immediately and of which I think I have reason to be solicitous, is the readiness with which Mr. Eaton throws different, quite *distinct*, species under one and the same name. I regret this, the more it may be inferred as if I purposely manufactured species for the sake of selling one and the same species over again under different numbers. Having pointed out in Mr. Eaton's set some of the more obscure characters of many species very much resembling each other, I thought I had done something to prevent mistakes. It always seemed to me, that authors who only see 1 or 2 dried specimens of each species ought to pay at least some slight regard to the opinion of a collector who had the best opportunities, and for 4 years availed himself of those opportunities to study the habits of the different ferns, and to observe them in their growing state in the different phases of their growth, not on single specimens or in single localities only, but in hundreds of different places and individuals." Fendler continued: "There may be a dozen species about which I was rather doubtful, but all the rest I consider genuine species; and as soon as I shall have time to examine Dr. Engelmann's set, I shall endeavor to point out the differences in species considered the same by Mr. Eaton. That even the most experient [sic] authors on ferns may sometimes take 2 different species to be one and the same is proved by Prof. Mettenius calling No. 161 'a young specimen of 162.' Now the former (No. 161) is not only different in form but has also 2 to 3 oval tubers, all the fronds die at a certain season of the year, and new fronds make their appearance rather suddenly but not before the commencement of the rainy season; the latter (No. 162) is a perennial plant to be seen at all times of the year and never possessing tubers" [Fendler to Gray, 24 March 1868, St. Louis]. In fact, these two numbers do represent two species (Appendix I), and Fendler was correct.

Nevertheless, Fendler's friendship with Eaton grew, as evidenced by Fendler's 15 letters to Eaton written from Trinidad between 1878 and Fendler's death in 1883. In Trinidad, as in Venezuela, he seems to have been preoccupied with collecting ferns and seems to have particularly relished discussing his Trinidad fern collections with Eaton. Fendler, however, much preferred Venezuela over Trinidad and in his letters to Eaton, Engelmann, and Gray from Trinidad, he often mentioned how much he would like to return to Colonia Tovar. In his last letter to Eaton before his death, Fendler stated, "I long for the cool alpine air (damp though it be) for the deep shades and the eternal silence of those primeval forests, where a quarter of century ago my footsteps were wandering in search of the treasures of botany—especially those of ferns—again to go and see them, and to draw them forth from out their hiding places in the deep dells, or to bring them down from the mountain's high summit" [Fendler to Eaton, 15 June 1882, Port-of-Spain, Trinidad]. At 69, forever the fervent collector, Fendler asked Eaton if the professor could find subscribers to about 40 sets of Venezuelan ferns [Fendler to Eaton, 15 June 1882, Port-of-Spain, Trinidad]. Fendler often wrote to his correspondents that he longed to return to the "land of perpetual peace . . . the happy region of the ferns."

Fendler's Fern Notebook and Collections

Fendler's field notebook in the GH archives is not chronological and consecutive, but rather a catalog of species in taxonomic order. Thus, the number sequence begins with 1 (Marattiaceae), proceeds through the more primitive fern families (Osmundaceae, Schizaeaceae, Hymenophyllaceae, Gleicheniaceae, Cyatheaceae), and then continues with the more advanced ferns, genus by genus, up to number 324. Numbers after 324 were collected

[4] Georg H. Mettenius (1823–1866), German pteridologist, whose fern herbarium is now mostly at B.

after a trip to the United States and after he had distributed some of his material. It is obvious that the notebook was compiled after many of the collections had already been made and put into sequence. Fendler combined collections made on different dates and at different places under a single number. For example, *Fendler 6*, *Anemia villosa*, was collected on nine different dates (according to data on the sheet at YU) and most likely at several different localities during the years 1854, 1855, and 1856.

Fendler probably revisited many collection sites in an attempt to amass additional material of a given number, because he intended to collect in large sets for sale to as many individuals or herbaria as possible. It appears that he tried to collect in sets of 20, although he gathered 40 sheets of *Fendler 23*, *Trichomanes reptans*. The number of collections appears in the upper right-hand corner of the labels on sheets at YU but does not appear on the labels of Fendler collections in other herbaria. In some cases, Fendler kept an account of material of varying stages, e.g., he collected 26 young and 12 old specimens of *Marattia laevis* (*Fendler 3*). In other instances, he recorded the number of specimens in different categories, e.g., he collected 20 specimens of no. 94, *Paesia glandulosa*, and 5 more with the rhizome. For many numbers through about 324, specimens were collected in rather large sets. Thereafter, the sets were generally much smaller, often only a few sheets. Most of the numbers after 324 were gathered in the years 1855 to 1858, whereas most collections of the numbers before 325 were made in 1854, with additions to the set made in 1855 and 1856.

Fendler's keen eye is evident by the fact that, even though he often collected the same species (or number) at different times and/or localities, there are very few mixed gatherings. He must have had a very discriminating eye for differences. When in doubt, he often gave aberrant collections Greek letter designations α and β under the same number, or labeled the additions "ad 56"; sometimes these represent noteworthy taxonomic variations (occasionally different species), sometimes only forms of little taxonomic significance. The following are taxonomically mixed collections: 16, 31, 64, 72, 73, 83, 98, 117, 143, 179, 181, 185, 187, 221, 224, 232, 258?, 259, 293, 294, 322, 324, 364, 378, 380, and 473. Some of these probably represent inadvertent mixing or misnumbering, whereas others are in large genera of great taxonomic difficulty, e.g., *Elaphoglossum*, *Thelypteris*, and *Selaginella*.

Fendler's collection numbers range from 1 to 499. Of these, 44 are thus far identified as types. We have seen specimens or notebook information for all numbers except 2 and 339. In addition, neither we nor Eaton (1861) saw specimens numbered 337, 345, 346, 384, 392, 401, 427, 442, 458, 462, 478, 484, or 490. The notebook at Harvard contains entries for numbers 58 to 499; inexplicably, the early numbers are missing.

Because Fendler gave the same collection number to plants collected at different times and localities, it often is impossible to determine the locality and date of a particular specimen. In a few cases there is only a single date on the specimen and in the notebook. In the list that follows (Appendix I), dates are given only where there is reasonable certainty that the entire gathering was made on a single date at a single place. For those numbers that were collected on more than one date, we give the total number of dates (as indicated from the notebook and on the specimens at YU). For all numbers, the size of the set, when known, is given.

Fendler's Venezuelan pteridophytes were widely distributed, and specimens have been located in the following 16 herbaria: B, BM, BR, CU, F, G, GH, GOET, K, MO, NY, P, PH, S, US, and YU.

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APPENDIX I

Determinations of Fendler's pteridophyte collections from Venezuela, Estado Aragua and adjacent states, Colonia Tovar, and vicinity, 1854–1855. The fractional number in square brackets is the number of collection dates listed by Fendler in his notebook and on the set at YU (numerator) over the number of sets (denominator), as indicated on specimens at YU. If a given number was collected on a single date only, the exact date is given. Determinations are by Alan Smith unless otherwise indicated. Abbreviations: JM = John T. Mickel; RT = Rolla M. Tryon; AT = Alice F. Tryon; ME = A. Murray Evans; DL = David B. Lellinger; RM = Robbin C. Moran; BO = Benjamin Øllgaard. (s) = data from specimen at YU; (n) = data from Fendler notebook at GH.

1. *Danaea moritziana* C. Presl, vel aff.; MO, YU. [7/20]; 6,000–7,000 ft. (s).
2. Not located.
3. *Marattia laevis* J. E. Smith; MO, YU—2. [3/38]; 6,500 ft. (s).
4. *Botrychium* sp.; YU; cited by Eaton (1861) as *B. decompositum* Mart. & Gal.
5. *Osmunda regalis* L.; MO, YU. [2/24]; 5,900 ft. (s).
6. *Anemia villosa* Humb. & Bonpl. ex Willd.; MO, YU; det. JM. [9/20]; 5,000–7,000 ft. (s).
7. *Anemia ferruginea* H.B.K. var. *ferruginea*; MO, YU; det. JM. [2/20]; 6,500 ft. (s).
8. *Anemia hirsuta* (L.) Sw.; MO, YU; det. JM. [6/17]; 5,500 ft. (s).
9. *Anemia oblongifolia* (Cav.) Sw.; MO, YU; det. JM. [4/20]; 5,500–6,000 ft. (s).

9β. *Anemia oblongifolia* (Cav.) Sw.; YU. [?/1?].

10. *Anemia oblongifolia* (Cav.) Sw.; MO—2, YU; det. JM. [6/20]; 6,000 ft. (s).
11. *Anemia pastinacaria* Moritz ex Prantl; MO—2, YU; det. JM. [7/20]; 6,000 ft. (s).
12. *Anemia* sp., undescribed?; YU. 11/9/54 [1/2]; 3,500 ft. (s).

12β. *Anemia* sp., undescribed?; YU.

13. *Anemia phyllitidis* (L.) Sw.; MO, YU; det. JM. [5/20]; 3,000–4,000 ft. (s).
14. *Lygodium venustum* Sw.; MO, YU. [6/19] (s).
15. *Anemia hirsuta* (L.) Sw.; MO, YU; det. JM. [3/9]; 5,200 ft. (s).
16. *Trichomanes* (*Pachychaetum*) *rigidum* Sw.; MO—2, YU—2. [13/30]; 6,000–7,000 ft. (s).

16. *Trichomanes* (*Lacosteopsis*) *diaphanum* H.B.K.; MO.

17. *Trichomanes* (*Lacosteopsis*) *diaphanum* H.B.K.; MO—2, YU. [7/50]; 6,000–7,000 ft. (s).
18. *Trichomanes* (*Lacosteopsis*) *diaphanum* H.B.K.; MO—2, US—2, YU. [2/21] (s).
19. *Trichomanes* (*Lacosteopsis*) *diaphanum* H.B.K.; US—not seen.
20. *Trichomanes* (*Lacosteopsis*) *radicans* Sw.; MO—3, US, YU—3. [10/30]; 6,000–6,500 ft. (s).
21. *Trichomanes* (*Lacosteopsis*) *rupestre* (Raddi) Bosch; MO—2, US, YU—2. [6/20]; 5,000–6,000 ft. (s).
22. *Trichomanes* (*Lacosteopsis*) *capillaceum* L.; MO—2, US, YU. [3/21]; 6,000–7,000 ft. (s).
23. *Trichomanes* (*Didymoglossum*) *reptans* Sw.; B, G, GH, MO—4, US, YU; cited by Wessels Boer (1962). [13/40]; 6,000–7,000 ft. (s).
24. *Trichomanes* (*Didymoglossum*) *pusillum* Sw.; B, G, GH, L, MO—2, S, US, YU; cited by Wessels Boer (1962). [6/25]; 6,500 ft. (s).

ad 24. *Trichomanes* (*Didymoglossum*) *pusillum* Sw.; YU. 18/3/56 [1/?] (s).

25. *Trichomanes* (*Didymoglossum*) *ovale* (Fourn.) W. Boer. *Didymoglossum ovale* Fourn., Bull. Soc. Bot. France 19: 240. 1872. HOLOTYPE, P; ISOTYPES, B, G, GH, MO—2, YU. Cited by Wessels Boer (1962). 24/7/56 [1/?]; 6,000 ft. (s).

ad 25. *Trichomanes* (*Didymoglossum*) *ovale* (Fourn.) W. Boer; YU. [2/20] (s).

26. *Trichomanes* (*Achomanes*) *robustum* Fourn.; MO, US, YU. [4/21]; 5,500 ft. (s).
27. *Hymenophyllum* (*Ptychophyllum*) *fucoides* (Sw.) Sw.; MO—2, US, YU. [14/20]; 7,000–8,000 ft. (s).

27β. *Hymenophyllum* (*Ptychophyllum*) *fucoides* (Sw.) Sw.; YU. [3/6] (s).

28. *Hymenophyllum* (*Mecodium*) *axillare* Sw.; MO—2, YU. [16/21]; 6,500 ft. (s).
29. *Hymenophyllum* (*Hymenophyllum*) *tunbrigense* (L.) J. E. Smith; MO, US, YU. 9/11/54 [1/5]; 7,000–8,000 ft. (s).
30. *Hymenophyllum* (*Mecodium*) *polyanthos* (Sw.) Sw.; MO—2, YU. [5/40]; 6,000–7,000 ft. (s).
31. *Hymenophyllum* (*Sphaerocionium*) sp., undescribed?; YU. [5/15]; 6,500–7,000 ft. (s).

31. *Hymenophyllum* (*Mecodium*) *fendlerianum* Sturm in Martius; MO.

31. *Hymenophyllum* (*Sphaerocionium*) *hirsutum* (L.) Sw., vel aff.; MO.
32. *Hymenophyllum* (*Mecodium*) *apiculatum* Mett. ex Kuhn, Linnaea 35: 391. 1868. ISOTYPES, MO, US, YU.

ad 32. *Hymenophyllum* (*Mecodium*) *apiculatum* Mett. ex Kuhn; YU. 26/7/56 [1/?] (s).

33. *Hymenophyllum* (*Sphaerocionium*) *microcarpum* Desv.; US, YU; cited by Morton (1947). [3/20]; 6,500–7,200 ft. (s).
34. *Hymenophyllum* (*Mecodium*) *undulatum* (Sw.) Sw.; MO, US, YU. [3/18]; 6,200 ft. (s).
35. *Hymenophyllum* (*Mecodium*) *fendlerianum* Sturm

in Martius, Fl. Bras. 1(2): 291. 1859. LECTOTYPE (chosen by Lellinger, 1984), US; ISOLECTOTYPES, BR, MO.

36. *Hymenophyllum* (*Mecodium*) *asplenioides* Sw.; MO, US.
37. *Hymenophyllum* (*Sphaerocionium*) *hirsutum* (L.) Sw.; GH, MO, NY, YU; cited by Morton (1947). [4/20]; 6,000 ft. (s).
37β. *Hymenophyllum* (*Sphaerocionium*) *hirsutum* (L.) Sw.; YU. 29/1/57 [1/1] (s).
38. *Hymenophyllum* (*Sphaerocionium*) *fragile* (Hedwig) C. Morton; GH, MO—2, NY, US, YU; cited by Morton (1947). [6/?]; 6,000–7,000 ft. (s).
39. *Hymenophyllum* (*Sphaerocionium*) *karstenianum* Sturm, Bot. Zeitung (Berlin) 17: 298. 1859. ISOSYNTYPES, GH, MO—2, US, YU. Cited by Morton (1947). [4/21]; 6,200 ft. (s).
40. *Sticherus rubiginosus* (Mett.) Nakai; MO, US, YU—2. [3/15]; 8,000 ft. (s).
41. *Sticherus nudus* (Moritz ex Reichardt) Nakai; MO, YU. [4/17]; 6,000–7,000 ft. (s).
42. *Sticherus bifidus* (Willd.) Ching; MO, YU—2. [3/11]; 6,000–7,000 ft. (s).
43. *Sticherus penniger* (Martius) Copel.; MO, YU. [5/19]; 6,000 ft. (s).
44. *Dicranopteris flexuosa* (Schrader) L. Underw.; MO, YU. [4/20]; 6,200 ft. (s).
45. *Diplopterygium bancroftii* (Hook.) A. R. Smith; MO, US—2, YU. [4/20]; 6,500 ft. (s).
46. *Cyathea speciosa* Willd.; GH, MO, YU—3; cited by R. Tryon (1976). 17/9/55 [1/20]; 4,800 ft. (s).
46β. *Cyathea speciosa* Willd.; YU. 12/12/56 [1/1] (s).
47. *Cyathea villosa* Willd.; MO, YU; cited by Barrington (1978) as *Trichipteris villosa* (Willd.) R. Tryon. 3/12/54 [1/21]; 6,500 ft. (s).
48. *Lophosoria quadripinnata* (J. Gmelin) C. Chr.; MO, YU—3. [2/21]; 7,800 ft. (s).
49. *Cyathea tryonorum* (Riba) Lellinger; MO—2, YU—4. [4/18]; 6,000–6,800 ft. (s).
49β. *Cyathea tryonorum* (Riba) Lellinger; YU. 12/12/56 [1/1] (s).
50. *Cyathea ebenina* Karsten; GH, YU—3; cited by R. Tryon (1976). [?/1] 6,500 ft. (s).
51. *Cyathea fulva* (Mart. & Gal.) Fée; YU. [3/?]; 6,500 ft. (s).
52. *Cyathea fulva* (Mart. & Gal.) Fée; F, GH, MO—2, YU—2; cited by R. Tryon (1976). [3/21]; 6,000–7,000 ft. (s).
53. *Cyathea squamata* (Klotzsch) Domin; F, GH, MO—2, NY, YU; these are ISOTYPES of *Alsophila caracasana* Klotzsch var. *fendleriana* Domin, Pterid. Dominica 95. 1919. Cited by Barrington (1978) as *Trichipteris microphylla* (Klotzsch) R. Tryon. [2/20]; 6,500–7,000 ft. (s).
54. *Cyathea gibbosa* (Klotzsch) Domin; GH, MO, US, YU; cited by Barrington (1978) as *Trichipteris gibbosa* (Klotzsch) Barrington. 26/8/54 [1/14]; 6,000–6,500 ft. (s).
55. *Cyathea pungens* (Willd.) Domin; GH, MO, NY, YU—2; cited by Barrington (1978) as *Trichipteris procera* (Willd.) R. Tryon. [2/20]; 6,500 ft.; seaside (s).
56. *Cyathea caracasana* (Klotzsch) Domin var. *caracasana*; GH, MO, YU—2; cited by R. Tryon (1976). [3/13]; 6,000–6,500 ft. (s).
ad 56. *Cyathea caracasana* (Klotzsch) Domin var. *caracasana*; YU. 28/6/56 [1/?] (s).
57. *Dicksonia sellowiana* Hook.; YU; 19/6/54 [1/16]; 6,800–7,800 ft. (s).
58. *Dennstaedtia cicutaria* (Sw.) T. Moore; YU. 1/6/54 [1/17]; 6,500 ft.; Colonia Tovar (n).
59. *Dennstaedtia dissecta* (Sw.) T. Moore; MO. [3/?]; 6,000 ft.; Colonia Tovar (n).
60. *Dennstaedtia arborescens* (Willd.) Ekman ex Maxon; MO. [4/?]; 6,500–7,500 ft.; Colonia Tovar (n).
61. *Saccoloma domingense* (Sprengel) C. Chr.; MO—2, YU—2. [6/20]; 6,000–7,000 ft.; Colonia Tovar (n).
61β. *Saccoloma domingense* (Sprengel) C. Chr.; YU. 29/1/57 [1/1] (s).
62. *Loxoscaphe theciferum* (H.B.K.) T. Moore; MO, YU. [10/28]; 6,000 ft.; Colonia Tovar (n).
63. *Lindsaea klotzschiana* Moritz in Ettingshausen; YU. [7/16]; 6,000–6,800 ft.; Colonia Tovar, also between Maracai and Choroni (n).
63α & β. *Lindsaea klotzschiana* Moritz in Ettingshausen; BR, G, GH, GOET, K, MO, PH, US; cited by Kramer (1957).
63β. *Lindsaea klotzschiana* Moritz in Ettingshausen; YU. 12/12/56 [1/8] (s).
64. *Hypolepis viscosa* Karsten; YU—2. [4/20]; 6,500 ft.; Colonia Tovar (n).
64. *Hypolepis bogotensis* Karsten?; MO.
64β. *Hypolepis bogotensis* Karsten?; YU. 17/6/56 [1/?]; highest mountains, Lagunassa (s).
64β. *Hypolepis viscosa* Karsten; YU.
65. *Cheilanthes microphylla* (Sw.) Sw.; MO. [5/?]; 2,000–4,000 ft.; La Victoria, also between Caracas and La Guayra (n).
66. *Hypolepis parallelogramma* (Kunze) C. Presl; MO, YU—4. [3/20]; 6,500 ft.; Colonia Tovar (n).
ad 66. *Hypolepis parallelogramma* (Kunze) C. Presl; YU. 6/1/57 [1/?] (s).
67. *Adiantopsis radiata* (L.) Fée; YU. [2/?]; Maya a few mi. S of Colonia Tovar (n).
68. *Adiantum braunii* Mett. ex Kuhn; MO, YU. 25/10/54 [1/20]; 3,500 ft.; a few mi. SW of Colonia [Tovar] (n).
69. *Adiantum tenerum* Sw.; MO. [3/?]; 3,000–3,500 ft.; lower valleys around Colonia [Tovar] (n).
70. *Adiantum tenerum* Sw.; MO, YU. [2/7]; 3,200 ft.; Biscaina, S of Colonia [Tovar], also near Caracas (n).
71. *Adiantum poiretii* Wikström; MO, YU. [2/15]; 3,000–4,000 ft.; a few mi. SW of Colonia Tovar, also near Caracas (n).
72. *Adiantum henslovianum* Hook.; YU. [4/20]; 4,000 ft.; a few mi. SW of Colonia Tovar (n).
72. *Adiantum capillus-veneris* L.; MO.
73. *Adiantum concinnum* Humb. & Bonpl. ex Willd.; YU. [3/14]; 3,000–4,000 ft.; Caracas, also a few mi. S of Colonia [Tovar] (n).
ad 73. *Adiantum concinnum* Humb. & Bonpl. ex Willd.; YU. 19/1/56 [1/?] (s). Same sheet as 73.
73. *Adiantum lunulatum* Burm. f.; MO, YU.
73/76. *Adiantum concinnum* Humb. & Bonpl. ex Willd.; MO.
74. *Adiantum raddianum* C. Presl; YU. [4/4]; 3,000–3,500 ft.; 6–9 mi. S of Colonia [Tovar] (n).
75. *Adiantum concinnum* Humb. & Bonpl. ex Willd.;

MO—2, YU—2. [5/20]; 3,000–4,000 ft.; 6–9 mi. S of Colonia [Tovar] (n).

ad 75. *Adiantum concinnum* Humb. & Bonpl. ex Willd.; YU. [4/7] (s).

75β. *Adiantum concinnum* Humb. & Bonpl. ex Willd.; YU. [3/17] (s).

76. *Adiantum concinnum* Humb. & Bonpl. ex Willd.; YU. 28/6/55 [1/3]; 5,000–6,000 ft.; 9 mi. S of Colonia [Tovar] (n).

77. *Adiantum concinnum* Humb. & Bonpl. ex Willd.; YU. [3/2]; 2,000–3,000 ft.; La Victoria to Biscaina (n).

78. *Adiantum henslovianum* Hook.; MO. [2/?]; 3,000–4,000 ft.; around Caracas (n).

79. *Adiantum patens* Willd.; MO, YU. [4/16]; 3,000–4,000 ft.; a few mi. S and SW of Colonia [Tovar] (n).

80. *Adiantum polyphyllum* Willd.; MO, YU—2. [5/20]; 3,000–4,000 ft.; a few mi. S and SW of Colonia [Tovar] (n).

81. *Adiantum deflectens* Martius; LECTOTYPE, US (chosen by Lellinger, Proc. Biol. Soc. Washington 89: 703. 1977) of *A. deflectens* var. *tremulum* Hieron., Bot. Jahrb. Syst. 34: 487 1904, as "*tremula*"; ISOLECTOTYPES, MO—2, YU. [2/20]; 2,000–3,000 ft.; between La Victoria and Biscaina, S of Colonia Tovar (n).

82. *Adiantum lunulatum* Burm. f.; MO, YU. [2/12]; 2,500 ft.; near La Victoria and south of Laguna de Valencia (n).

83. *Adiantum pulverulentum* L.; YU. [3/16]; 2,500–4,000 ft.; a few mi. S and SW of Colonia [Tovar], also Piedernales (n).

83. *Adiantum fructuosum* Sprengel; MO.

84. *Adiantum serratodentatum* Willd.; MO, YU. [2/18]; 2,500–3,500 ft.; Biscaina and Piedernales in savannahs at margin of woods (n).

85. *Adiantum villosum* L.; MO, YU—2. [4/8]; 2,000–3,000 ft.; Piedernales, La Victoria, between Caracas and La Guayra (n).

ad 85. *Adiantum tetraphyllum* Humb. & Bonpl. ex Willd.; YU.

86. *Adiantum pulverulentum* L.; MO, YU. [8/20]; 3,000–4,000 ft.; a few mi. S and SW of Colonia Tovar, also Piedernales (n).

87. *Adiantum petiolatum* Desv.; YU. 25/1/55 [1/2]; 2,000 ft.; Piedernales, near Güigüe (n).

88. *Adiantum macrophyllum* Sw.; MO. [7/21]; 2,500–3,500 ft.; valley of the Tuy River, Maya Piedernales (n).

89. *Pellaea ovata* (Desv.) Weath.; MO—2, YU; det. AT. [7/20]; 6,500 ft.; a few mi. S of Colonia Tovar in a savannah between rocks (n).

90. *Cheilanthes marginata* H.B.K.; MO, YU. [3/20]; 7,000 ft.; a few mi. W of Colonia Tovar (n).

91. *Doryopteris pedata* (L.) Fée var. *palmata* (Willd.) Hicken; MO; YU—2; det. RT. [6/20]; 3,000–4,000 ft.; lower valleys S and SW of Colonia Tovar (n).

92. *Cheilanthes concolor* (Langsd. & Fischer) R. & A. Tryon; MO, YU. [2/20]; 2,000–3,000 ft.; seaside of mountain range between Caracas and Guayra and between Maracai and Choroni (n).

93. *Histiopteris incisa* (Thunb.) J. Smith; MO, YU—3. [2/25]; 7,500 ft.; highest mountains east of Colonia Tovar (n).

94. *Paesia glandulosa* (Sw.) Kuhn; MO, YU—2. [2/25]; 7,500 ft.; highest mountains E of Colonia Tovar (n).

95. *Pteris gigantea* Willd.; MO, US, YU—2. [3/18]; 3,500 ft.; lower valleys S of Colonia [Tovar] (n).

96. *Pteris grandifolia* L.; MO, YU—2. [2/14]; 2,000–2,500 ft.; between Caracas and La Guayra, also above Hacienda Curisal (n).

97. *Pteris consanguinea* Mett. ex Kuhn, Linnaea 36: 89. 1869. ISOSYNTYPES, K—photo US, MO, YU—3. [2/16]; 6,700 ft.; mountains south of Colonia [Tovar] (n).

98. *Pteris podophylla* Sw.; MO, US, YU—2. [4/26]; 5,500–7,000 ft.; valley of the Tuy and headwaters of San Carlos River (n).

98. *Pteris propinqua* Agardh; YU. [?/3]; 7,000 ft. (s).

99. *Pteris propinqua* Agardh; YU. 25/1/55 [1/3]; 2,300 ft.; Piedernales near Güigüe (n).

100. *Lonchitis hirsuta* L.; MO, YU. 5/6/55 [1/20]; 3,200 ft.; small distance above Biscaina, 9 mi. S of Colonia [Tovar] (n).

101. *Pteris deflexa* Link; MO, YU. [5/10]; 6,000 ft.; Colonia Tovar (n).

102. *Pteris deflexa* Link; MO, US, YU—3. [7/20]; 7,000 ft.; a few mi. W of Colonia Tovar, high mountains (n).

103. *Pteris quadriaurita* Retz.; MO, YU. [3/1]; 4,000 ft.; a few mi. S and SW of Colonia [Tovar] (n).

103β. *Pteris quadriaurita* Retz.; YU—2. 26/1/57 [1/1] (s).

104. *Pteridium arachnoideum* (Kaulf.) Maxon; MO, YU—3. [4/20]; 5,000–7,000 ft.; Colonia Tovar (n).

105. *Pteris longifolia* L.; MO, US, YU. [7/20]; 6,000–6,500 ft.; savannah a few mi. S of Colonia [Tovar] (n).

106. *Blechnum occidentale* L.; MO—2. [3/?]; 4,000–6,500 ft.; mountains S of Colonia, also Caracas (n).

107. *Blechnum occidentale* L.; YU; cited by Eaton (1861). [3/?]; 6,800 ft.; a few mi. W of Colonia Tovar (n).

108. *Blechnum occidentale* L.; YU; cited by Eaton (1861). 27/5/54 [1/?]; 6,000 ft.; a few mi. SW of Colonia [Tovar] (n).

109. *Blechnum* hybrid?, possibly *B. occidentale* L. × *B. polypodioides* Raddi; MO—2. [3/?]; 2,000–3,500 ft.; near Caracas, also low valleys S of Colonia [Tovar], Piedernales (n).

110. *Blechnum polypodioides* Raddi; MO—2. [4/?]; 2,000–4,000 ft.; near Caracas, La Victoria (n).

110β. *Blechnum* sp.; YU; cited by Eaton (1861) as *B. polypodioides.*

111. *Blechnum* sp.; YU; cited by Eaton (1861) as *B. longifolium* H.B.K. 25/1/55 [1/?]; 2,300 ft.; Piedernales (n).

112. *Blechnum* ×*caudatum* Cav. [*B. fraxineum* Willd. × *B. occidentale* L.]; MO. [3/?]; 3,000–4,000 ft.; lower valleys a few mi. S and SW of Colonia Tovar (n).

113. *Blechnum* ×*caudatum* Cav. [*B. fraxineum* Willd. × *B. occidentale* L.]; MO. [3/?]; 5,500 ft.; Tuy River valley below Colonia [Tovar] (n).

114. *Blechnum fraxineum* Willd.; MO. [3/?]; 3,000–3,500 ft.; Macarao valley, 9 mi. above Las Aguntas (n).

115. *Blechnum* sp.; YU; cited by Eaton (1861) as *B.*

longifolia H.B.K. [2/?]; 3,000 ft.; Piedernales, also between Caracas and La Guayra (n).

116. *Blechnum* sp.; YU; cited by Eaton (1861) as *B. fendleri* Hook. 25/1/55 [1/?]; 2,300 ft.; Piedernales (n).
117. *Salpichlaena volubilis* (Kaulf.) J. Smith; MO—2. [3/?]; 6,000–7,000 ft.; Colonia Tovar (n).
117. *Arachniodes denticulata* (Sw.) Ching; MO.
118. *Blechnum cordatum* (Desv.) Hieron.; MO. [3/?]; 6,500–7,200 ft.; a few mi. W of Colonia [Tovar] (n).
119. *Blechnum cordatum* (Desv.) Hieron.; MO. [5/?]; 7,000 ft.; a few mi. S and SW of Colonia Tovar (n).
120. *Blechnum* sp.; YU; cited by Eaton (1861) as *Lomaria procera* Sprengel [possibly *B. cordatum* (Desv.) Hieron.]. 16/8/55 [1/?]; 3,000 ft.; between Caracas and La Guayra (n).
121. *Blechnum* aff. *cordatum* (Desv.) Hieron.; MO. 24/6/55 [1/?]; 8,000 ft.; highest mountains 12 mi. E of Colonia Tovar (n).
122. *Blechnum* sp.; YU; cited by Eaton (1861) as *Lomaria procera* Sprengel [possibly *B. cordatum* (Desv.) Hieron.]. No data in notebook.
123. *Asplenium rutaceum* (Willd.) Mett.; MO, US, YU. [3/21]; 6,500 ft.; Colonia Tovar and seaside of mountains (n).
124. *Asplenium cristatum* Lam.; MO, YU. [15/23]; 6,000–7,000 ft.; Colonia Tovar (n).

ad 124. *Asplenium cristatum* Lam.; YU. 25/1/55 [1/8] (s).

124β. *Asplenium* aff. *cristatum* Lam.; MO, US, YU. [5/11]; rachis winged.
125. *Asplenium flabellulatum* Kunze; MO, US, YU—3. [6/23]; 6,000–7,000 ft.; Colonia Tovar (n).
125. *Asplenium flabellulatum* Kunze var. *partitum* Klotzsch; MO.
126. *Asplenium radicans* L.; MO—2, US, YU. [5/13]; 6,000–7,000 ft.; around Colonia Tovar (n).
126β. *Asplenium radicans* L.; YU. [?/4].
127. *Asplenium radicans* L.?; MO—2, US, YU. [6/21]; 4,000–5,000 ft.; a few mi. S and SW of Colonia [Tovar] (n).
127β. *Asplenium flabellulatum* Kunze var. *partitum* Klotzsch; YU. 8/1/57 [1/1] (s).
128. *Diplazium cristatum* (Desr.) Alston; MO, US, YU. [6/18]; 6,500 ft.; Colonia Tovar (n).
128β. *Diplazium cristatum* (Desr.) Alston; YU. 9/2/57 [1/1] (s).
129. *Diplazium caracasanum* (Willd.) Kunze ex T. Moore; MO, US, YU. [7/16]; 6,500 ft.; Colonia Tovar (n).
129β. *Diplazium caracasanum* (Willd.) Kunze ex T. Moore; MO, YU. 8/1/57 [1/9] (s).
130. *Asplenium pumilum* Sw.; MO, US, YU. [6/24]; 2,000–4,000 ft.; a few mi. SW of Colonia [Tovar], also near La Victoria and between Caracas and La Guayra (n).
131. *Asplenium obtusifolium* L.; MO, US, YU. [3/22]; 5,000–5,500 ft.; around Colonia Tovar, in wet places on rocks (n).
132. *Asplenium squamosum* L.; MO, YU—2; cited by Morton & Lellinger (1966) at GH, NY. 8/10/55 [1/11]; 7,200 ft.; 5 mi. W of Colonia Tovar, upon rocks (n).
133. *Asplenium formosum* Willd.; MO, US, YU. [5/27]; 4,000 ft.; a few mi. SW of Colonia Tovar, also several mi. above Choroni (n).
134. *Asplenium monanthes* L.; MO, US, YU. [2/23]; 4,000 ft.; a few mi. SW of Colonia [Tovar] (n). One other sheet at MO is *Asplenium cristatum* Lam.
135. *Asplenium harpeodes* Kunze; MO—3, YU. [13/22]; 6,500–7,500 ft.; around Colonia Tovar (n).
136. *Asplenium laetum* Sw., vel aff.; MO, US, YU. [5/20]; 3,000–4,000 ft.; a few mi. S and SW of Colonia [Tovar] (n).
137. *Asplenium raddianum* Gaud.; MO, US, YU—2. [14/20]; 6,000–7,000 ft.; Colonia Tovar (n).
138. *Asplenium claussenii* Hieron., Hedwigia 60: 241. 1918. LECTOTYPE (chosen by Morton & Lellinger, 1966), B; ISOLECTOTYPES, MO, US, YU. [5/20]; 4,000–5,000 ft.; near Colonia Tovar (n).

138β. *Asplenium claussenii* Hieron.; YU. 4/2/57 [1/?] (s).

139. *Asplenium ruizianum* Klotzsch; MO, YU. [3/20]; 4,000 ft.; a few mi. S and SW of Colonia [Tovar] (n).

139β. *Asplenium ruizianum* Klotzsch; US, YU. [2/18] (s).

139γ. *Asplenium claussenii* Hieron.; YU. 25/1/55 [1/1] (s).

140. *Asplenium cirrhatum* Rich. ex Willd.; MO, YU. Mixed with *A. radicans* L. at YU. [5/23]; 7,000 ft.; seaside of mountains N of Colonia [Tovar] (n).
141. *Asplenium auritum* Sw. var. *obtusum* Kunze ex Mett.; MO. [2/?]; 4,000 ft.; a few mi. SW of Colonia Tovar (n).
142. *Asplenium monodon* Liebm.?; MO, YU. [6/20]; 6,000 ft.; Colonia Tovar (n).

ad 142. *Asplenium monodon* Liebm.?; YU. [4/?] (s).

142β. *Asplenium monodon* Liebm.; YU. [2/1] (s).
143. *Asplenium abscissum* Willd.; MO, YU. [9/20]; 6,400 ft.; Colonia Tovar (n).
143. *Asplenium oligophyllum* Kaulf.; MO.
143β. *Asplenium abscissum* Willd.; MO, YU. 4/10/54 [1/13] (s).
143γ. *Asplenium melanopus* Sodiro; YU. 19/12/54 [1/1] (s).
144. *Asplenium auriculatum* Sw., vel aff.; MO—2, YU. [11/22]; 6,000–7,000 ft.; Colonia Tovar (n).
145. *Asplenium alatum* Humb. & Bonpl. ex Willd.; MO, US, YU. [6/20]; 6,500 ft.; Colonia Tovar (n).
146. *Diplazium diplazioides* (Klotzsch & Karsten ex Klotzsch) Alston; YU. 28/9/55 [1/2]; 6,500 ft.; seaside of mountains N of Colonia [Tovar] (n).
147. *Diplazium hians* Kunze ex Klotzsch; US, YU—2. 28/6/54 [1/9]; 6,000 ft.; Colonia Tovar (n).
148. *Diplazium hians* Kunze ex Klotzsch; MO, YU—2. [2/5]; 5,600 ft.; Tuy River valley below Colonia [Tovar], seaside of mountains (n).
149. *Diplazium diplazioides* (Klotzsch & Karsten ex Klotzsch) Alston; MO, US, YU. [5/9]; 7,000–8,000 ft.; highest mountains around Colonia [Tovar] (n).
150. *Diplazium* aff. *striatum* (L.) C. Presl; MO, US, YU. [3/13]; 4,000 ft.; San Carlos River valley, a few mi. SW of Colonia [Tovar] (n).
151. *Diplazium mutilum* Kunze; MO, US, YU. [3/11]; 4,500 ft.; a few mi. S and SW of Colonia [Tovar] (n).
152. *Diplazium centripetale* (Baker) Maxon, vel aff.; MO, US, YU. 28/9/54 [1/10]; 6,000 ft.; seaside of mountains N of Colonia [Tovar] (n).
153. *Diplazium celtidifolium* Kunze; MO, US—3, YU. [5/20]; 6,000–7,000 ft.; around Colonia Tovar (n).

154. *Diplazium plantaginifolium* (L.) Urban; MO, US—2, YU. 29/8/54 [1/26]; 5,000–6,000 ft.; Tuy River valley below Colonia [Tovar] (n).
155. *Asplenium serra* Langsd. & Fischer; MO, YU—3. [9/20]; 7,000 ft.; around Colonia Tovar (n).
156. *Asplenium lividum* Mett. ex Kuhn; ISOTYPES, MO, US. Cited by Morton & Lellinger (1966). 25/10/54 [1/17]; 4,000 ft.; San Carlos River valley (n).
157. *Asplenium praemorsum* Sw.; MO, YU. [9/21]; 4,000–7,000 ft.; around Colonia Tovar, also 15 mi. W of Caracas (n).

157β. *Asplenium praemorsum* Sw.; YU. 27/2/57 [1/1] (s).

157?. *Asplenium praemorsum* Sw.; YU. [2/?].

158. *Thelypteris* (*Amauropelta*) *pilosohispida* (Hook.) Alston; GH, MO, YU—2. [9/20]; 6,000–7,000 ft.; Colonia Tovar (n).
159. *Thelypteris* (*Amauropelta*) *diplazioides* (Moritz ex Mett.) Ching; B, CU, GH—2, MO, US, YU—2. [3/16]; 5,500–6,000 ft.; seaside of mountains N of Colonia Tovar (n).
160. *Didymochlaena truncatula* (Sw.) J. Smith; MO, YU—3. [12/18]; 6,000–7,000 ft.; Colonia Tovar, also seaside of mountains N of Colonia Tovar (n).
161. *Nephrolepis occidentalis* Kunze; MO—2, YU. [2/22]; 3,000–4,000 ft.; a few mi. S of Colonia Tovar, also La Victoria (n). "Plant annual from tubers" (s).
162. *Nephrolepis pendula* (Raddi) J. Smith; MO—2, YU—2. [5/21]; 4,000–6,000 ft.; a few mi. S of Colonia [Tovar], also mountains N of Caracas (n).

162β. *Nephrolepis pendula* (Raddi) J. Smith, YU. [?/1].

163. *Athyrium skinneri* (Baker) C. Chr.; YU. 25/1/55 [1/1]; 3,000 ft.; Piedernales near Güigüe (n).
164. *Tectaria heracleifolia* (Willd.) L. Underw.; MO, US, YU. [5/9]; 3,000–4,000 ft.; a few mi. S and SW of Colonia Tovar (n).

164β. *Tectaria heracleifolia* (Willd.) L. Underw.; YU. [2/3].

165. *Tectaria incisa* Cav., vel aff.; MO, YU—3. [6/17]; 4,000 ft.; a few mi. SW of Colonia Tovar (n).

165 additional. *Tectaria trifoliata* (L.) Cav.; YU. 12/12/56 [1/1] (s).

165β. *Tectaria incisa* Cav.; YU. 22/4/58 [1/1]; 4,000 ft.; seaside of mountains N of Petaquire (s).

166. *Tectaria incisa* Cav.; YU. [3/1]; 2,000–4,000 ft.; a few mi. SW of Colonia Tovar (n).
167. *Hemidictyum marginatum* (L.) C. Presl; MO, YU—2. 7/3/57 [1/?]; 3,000 ft.; seaside of mountain range between Valencia and San Estevan (n).
168. *Dryopteris patula* (Sw.) L. Underw.; MO—2, US, YU—2. [3/34]; 7,000 ft.; a few mi. W of Colonia Tovar (n).
169. *Dryopteris patula* (Sw.) L. Underw.; YU. 21/10/54 [1/2]; 3,200 ft.; Maya River valley, a few mi. S of Colonia Tovar (n).
170. *Arachniodes denticulata* (Sw.) Ching; MO. [4/?]; 7,000–8,000 ft.; highest mountains around Colonia Tovar (n).
171. *Polystichum* sp., aff. *polyphyllum* (C. Presl) C. Presl; US; mixed with *Polypodium* sp. [3/?]; 8,200 ft.; highest mountains E of Colonia [Tovar], in an open glade (n).
172. *Polystichum muricatum* (L.) Fée; US—2. [2/?]; 6,500 ft.; Colonia Tovar (n).
173. *Polystichum* sp.; YU; cited by Eaton (1861) as *Aspidium moritzianum* Klotzsch [possibly *P. muricatum* (L.) Fée]. [2/?]; 6,500 ft.; Colonia Tovar (n).
174. *Polystichum muricatum* (L.) Fée; US. [2/?]; 7,000 ft.; Colonia Tovar (n).
175. *Polystichum platyphyllum* (Willd.) C. Presl; YU; cited by Eaton (1861) as *Phegopteris platyphylla* (Willd.) Mett. [3/?]; 6,500 ft.; Colonia Tovar (n).
176. *Thelypteris* (*Amauropelta*) *concinna* (Willd.) Ching, vel aff.; CU, G, GH, MO, US. [2/?]; 2,500–3,000 ft.; Biscaina and Hacienda Carisal S of Colonia Tovar (n).
177. *Thelypteris* (*Amauropelta*) *opposita* (Vahl) Ching; MO, US, YU. [2/7]; 3,200 ft.; Caracas (n).
178. *Thelypteris* (*Amauropelta*) *pilosula* (Mett.) R. Tryon; GH, MO, US, YU. [3/15]; 7,000 ft.; Colonia Tovar (n).
179. *Thelypteris* (*Amauropelta*) *concinna* (Willd.) Ching; MO, YU—3. [2/20]; 7,000 ft.; a few mi. W of Colonia Tovar (n).

179. *Thelypteris* (*Amauropelta*) *oligocarpa* (Humb. & Bonpl. ex Willd.) Ching; MO.

180. *Thelypteris* (*Amauropelta*) *pilosula* (Mett.) R. Tryon; GH, MO, YU. [9/16]; 6,000–6,500 ft.; Colonia Tovar (n).
181. *Thelypteris* (*Amauropelta*) *scalaris* (Christ) Alston; GH, MO, US. [3/7]; 3,000–4,000 ft.; a few mi. S and SW of Colonia Tovar (n).

181. *Thelypteris* (*Amauropelta*) *oligocarpa* (Humb. & Bonpl. ex Willd.) Ching; YU.

182. *Thelypteris* (*Amauropelta*) *opposita* (Vahl) Ching, vel aff.; MO, US, YU. [4/13]; 2,000–4,000 ft.; lower valleys S of Colonia [Tovar], also between Caracas and La Guayra (n).
183. *Thelypteris* (*Amauropelta*) *pilosula* (Mett.) R. Tryon; YU. 24/6/55 [1/1]; 8,000 ft.; highest mountains E of Colonia Tovar (n).
184. *Thelypteris* (*Amauropelta*) *pilosula* (Mett.) R. Tryon; YU. 13/10/54 [1/1]; 6,500 ft.; San Carlos River valley near Colonia [Tovar] (n).
185. *Thelypteris* (*Amauropelta*) *rudis* (Kunze) Proctor & *T. concinna* (Willd.) Ching; MO [*T. rudis* at US]. [4/13]; 5,800 ft.; a few mi. S of Colonia Tovar in wet places of savannah (n).

ad 185. *Thelypteris* (*Amauropelta*) *rudis* (Kunze) Proctor; YU. 1/6/54 [1/?] (s).

185. *Thelypteris* (*Amauropelta*) *proctorii* A. R. Smith & Lellinger?; YU.

186. *Thelypteris* (*Amauropelta*) *deflexa* (C. Presl) R. Tryon; B, G, GH, MO—3, P, YU. [3/20]; 7,000 ft.; a few mi. W of Colonia Tovar (n).
187. *Thelypteris* (*Amauropelta*) *rudis* (Kunze) Proctor; YU—2. 27/8/55 [1/4]; 6,500 ft.; a few mi. W of Colonia Tovar (n).

187. *Thelypteris* (*Amauropelta*) *cheilanthoides* (Kunze) Proctor; GH.

187. *Thelypteris* (*Amauropelta*) *pachyrhachis* (Kunze ex Mett.) Ching var. *pachyrhachis*; GH.

188. *Thelypteris* (*Cyclosorus*) *grandis* A. R. Smith var. *aequatorialis* (C. Chr.) A. R. Smith; MO, YU—2. [4/9]; 3,000–4,000 ft.; a few mi. S and SW of Colonia Tovar (n).
189. *Thelypteris* (*Cyclosorus*) *patens* (Sw.) Small var. *patens*; MO, YU. [3/10]; 3,000 ft.; river valleys near Caracas, also Biscaina S of Colonia [Tovar] (n).
190. *Thelypteris* (*Cyclosorus*) *patens* (Sw.) Small var. *scabriuscula* (C. Presl) A. R. Smith; MO, YU—2.

25/10/54 [1/6]; 3,600 ft.; a few mi. SW of Colonia Tovar (n).

191. *Thelypteris* (*Cyclosorus*) *hispidula* (Decne.) Reed; YU. [3/4]; 3,000–4,000 ft.; a few mi. S and SW of Colonia Tovar (n).
192. *Thelypteris* (*Cyclosorus*) *patens* (Sw.) Small var. *patens*; MO, YU. 20/2/54 [1/6]; 3,200 ft.; near Caracas (n).
193. *Thelypteris* (*Goniopteris*) *gemmulifera* (Hieron.) A. R. Smith; GH, MO, NY, YU. [2/3]; 3,000 ft.; a few mi. S of Colonia [Tovar], also seaside of mountains between Maracai and Choroni (n).

193γ. *Thelypteris* (*Goniopteris*) *gemmulifera* (Hieron.) A. R. Smith; YU. [3/6] (s).

194. *Ctenitis nigrovenia* (Christ) Copel.; MO, US, YU. [3/16]; 4,000 ft.; a few mi. S and SW of Colonia Tovar (n).
195. *Ctenitis submarginalis* (Langsd. & Fischer) Ching; YU. [3/1]; 3,200 ft.; Maya River, a few mi. S of Colonia [Tovar] (n).
196. *Thelypteris* (*Goniopteris*) *tetragona* (Sw.) Small; GH, MO, YU. [3/9]; 3,000–4,000 ft.; a few mi. S and SW of Colonia Tovar (n).
197. *Ctenitis submarginalis* (Langsd. & Fischer) Ching; MO, US, YU—2. [2/16]; 3,200 ft.; valley of Maya, a few mi. S of Colonia [Tovar] (n).
198. *Stigmatopteris nephrodioides* (Klotzsch) C. Chr.; MO, US, YU—2. 29/8/54 [1/30]; 5,600 ft.; River Tuy below Colonia Tovar (n).
199. *Thelypteris* (*Goniopteris*) *poiteana* (Bory) Proctor; GH, MO, YU. [2/6]; 2,000 ft.; Piedernales, also between Caracas and La Guayra (n).
200. *Thelypteris* (*Goniopteris*) *pennata* (Poiret in Lam.) C. Morton; YU. 3,000–5,000 ft.; River Tuy below Colonia Tovar, also between Caracas and La Guayra (n); [2/2] (s).
201. *Thelypteris* (*Goniopteris*) *asterothrix* (Fée) Proctor; GH, MO—2, YU. 19/12/54 [1/22]; 3,200 ft.; Maya River a few mi. S of Colonia Tovar (n).
202. *Ctenitis subincisa* (Willd.) Ching; MO—3, YU—3. [8/20]; 6,000 ft.; Colonia Tovar (n).
203. *Ctenitis sloanei* (Sprengel) C. Morton; YU—2. 5/1/55 [1/1]; Piedernales near Güigüe (n).
204. *Ctenitis ampla* (Humb. & Bonpl. ex Willd.) Ching; MO, US—2, YU. [4/6]; 3,000–4,000 ft.; a few mi. S and SW of Colonia Tovar (n).
205. *Lastreopsis effusa* (Sw.) Tindale subsp. *divergens* (Willd.) Tindale; MO, YU—2. [3/20]; 3,000–4,000 ft.; a few mi. SW of Colonia Tovar (n).
206. *Thelypteris* (*Amauropelta*) *pteroidea* (Klotzsch) R. Tryon; CU, GH, MO, US, YU—3. [5/12]; 7,500 ft.; 9 mi. E of Colonia Tovar (n).
207. *Grammitis phlegmaria* (J. Smith) Proctor; YU. [2/4] 6/5/58; 7,000–8,000 ft.; Colonia Tovar (n).
208. *Grammitis alfarii* (J. D. Smith) C. Morton; MO, YU; these are ISOSYNTYPES of *Polypodium oligosorum* Mett. ex Kuhn, Linnaea 36: 132. 1869 (non Klotzsch, 1847). [4/21]; 7,000–8,000 ft.; highest mountains E of Colonia Tovar, also between Maracai and Choroni (n). Specimens at MO and YU mixed with *G. senilis* (Fée) C. Morton.
209. *Grammitis senilis* (Fée) C. Morton; MO, US, YU, cited by Copeland (1955) as *Ctenopteris senilis* (Fée) Copel. [9/20]; 8,000 ft.; highest mountains around Colonia Tovar (n).
210. *Grammitis cultrata* (Willd.) Proctor; US, YU. [9/20]; 7,000–8,000 ft.; highest mountains around Colonia Tovar (n).
211. *Grammitis truncicola* (Klotzsch) C. Morton; MO, US—2, YU. [13/20]; 7,000–8,000 ft.; highest mountains around Colonia Tovar and W to Valencia (n).

211β. *Grammitis* sp.; YU; cited by Eaton (1861) as *Polypodium truncicola* Klotzsch.

211, pt. *Grammitis trichomanoides* (Sw.) Ching; US.

212. *Grammitis concinna* A. R. Smith, nom. nov.; GH, MO, YU; ISOTYPES of *Polypodium concinnum* Mett. ex Kuhn, Linnaea 36: 132. 1869 (non Willd., 1810). 25/6/54 [1/8]; 7,500 ft.; high mountains E of Colonia Tovar (n).
213. *Grammitis chrysleri* (Copel.) Proctor; MO, US, YU. [10/20]; 6,500 ft.; Colonia Tovar (n).

213β. *Grammitis asplenifolia* (L.) Proctor; YU. 6/5/58 [1/8] (s).

214. *Polypodium moritzianum* Link; MO, US, YU—2. [9/30]; 6,000–7,000 ft.; Colonia Tovar (n).
215. *Grammitis fendleri* (Copel.) Lellinger; MO, US, YU; these are ISOSYNTYPES of *Polypodium radicale* Moritz ex Hieron., Bot. Jahrb. Syst. 34: 511. 1904 (non Baker, 1867). Cited by Copeland (1955). [7/20]; 6,000–8,000 ft.; Colonia Tovar (n).
216. *Grammitis longisetulosa* (Copel.) C. Morton; MO, US, YU. [3/20]; 6,000–7,000 ft.; Colonia Tovar (n).
217. *Grammitis firma* (J. Smith) C. Morton; MO, YU. [6/20]; 6,000–7,000 ft.; Colonia Tovar (n).
218. *Grammitis apiculata* (Kunze ex Klotzsch) Seymour; MO, US, YU; cited by Copeland (1955) as *Ctenopteris apiculata* (Kunze) Copel. [9/20]; 6,000–7,000 ft.; Colonia Tovar (n).
219. *Grammitis xiphopteroides* (Liebm.) A. R. Smith; MO, YU; cited by Copeland (1955) as *Ctenopteris pilosissima* (Mart. & Gal.) Copel. [14/20]; 6,000–8,000 ft.; Colonia Tovar (n).
220. *Polypodium consimile* Mett. var. *consimile*; B, GH, MO, US, YU; cited by Evans (1969). [6/20]; 6,500 ft.; Colonia Tovar (n).

220β. *Polypodium consimile* Mett. var. *consimile*; GH, MO, US, YU; cited by Evans (1969).

221. *Polypodium eurybasis* C. Chr. var. *eurybasis*; MO, YU; det. ME at MO. At YU there are also specimens of *P. plumula* Humb. & Bonpl. ex Willd. and *P. dispersum* A. M. Evans on the same sheet. [12/20]; 6,000–8,000 ft.; Colonia Tovar (n).

221β. *Polypodium eurybasis* C. Chr.; YU. [8/13] (s).

221γ. *Polypodium camptophyllarium* Fée var. *lachniferum* (Hieron.) A. M. Evans; YU. 19/9/55 [1/1] (s).

221δ. *Polypodium* sp.; YU; cited by Eaton (1861) as *P. paradiseae* Langsd. & Fischer.

222. *Niphidium mortonianum* Lellinger; MO, YU; det. DL. [6/18]; 6,000–8,000 ft.; Colonia Tovar (n).
223. *Niphidium crassifolium* (L.) Lellinger; MO, YU; det. DL. [2/11]; 3,500–4,000 ft.; a few mi. SW of Colonia Tovar (n).
224. *Campyloneurum angustifolium* (Sw.) Fée; YU; det. DL. 5/6/55 [1/5]; 7,000–8,000 ft.; highest mountains E of Colonia Tovar, also between Maracai and Choroni (n).

224. *Campyloneurum chlorolepis* Alston; YU. 29/1/57 [1/1] (s).

225. *Campyloneurum chlorolepis* Alston; MO, YU. 3/7/55 [1/6]; 5,000 ft.; a few mi. S of Colonia Tovar (n).
226. *Campyloneurum amphostenon* (Kunze ex Klotzsch)

Fée; MO, YU. [13/20]; 7,000–8,000 ft.; a few mi. W of Colonia Tovar (n).

ad 226. *Campyloneurum amphostenon* (Kunze ex Klotzsch) Fée; YU; det. DL. [2/1]; highest mountains (s).

227. *Campyloneurum phyllitidis* (L.) C. Presl; MO, YU. [6/21]; 2,000–4,000 ft.; a few mi. SW of Colonia Tovar, also between Caracas and La Guayra, Piedernales (n).

228. *Campyloneurum chrysopodum* (Klotzsch) Fée; det. DL; MO—2, YU; these are ISOTYPES of *Campyloneurum fendleri* T. Moore, Ind. Fil. 224. 1861. 5/10/54 [1/19]; 5,500 ft.; seaside of mountains north of Colonia Tovar (n).

228β. *Campyloneurum chrysopodum* (Klotzsch) Fée; det. DL; MO, YU. 7/3/57 [1/6] (s).

229. *Campyloneurum repens* (Aubl.) C. Presl; MO, YU; det. DL. [2/10]; 5,500 ft.; seaside of mountains N of Colonia Tovar (n).

230. *Campyloneurum repens* (Aubl.) C. Presl; MO, YU; det. DL. [5/20]; 6,000 ft.; seaside of mountains N of Colonia Tovar (n).

231. *Campyloneurum decurrens* (Raddi) C. Presl; YU; det. DL. [3/4]; 5,000 ft.; seaside of mountains N of Colonia Tovar (n).

232. *Thelypteris* (*Meniscium*) *salzmannii* (Fée) C. Morton; GH, K, MO, YU—2; cited by Maxon & Morton (1938) as *Dryopteris ensiformis* C. Chr., in part [= *Thelypteris ensiformis* (C. Chr.) R. Tryon]. [2/14]; 4,000 ft.; Piedernales, also seaside of mountains between Valencia and San Estevan (n). One collection at YU contains both species.

232β. *Thelypteris* (*Meniscium*) *arborescens* (Humb. & Bonpl. ex Willd.) C. Morton; YU. [?/1].

233. *Phanerophlebia juglandifolia* (Humb. & Bonpl. ex Willd.) J. Smith; US, YU. [5/23]; 5,500 ft.; Tuy River valley below Colonia Tovar (n).

234. *Polypodium fraxinifolium* Jacq.; YU. 18/10/54 [1/1]; 7,000 ft.; a few mi. W of Colonia Tovar (n).

235. *Polypodium fraxinifolium* Jacq.; MO, YU. 24/6/55 [1/20]; 7,000 ft.; high mountains around Colonia Tovar (n).

236. *Polypodium fraxinifolium* Jacq.; YU; cited by Eaton (1861). 28/9/55 [1/?]; 7,000 ft.; seaside of mountains N of Colonia Tovar (n).

237. *Polypodium* aff. *fraxinifolium* Jacq.; YU. With acicular, spreading rhizome scales. 19/12/54 [1/3]; 6,000 ft. a few mi. S of Colonia Tovar (n). "Rhizome very different from no. 236" (s).

238. *Polypodium dissimile* L.; YU. [2/3]; 4,000–5,000 ft.; seaside of mountain range between Maracai and Choroni (n).

238β. *Polypodium dissimile* L.; YU. [?/1]. Mounted on same sheet as 238.

239. *Polypodium* sp.; YU; cited by Eaton (1861) as *P. latipes* Langsd. & Fischer. 15/7/54 [1/?]; 4,000 ft.; a few mi. SW of Colonia Tovar (n).

240. *Polypodium sessilifolium* Desv.; MO, YU. [6/10]; 7,000–8,000 ft.; high mountains around Colonia Tovar (n).

241. *Polypodium* (*Phlebodium*) *pseudoaureum* Cav.; MO, YU—2. [10/18]; 5,000–7,000 ft.; a few mi. S and SW of Colonia Tovar (n).

242. *Polypodium fuscopetiolatum* A. R. Smith; MO—2, YU—2. [2/23]; 3,000–4,000 ft.; a few mi. S and SW of Colonia Tovar (n).

243. *Polypodium funckii* Mett.; US—2, YU. [2/14]; 8,000 ft.; highest mountains E of Colonia Tovar (n).

243?. *Polypodium* sp.; YU; cited by Eaton (1861) as *P. loriceum* L.

244. *Polypodium lasiopus* Klotzsch; MO, US, YU. [10/21]; 6,000–7,000 ft.; a few mi. S of Colonia Tovar (n).

245. *Polypodium remotum* Desv.; MO, US, YU. [6/17]; 6,200 ft.; Colonia Tovar (n).

246. *Polypodium buchtienii* Christ & Rosenstock; YU. [2/4]; 7,000–8,000 ft.; high mountains around Colonia Tovar (n).

247. *Polypodium steirolepis* C. Chr.; MO, NY, US, YU. ISOTYPES of *P. nigripes* Hook., Sp. Fil. 5: 17. 1863 (non Hassk., 1844). [5/17]; 3,500 ft.; a few mi. S and SW of Colonia Tovar (n).

248. *Microgramma vacciniifolia* (Langsd. & Fischer) Copel.; MO, YU. [2/6]; 1,000 ft.; seaside of mountains near San Estevan, also between Caracas and La Guayra (n).

249. *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf.; YU. 27/8/55 [1/4]; 6,500 ft.; a few mi. W of Colonia Tovar (n).

250. *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf.; MO, YU. [14/23]; 7,000 ft.; Colonia Tovar (n).

251. ×*Pleopodium leucosporum* (Klotzsch) Mickel & Beitel [*Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf. × *Polypodium thyssanolepis* A. Braun ex Klotzsch]; MO, US, YU. 23/2/54 [1/?]; 4,000 ft.; mountains N of Caracas (n).

252. *Polypodium thyssanolepis* A. Braun ex Klotzsch; MO, YU. [4/20]; 3,000–4,000 ft.; valley of Macarao W of Caracas (n).

253. *Polypodium polypodioides* (L.) Watt var. *burchellii* (Baker) Weath.; MO, YU. [6/20]; 3,000–4,000 ft.; a few mi. S and SW of Colonia Tovar (n).

254. *Polypodium ursipes* Moritz ex C. Chr.; MO, US; these are ISOSYNTYPES of *P. ambiguum* Mett. ex Kuhn, Linnaea 36: 134. 1869 (non Desv., 1827). [3/?]; 8,000 ft.; highest mountains E of Colonia Tovar (n).

255. *Grammitis jamesonii* (Hook.) C. Morton; US, YU. 7,000–8,000 ft.; Colonia Tovar (n); [5/20] (s). On same sheet as *356* at YU.

256. *Grammitis leptopoda* (C. H. Wright) Copel.; MO, US. [2/?]; 7,000 ft.; Colonia Tovar (n).

257. *Grammitis jungermannioides* (Klotzsch) Ching; YU; cited by Eaton (1861) as *Polypodium jungermannioides* Klotzsch. [2/?]; 6,800 ft.; Colonia Tovar (n).

258. *Vittaria graminifolia* Kaulf.; MO, YU. [9/20]; 6,700 ft.; Colonia Tovar (n).

258. *Selaginella viticulosa* Klotzsch; NY; cited by Alston et al. (1981); erroneous citation?

259. *Vittaria moritziana* Mett. + *V. stipitata* Kunze; MO, YU. [6/19]; 6,000–7,000 ft.; Colonia Tovar (n).

259β. *Vittaria gardneriana* Fée; MO, YU. 6,000 ft. (n); [2/17] (s).

260. *Vittaria remota* Fée; MO, YU. [2/20]; 7,000 ft.; Colonia Tovar (n).

261. *Polybotrya serratifolia* (Fée) Klotzsch; MO—2, YU; det. RM. [5/17]; 6,000 ft.; Colonia Tovar (n).

262. *Polybotrya canaliculata* Klotzsch; MO—2, YU—

3; det. RM. [2/10 + 9]; 5,000 ft.; seaside of mountain range opposite the Colony [Tovar] (n).

263. *Elaphoglossum peltatum* (Sw.) Urban forma *flabellatum* (Humb. & Bonpl. ex Willd.) Mickel; MO, YU. [4/19]; 6,000 ft.; River Tuy below Colony (n).
264. *Elaphoglossum erinaceum* (Fée) T. Moore; MO, YU; det. JM. [6/5]; 5,000–6,000 ft.; Tuy valley below Colonia [Tovar] (n).
265. *Elaphoglossum eximium* (Mett.) Christ; GH, MO—2, PH, YU; these are ISOSYNTYPES of *Acrostichum reichenbachii* Moritz ex Kuhn, Linnaea 36: 42. 1869. [3/20]; 7,200 ft.; headwaters of San Carlos River (n).
266. *Elaphoglossum moritzianum* (Klotzsch) T. Moore; GH, MO, NY, PH, US, YU; det. JM. [6/20]; 5,900 ft.; valley of the Tuy River, below Colonia [Tovar] on rocks (n).
267. *Elaphoglossum piloselloides* (C. Presl) T. Moore; GH, MO, US, YU; det. JM. 19/9/55 [1/17]; 6,600 ft., San Carlos valley in a cave in rocks in the savannah (n).
268. *Elaphoglossum hieracioides* Mickel; HOLOTYPE, US; ISOTYPES, GH, MO, YU. [9/20]; 6,500 ft.; San Carlos valley (n).
269. *Elaphoglossum meridense* (Klotzsch) T. Moore; MO, NY, YU; det. JM. [9/20]; 6,300 ft.; mountain range S of Colonia [Tovar] (n).

269β. *Elaphoglossum deorsum* (Karsten) Vareschi; MO; det. JM.

270. *Elaphoglossum bellermannianum* (Klotzsch) T. Moore; MO, NY, US, YU; det. JM. [7/21]; 6,500–7,000 ft.; mountain range S of Colonia [Tovar].
271. *Elaphoglossum cuspidatum* (Willd.) T. Moore; MO, NY, YU; det. JM. [4/20]; 6,300 ft.; mountains S of Colonia [Tovar] (n).
272. *Elaphoglossum tenuiculum* (Fée) T. Moore; P; this is the HOLOTYPE of *Acrostichum tenuiculum* Fée, Mém. Fam. Foug. 10: 6, t. 2, f. 2. 1865. ISOTYPE, YU. [2/18]; 6,600 ft.; 7 mi. SW of Colonia [Tovar] between rocks in savannahs (n).
273. *Elaphoglossum tectum* (Humb. & Bonpl. ex Willd.) T. Moore; MO, YU; det. JM. [5/23]; 6,500 ft.; Colonia Tovar (n).

ad 273. *Elaphoglossum tectum* (Humb. & Bonpl. ex Willd.) T. Moore; YU. 3/7/55 [1/1] (s).

274. *Elaphoglossum tectum* (Humb. & Bonpl. ex Willd.) T. Moore; YU. 27/8/55 [1/3]; 6,600 ft.; 7 mi. SW of Colonia [Tovar] (n).
275. *Elaphoglossum succubus* Mickel; HOLOTYPE, NY; ISOTYPES, MO, US. [5/21]; 6,000 ft.; Maya valley near Colonia [Tovar] (n).

275α. *Elaphoglossum affine* (Mart. & Gal.) T. Moore; MO, not seen; cited by Mickel in Smith (1985).

276. *Elaphoglossum huacssaro* (Ruiz) Christ; MO, US; det. JM. [3/?]; 6,000 ft.; mountain range S of Colonia [Tovar], in wet ground full of springs (n).
277. *Elaphoglossum* sp.; YU; cited by Eaton (1861) as *Acrostichum leptophyllum* Fée. 23/8/55 [1/?]; 7,500 ft.; Lagunassa, 12 mi. E of Colonia [Tovar] (n).
278. *Elaphoglossum chrysopogon* Mickel; MO, YU; det. JM. [2/14]; 6,900 ft.; 6 mi. SE of Colonia [Tovar] (n).
279. *Elaphoglossum chrysopogon* Mickel; HOLOTYPE, NY; ISOTYPE, NY. [3/8]; 6,700 ft.; Lagunita, 6 mi. SW of Colonia [Tovar], between rocks (n).
280. *Elaphoglossum burchellii* (Baker) C. Chr.; MO, YU; det. JM. these are ISOSYNTYPES of *Elaphoglossum xanthoneuron* Christ. [5/20]; 6,300 ft.; mountain range S of Colonia [Tovar] (n).
281. *Elaphoglossum eximium* (Mett.) Christ; MO, YU; det. JM. [4/20]; 6,800 ft.; headwaters of San Carlos River, 3 mi. W of Colonia [Tovar].
282. *Elaphoglossum brachyneuron* (Fée) J. Smith; GH, MO, NY, US, YU; det. JM. [2/20]; 6,500 ft.; mountain range S of Colonia [Tovar] (n).
283. *Elaphoglossum ambiguum* (Mett. ex Christ) Alston; MO, US, YU—2; these are ISOTYPES of *Acrostichum ambiguum* Mett. ex Christ, Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. 36: 60. 1899. [5/20]; 6,400 ft.; Colonia [Tovar] (n).
284. *Elaphoglossum ambiguum* (Mett. ex Christ) Alston; MO, YU—2; det. JM. 28/9/54 [1/11]; 6,000–7,000 ft.; seaside of mountain range near Colonia [Tovar] (n).
285. *Elaphoglossum lingua* (C. Presl) Brackenr.; MO, US, YU; det. JM. [2/6]; 6,300 ft.; mountain range S of Colonia [Tovar] (n).
286. *Elaphoglossum lloense* (Hook.) T. Moore; MO, NY, YU; det. JM. [7/20]; 6,300 ft.; mountain range S of Colonia [Tovar] (n).
287. *Elaphoglossum macrophyllum* (Klotzsch) Christ; MO, NY, YU; det. JM. [3/12], 6,300 ft.; mountain range S of Colonia [Tovar].
288. *Elaphoglossum sellowianum* (Klotzsch ex Kuhn) C. Chr.; YU. [3/1]; 6,300 ft.; mountain range S of Colonia [Tovar] (n).
289. Not located, most likely an *Elaphoglossum*. 27/9/55 [1/?]; 6,800 ft.; Colonia Tovar, plant easily drying, somewhat viscose, sticking to the paper, sterile (n).
290. *Elaphoglossum hoffmannii* (Mett. ex Kuhn) Christ; BM, MO, NY, US, YU; these are ISOSYNTYPES of *Acrostichum attenuatum* Kunze ex Kuhn, Linnaea 36: 56. 1869 (non Fée, 1853). [4/20]; 6,300 ft.; mountains S of Colonia [Tovar], on trunks of trees and upon the ground (n).
291. *Elaphoglossum sporadolepis* (Kunze ex Kuhn) C. Chr.; YU. 2/10/54 [1/1]; 6,300 ft.; mountains S of Colonia [Tovar] (n).
292. *Elaphoglossum tovarense* (Moritz ex Kuhn) T. Moore; BM, MO, NY, US, YU; these are ISOSYNTYPES of *Acrostichum tovarense* Moritz ex Kuhn, Linnaea 36: 60. 1869. [4/20]; 6,300 ft.; mountain range S of Colonia [Tovar], upon the ground (n).
293. *Elaphoglossum sporadolepis* (Kunze ex Kuhn) C. Chr.; MO—2, YU; these are ISOSYNTYPES of *Acrostichum corpulentum* Kunze ex Kuhn, Linnaea 36: 61. 1869. [3/20]; 6,300 ft.; mountain range S of Colonia [Tovar] (n).

293. *Elaphoglossum andicola* (Fée) T. Moore; NY; cited by Mickel in Smith (1985).

294. *Elaphoglossum sporadolepis* (Kunze ex Kuhn) C. Chr.; MO, NY, US, YU; these are ISOLECTOTYPES of *Acrostichum sporadolepis* Kunze ex Kuhn, Linnaea 36: 59. 1869. [5/21]; 6,300 ft.; mountain range S of Colonia [Tovar] (n).

294, pt. *Elaphoglossum sporadolepis* (Kunze ex Kuhn) C. Chr.; B, YU; the former is the HOLOTYPE of *Acrostichum compactum* Mett. ex Kuhn, Linnaea 36: 59. 1869; cited by Mickel in Smith (1985).

295. *Elaphoglossum sellowianum* (Klotzsch ex Kuhn)

C. Chr.; US, YU; these are ISOSYNTYPES of *Acrostichum sellowianum* Klotzsch ex Kuhn, Linnaea 36: 52. 1869. [10/22]; 6,400 ft.; Colonia Tovar (n).

295α, pt. *Elaphoglossum tenuiculum* (Fée) T. Moore; MO, not seen; cited by Mickel in Smith (1985).

295β. *Elaphoglossum sellowianum* (Klotzsch ex Kuhn) Christ; YU; this is an ISOSYNTYPE of *Acrostichum sellowianum* Klotzsch ex Kuhn, Linnaea 36: 52. 1869. [4/16] (s).

296. *Elaphoglossum sporadolepis* (Kunze ex Kuhn) C. Chr.; MO, YU; these are ISOSYNTYPES of *Acrostichum sporadolepis* Kunze ex Kuhn, Linnaea 36: 59. 1869; det. JM. [3/8]; 6,300 ft.; mountains S of Colonia [Tovar].

297. *Pityrogramma trifoliata* (L.) R. Tryon; MO, YU. [2/19]; 3,000–4,000 ft.; warmer parts of river valleys, not far from the water (n).

298. *Pityrogramma calomelanos* (L.) Link; MO, US; these are ISOTYPES of *P. calomelanos* var. *venezuelae* Domin., Rozpr. Ceské Akad. Věd, Tř. 2, Vědy Mat. Přír., II. 51(18): 12. 1941. [2/?]; 3,000 ft.; between Caracas and La Guayra (n).

299. *Pityrogramma tartarea* (Cav.) Maxon; MO, YU—3. [10/20]; 6,300 ft., Colonia Tovar (n).

300. *Eriosorus flexuosus* (H.B.K.) Copel. var. *flexuosus*; G, GH, K, MO, P, US, YU; cited by A. Tryon (1970). [3/13]; 7,400 ft.; 12 mi. E of Colonia [Tovar] (n).

301. *Eriosorus hirtus* (H.B.K.) Copel. var. *hirtus*; B. BM, F, G, GH, K, MO—2, NY, YU—2; cited by A. Tryon (1970). [10/20]; 7,000 ft.; a few mi. W of Colonia [Tovar].

302. *Hemionitis rufa* (L.) Sw.; YU; cited by Eaton (1861) as *Gymnogramme rufa* Desv. 2,500 ft.; Piedernales, a little S of the lake of Valencia (n).

303. *Hemionitis palmata* L.; YU. [2/18]; 2,500–3,000 ft.; Piedernales, a little S of the lake of Valencia, [also] between La Guayra and Caracas (n).

304. *Antrophyum lineatum* (Sw.) Kaulf.; MO, YU. [12/20]; 6,000–7,000 ft.; Colonia Tovar (n).

305. *Antrophyum cajenense* (Desv.) Sprengel; MO, YU. Mixed on same sheet with *Antrophyum brasilianum* (Desv.) C. Chr. at YU. [3/23]; 6,000–7,000 ft.; Colonia Tovar, near Tuy River (n).

306. *Thelypteris* (*Amauropelta*) *aspidioides* (Willd.) R. Tryon; G, MO, US, YU. [4/13]; 5,600 ft.; Tuy River below Colonia [Tovar]; San Carlos River (n).

307. *Thelypteris* (*Amauropelta*) *rupestris* (Klotzsch) Reed; GH, MO, US. [2/?]; Colonia Tovar (n).

308. *Blechnum fragile* (Liebm.) C. Morton & Lellinger, vel aff.; MO. [3/?]; 7,800 ft.; 12 mi. E of Colonia [Tovar] (n).

309. *Blechnum divergens* (Kunze) Mett.; MO. [3/?]; 6,000–7,000 ft.; Colonia Tovar (n).

310. *Blechnum lehmannii* Hieron.; MO. [3/?]; 6,000–7,000 ft.; Colonia Tovar (n).

311. *Bolbitis serratifolia* (Mertens ex Kaulf.) Schott; BM, BR, G, K, MO, P, US, YU; cited by Hennipman (1977). [2/20]; 4,000 ft.; valley of San Carlos, SW of Colonia [Tovar] (n).

312. *Ophioglossum reticulatum* L.; MO. [3/?]; 6,500 ft.; several mi. SW of Colonia [Tovar].

313. *Lycopodium thyoides* Humb. & Bonpl. ex Willd.; MO, YU—2. [4/22]; 6,500–7,500 ft.; a few mi. S of Colonia Tovar (n).

314. *Lycopodium clavatum* L.; MO, YU. [4/12]; 7,000 ft.; a few mi. W of Colonia Tovar (n).

314β. *Lycopodium clavatum* L.; YU. 19/7/56 [1/2]; 7,000 ft. (s).

315. *Lycopodium alopecuroides* L.; YU. [2/17]; 6,000 ft.; a few mi. S of Colonia Tovar, wet places in the savannah (n).

316. *Lycopodium reflexum* Lam.; MO, YU. [7/20]; 7,000 ft.; a few mi. W of Colonia Tovar (n).

317. *Lycopodium acerosum* Sw.; YU. [2/7]; 3,500 ft.; valley a few mi. SW of Colonia Tovar (n).

318. *Lycopodium cernuum* L.; YU. [2/1]; 7,500 ft.; highest mountains E of Colonia Tovar (n).

319. *Lycopodium taxifolium* Sw.; MO, YU; det. BO. [6/17]; 6,500–8,000 ft.; around Colonia Tovar (n).

320. *Lycopodium myrsinites* Lam.; MO, YU; det. BO. [3/20]; 8,000 ft.; highest mountains E of Colonia Tovar (n).

321. *Selaginella pallescens* (C. Presl) Spring in Martius; MO, NY, YU. [4/22]; 2,000–4,000 ft.; valleys SW of Colonia Tovar, also La Victoria (n).

321β. *Selaginella pallescens* (C. Presl) Spring; YU. 23/8/56 [1/1]; 2,000 ft.; [La] Victoria (s).

322. *Selaginella viticulosa* Klotzsch; MO, YU. 16/8/55 [1/18]; 2,500 ft.; seaside of mountains between Caracas and La Guayra (n).

322. *Selaginella cavifolia* A. Braun; BM; this is an ISOSYNTYPE of *S. moritziana* var. *elongata* A. Braun, Ann. Sci. Nat. Bot., V. 3: 285. 1865; cited by Alston et al. (1981).

323. *Selaginella cavifolia* A. Braun; MO, YU; these are ISOSYNTYPES of *S. moritziana* var. *elongata* A. Braun, Ann. Sci. Nat. Bot., V. 3: 285. 1865. [4/17]; 7,000 ft.; high mountains around Colonia Tovar (n).

324. *Selaginella flagellata* Spring; BM, MO, YU; these are ISOSYNTYPES of *S. ambigua* A. Braun, Ann. Sci. Nat. Bot., V. 3: 286. 1865; cited by Alston et al. (1981). [2/22]; 2,300 ft.; La Victoria and Piedernales (n).

324, pt. *Selaginella cladorrhizans* A. Braun, Ann. Sci. Nat. Bot., V. 3: 282. 1865; SYNTYPES, B, BM, YU; cited by Alston et al. (1981). At YU, this species and *S. flagellata* are mixed on the same sheet.

325. *Plagiogyria semicordata* (C. Presl) Christ; MO, YU. 23/8/55 [1/18]; 8,000 ft.; highest mountains, 12 mi. E of Colonia [Tovar] (n).

326. *Asplenium oligophyllum* Kaulf.; MO, US, YU. 3,500 ft.; a few mi. SW of Colonia Tovar, river bottom (n); 17/5/55 [1/26] (s).

327. *Hymenophyllum* (*Sphaerocionium*) *trichophyllum* H.B.K.; GH; YU cited by Morton (1947). 25/8/56 [1/20]; 8,000 ft.; 10 mi. E of Colonia [Tovar], highest mountains (n); Lagunassa (s).

328. *Hymenophyllum* (*Sphaerocionium*) *lanatum* Fée; YU. 12/7/56 [1/8]; 7,500 ft.; a few mi. W of Colonia [Tovar] (n).

ad 328. *Hymenophyllum* (*Sphaerocionium*) *lanatum* Fée; YU. 12/7/56 [1/10]; high mountains, La Victoria pass (s).

329. *Trichomanes* (*Acarpacrium*) *polypodioides* L.; MO, US, YU—2. [2/20]; 6,500–7,000 ft.; seaside of mountains north of Colonia Tovar (n).

330. *Lastreopsis exculta* (Mett.) Tindale; MO. 28/6/56, 8/1/57 [2/?]; 6,000 ft.; Colonia Tovar (n).

331. *Asplenium salicifolium* L.; YU—2. 12/7/56 [1/?]; 6,000–7,000 ft.; Colonia Tovar (n).
331β. *Asplenium auriculatum* Sw.; YU. 22/4/58 [1/?] (s).
332. *Asplenium serra* Langsd. & Fischer; YU—2. [?/2]; 7,000–8,000 ft.; Colonia Tovar (n). "Has been mixed up with no. 155, but pinnae very different; also the meshes of veinlets in the scales of rhizome smaller" (s).
333. *Asplenium serra* Langsd. & Fischer; YU. 22/1/56 [1/3]; 7,000 ft.; seaside of mountains N of Colonia [Tovar] (n).
334. *Diplazium macrophyllum* Desv.; YU—2. [2/1]; 6,000 ft.; seaside of mountains N of Colonia [Tovar], also between Valencia and San Estevan (n).
335. *Lomariopsis fendleri* D. Eaton, Mem. Amer. Acad. Arts, n.s. 8: 195. 1861; SYNTYPES, YU—3 sheets, collected on two different dates; ISOSYNTYPE, K. [2/16]; 6,000 ft.; seaside of mountain range between Colonia [Tovar] and Chichiribichi (n).
ad 335. *Lomariopsis fendleri* D. Eaton; YU. 22/1/56 [1/?] (s).
336. *Bolbitis portoricensis* (Sprengel) Hennipman; MO, YU—2; cited by Hennipman (1977). One collection at YU mixed with juveniles of *Pteris altissima* Poiret in Lam. 29/1/57 [1/13]; 3,500 ft.; seaside of mountain range between Maracai and Choroni (n).
337. Not located, *Lycopodium* (n). 17/7/56 [1/?]; 7,500 ft.; high mountains E of Colonia Tovar, upon trees (n).
338. *Grammitis pilosissima* (Mart. & Gal.) C. Morton; YU. 12/7/56 [1/1]; 7,500 ft.; Colonia Tovar (n).
339. Not located, no data in notebook.
340. *Blechnum schomburgkii* (Klotzsch) C. Chr.; MO. [3/7]; 7,000–8,000 ft.; Petaquire mountains, also highest mountains E of Colonia [Tovar] (n).
341. *Polypodium fuscopetiolatum* A. R. Smith; YU. 26/5/54 [1/1]; 3,500 ft.; Biscaina, S of Colonia [Tovar] (n).
342. *Ophioglossum nudicaule* L. f.; MO. 5,000 ft.; a few mi. S of Colonia [Tovar], beneath low shrubs at margin of woods (n).
343. *Polypodium bolivari* Sota; YU. 3/9/56 [1/3]; 5,000 ft.; a few mi. S of Colonia Tovar (n); near Maya (s).
344. *Cyathea villosa* Willd.; B; this is the HOLOTYPE of *Alsophila vernicosa* Mett. ex Kuhn, Linnaea 36: 155. 1869; ISOTYPES, GH, MO, YU; cited by Barrington (1978) as *Trichipteris villosa* (Willd.) R. Tryon. 21/8/56 [1/6]; 5,800 ft.; a few mi. S of Colonia [Tovar], in savannahs (n).
345. Not located. 2/9/56; 6,000 ft.; Colonia Tovar (n).
346. Not located. 5,000 ft.; beneath low shrubs, margin of woods, Maya near Colonia [Tovar] (n).
347. *Lycopodium* cf. *pendulinum* Hook.; MO, YU. 21/8/56 [1/21]; 6,000 ft.; a few mi. S of Colonia Tovar in wet places in the savannah (n).
348. *Grammitis* cf. *senilis* (Fée) C. Morton; MO. [2/?]; 7,000 ft.; seaside of mountain range between Maracai and Choroni (n).
349. *Grammitis* aff. *subtilis* (Kunze ex Klotzsch) C. Morton; MO, YU. 12/12/56 [1/7]; 6,500 ft.; seaside of mountain range between Maracai and Choroni (n).
350. *Grammitis* sp.; YU; cited by Eaton (1861) as *Polypodium pendulum* Sw. 12/12/56; 6,500 ft.; seaside of mountain range between Maracai and Choroni (n).
351. *Grammitis asplenifolia* (L.) Proctor?; YU. Juvenile. 12/12/56 [1/1]; 6,000 ft.; seaside of mountain range between Maracai and Choroni (n).
352. *Polypodium triseriale* Sw.; YU. 25/1/55 [1/1]; 3,500 ft.; Piedernales near Güigüe (n).
353. *Polypodium loriceum* L.; MO, YU—2. [2/3]; 6,000 ft.; seaside of mountains between Maracai and Choroni (n).
354. *Microgramma reptans* (Cav.) A. R. Smith; MO, YU. [2/11] 2,500 ft.; seaside of mountains between Maracai and Choroni (n).
355. *Cochlidium rostratum* (Hook.) Maxon ex C. Chr.; MO. [2/?]; 6,000 ft.; in crossing the mountains from Maracai towards Choroni (n).
356. *Cochlidium serrulatum* (Sw.) L. E. Bishop; MO, YU. [2/20]; 6,000–7,000 ft.; seaside of mountains between Maracai and Choroni, and between Valencia and San Estevan (n).
357?. *Pityrogramma chrysoconia* (Desv.) Maxon ex Domin; YU. [4/?]; 6,000 ft.; seaside of mountain range between Maracai and Choroni (n).
358. *Eriosorus hirtus* (H.B.K.) Copel. var. *hirtus*; GH, YU; cited by A. Tryon (1970). [3/1]; 6,000–7,000 ft.; a few mi. W of Colonia [Tovar] (n).
359. *Eriosorus hispidulus* (Kunze) Vareschi var. *hispidulus*; K, YU; cited by A. Tryon (1970). 12/12/56 [1/3]; 6,000 ft.; seaside of mountain range between Maracai and Choroni (n).
360. *Thelypteris* (*Amauropelta*) *aspidioides* (Willd.) R. Tryon; YU. 12/12/56 [1/2]; 2,500 ft.; seaside of mountain range between Maracai and Choroni (n).
361. *Elaphoglossum peltatum* (Sw.) Urban; MO, YU. [3/11]; 7,000 ft.; seaside of mountain range between Maracai and Choroni (n).
362. *Elaphoglossum pusillum* (Mett. ex Kuhn) C. Chr.; GH, NY, PH; these are ISOSYNTYPES of *Acrostichum fraseri* Mett. ex Kuhn, Linnaea 36: 43. 1869. 12/12/56 [1/?]; 2,000 ft.; near Esmeralda above Choroni (n).
363. *Elaphoglossum crinitum* (L.) Christ; YU. [2/2]; 2,500 ft.; seaside of mountain range between Maracai and Choroni (n).
364. *Adiantum tetraphyllum* Humb. & Bonpl. ex Willd.; YU. 12/12/56 [1/3]; 2,000 ft.; seaside of mountain range between Maracai and Choroni (n).
364. *Elaphoglossum pusillum* (Mett. ex Kuhn) C. Chr.; MO; det. JM.
365. *Pteris altissima* Poiret in Lam.; YU. 12/12/56 [1/1]; 2,500 ft.; seaside of mountain range between Maracai and Choroni (n).
366. *Doryopteris sagittifolia* (Raddi) J. Smith; MO, YU, [2/19]; 2,500 ft.; seaside of mountain range between Maracai and Choroni (n).
367. *Asplenium cirrhatum* Rich. ex Willd.; YU. [2/1]; 4,000 ft.; seaside of mountain range between Maracai and Choroni (n).
368. *Asplenium tenerrimum* Mett. ex Kuhn, Linnaea 36: 97. 1869; ISOTYPES, MO, NY, US; cited by Morton & Lellinger (1966) as *A. cuspidatum* Lam. var. *tenerrimum* (Mett. ex Kuhn) C. Morton & Lellinger. 21/11/56 [1/?]; 2,300 ft.; near La Victoria (n).

369. *Diplazium expansum* Willd.; YU—2. 12/12/56 [1/1]; 4,000 ft.; seaside of mountain range between Maracai and Choroni (n).
370. *Nephrolepis rivularis* (Vahl) Mett. ex Krug; MO, YU. 29/1/57 [1/7]; 5,000 ft.; seaside of mountain range between Maracai and Choroni (n).
371. *Thelypteris* (*Steiropteris*) *praetervisa* (Kuhn) A. R. Smith; K, YU; these are ISOTYPES of *Aspidium praetervisum* Kuhn, Linnaea 36: 111. 1869; cited by Smith (1980). 12/12/56 [1/2]; 2,500 ft.; seaside of mountains between Maracai and Choroni (n).
372. *Thelypteris* (*Steiropteris*) *fendleri* (D. Eaton) Reed; YU—2; HOLOTYPE of *Aspidium fendleri* D. Eaton, Mem. Amer. Acad. Arts, n.s. 8: 210. 1861; ISOTYPES, B, GH, K; cited by Smith (1980). [2/9]; 2,500 ft.; seaside of mountains between Maracai and Choroni (n).
373. *Thelypteris* (*Steiropteris*) *decussata* (L.) Proctor var. *decussata*; MO, YU—2; cited by Smith (1980). [2/8]; 3,000 ft.; seaside of mountains between Choroni and Maracai, also between Valencia and San Estevan (n).
374. *Dennstaedtia obtusifolia* (Willd.) T. Moore; YU. 12/12/56 [1/4]; 6,000 ft.; seaside of mountain range between Maracai and Choroni (n).
375. *Saccoloma inaequale* (Kunze) Mett.; MO, YU—2. [2/9]; 5,000 ft.; seaside of mountain range between Maracai and Choroni (n).
376. *Saccoloma elegans* Kaulf.; YU. 12/12/56 [1/2]; 3,000 ft.; seaside of mountain range between Maracai and Choroni (n).
377. *Lindsaea stricta* (Sw.) Dryander var. *stricta*; B, BR, C, F, G, GH, GOET, K, MO, PH, US, YU; cited by Kramer (1957). [2/22]; 4,000 ft.; seaside of mountain range between Maracai and Choroni (n).
378. *Lindsaea lancea* (L.) Beddome var. *lancea*; MO, YU; this number cited by Kramer (1957) as this species and also as *L. stricta* (Sw.) Dryander var. *stricta*. 12/12/56 [1/18]; 4,500 ft.; seaside of mountain range between Maracai and Choroni (n).

378, pt. *Lindsaea stricta* (Sw.) Dryander var. *stricta*; YU. This sheet is, in part, juvenile material of some other species of *Lindsaea*.

379. = 63*β* (n & s), which is *Lindsaea klotzschiana* Moritz in Ettingshausen. Without locality data in notebook.
380. *Lindsaea stricta* (Sw.) Dryander var. *stricta*; cited by Kramer (1957). 12/12/56 [1/6]; 5,000 ft.; seaside of mountain range between Maracai and Choroni (n).
380. *Lindsaea klotzschiana* Moritz in Ettingshausen; YU. 12/12/56 [1/?]; 5,000 ft. (s).
381. *Grammitis taxifolia* (L.) Proctor; YU. 30/1/58 [1/1]; 6,500 ft.; seaside of mountains between Agua Blanca and Cumbote (n).
382. *Cyathea gibbosa* (Klotzsch) Domin; YU. 12/12/56 [1/1]; 5,000 ft.; seaside of mountain range between Maracai and Choroni (n).
383. *Cyathea senilis* (Klotzsch) Domin; YU—2. [2/3]; 6,500 ft.; seaside of mountain range between Maracai and Choroni and further west (n).
384. Not located. 29/1/57 [1/?]; 6,000 ft.; seaside of mountains between Maracai and Choroni (n).
385. *Cnemidaria horrida* (L.) C. Presl; MO, YU; cited by Stolze (1974). [3/13]; 2,000–3,000 ft.; seaside of mountain range between Maracai and Choroni, also between Valencia and San Estevan (n).
386. *Cnemidaria karsteniana* (Klotzsch) R. Tryon; MO; cited by Stolze (1974). [3/8]; 5,000 ft.; seaside of mountain range between Maracai and Choroni and further west (n).
387. *Hymenophyllum* (*Sphaerocionium*) *lanatum* Fée; GH, MO, YU; cited by Morton (1947). 12/12/56 [1/11]; 6,000 ft.; seaside of mountains between Maracai and Choroni (n).
388. *Trichomanes* (*Achomanes*) *crispum* L.; YU. [2/21]; 4,000–5,000 ft.; seaside of mountains between Maracai and Choroni (n).
388*β*. *Trichomanes* (*Achomanes*) sp., undescribed? (same as 389); YU. 29/1/57 [1/2] (s).
389. *Trichomanes* (*Achomanes*) sp., undescribed?; MO, YU. [3/10]; 5,000 ft.; seaside of mountains between Maracai and Choroni (n).
390. *Trichomanes* (*Neurophyllum*) *pinnatum* Hedwig; MO, YU. [2/11]; 4,000 ft.; seaside of mountains between Maracai and Choroni (n).
391. *Elaphoglossum glabellum* J. Smith; YU. [2/4]; 7,000 ft.; in crossing mountains from Maracai to Choroni (n).
392. Not located. 12/12/54 [1/?]; 6,500 ft.; Colonia Tovar (n).
393. *Hymenophyllum* (*Mecodium*) *apiculatum* Mett. ex Kuhn; YU. 12/12/56 [1/1]; 6,000 ft.; seaside of mountain range between Maracai and Choroni (n).
394. *Hymenophyllum* (*Mecodium*) *polyanthos* (Sw.) Sw.; YU. 12/12/56 [1/3]; 6,500 ft.; seaside of mountain range between Maracai and Choroni (n).
395. *Trichomanes* (*Lacosteopsis*) *capillaceum* L.; YU. 6,500 ft.; Colonia Tovar, on rocks near a rivulet (n); 4,000 ft.; (s).
396. *Schizaea elegans* (Vahl) Sw.; MO. 12/12/56 [1/?]; 4,500 ft.; seaside of mountain range between Maracai and Choroni (n).
397. *Selaginella diffusa* (C. Presl) Spring; MO, YU. 12/12/56 [1/12]; 4,000 ft.; seaside of mountain range between Maracai and Choroni (n).
398. *Lycopodium* (n), not located. 12/12/56 [1/?]; 5,000 ft.; seaside of mountain range between Maracai and Choroni (n).
399. *Lycopodium cernuum* L.; YU. 12/12/56 [1/3]; 5,500 ft.; seaside of mountains between Maracai and Choroni (n).
399*β*. *Lycopodium cernuum* L.; YU, mounted on same sheet as *399*. 12/12/56 [1/1]; 6,000 ft.; mountains between Maracai and Choroni on dry south side (s).
400. *Lycopodium thyoides* Humb. & Bonpl. ex Willd.; YU. 12/12/56 [1/1]; 6,500 ft.; seaside of mountains between Maracai and Choroni (n).
401. Not located. 6/1/57 [1/?]; highest mountains E of Colonia Tovar (n).
402. *Selaginella porphyrospora* A. Braun; YU. 12/12/56 [1/3]; 5,000 ft.; seaside of mountains between Maracai and Choroni (n).
403. *Selaginella flagellata* Spring; YU. 12/12/56 [1/4]; 3,000 ft.; seaside of mountains between Maracai and Choroni (n).
404. *Cheilanthes* sp.; YU; cited by Eaton (1861) as *Pellaea decomposita* Hook. [could be *C. marginata* H.B.K.]. 7/3/57 [1/?]; 3,500 ft.; seaside of

mountain range between Valencia and San Estevan (n).

405. *Athyrium filix-femina* (L.) Roth; MO, YU. 6/1/57 [1/22]; 8,000 ft.; 12 mi. E of Colonia Tovar, highest mountains (n).
406. *Grammitis moniliformis* (Lagasca ex Sw.) Kaulf.; YU; cited by Eaton (1861). 29/1/57 [1/?]; 7,000 ft.; seaside of mountains between Maracai and Choroni (n).
407. *Polypodium hygrometricum* Splitg.; YU. 28/1/57 [1/1]; 3,000 ft.; seaside of mountains between Maracai and Choroni (n).
408. *Bolbitis hemiotis* (Maxon) Ching; YU. 29/1/57 [1/5]; 4,000 ft.; seaside of mountains between Maracai and Choroni (n).
409. *Campyloneurum occultum* (Christ) L. D. Gómez; YU. 29/1/57 [1/3]; 6,000 ft.; seaside of mountains between Maracai and Choroni (n).
410. *Campyloneurum magnificum* T. Moore; YU—4 sheets, collected on two different dates; these are SYNTYPES of *Polypodium fendleri* D. Eaton, Mem. Amer. Acad. Arts, n.s. 8: 199. 1861; ISOSYNTYPES, MO—2. [2/13]; 4,000 ft.; seaside of mountains between Petaquire and the sea (n).
411. *Asplenium* sp.; YU; cited by Eaton (1861) as *A. salicifolium* L. 12/2/58 [1/?]; 4,000 ft.; seaside of mountains between Petaquire and Cariaca (n).
412. *Tectaria plantaginea* (Jacq.) Maxon var. *plantaginea*; MO, YU—2. 9/2/57 [1/18]; 4,000 ft.; seaside of mountains between Petaquire and the sea (n).
413. *Polypodium sessilifolium* Desv.; YU. 9/2/57 [1/2]; 5,000 ft.; seaside of mountains between Petaquire and the sea (n).
414. *Polypodium* aff. *fraxinifolium* Jacq.; YU. 29/1/57 [1/1]; 6,500 ft.; seaside of mountains between Maracai and Choroni (n).
415. *Polypodium triseriale* Sw.; YU. 29/1/57 [1/1]; 6,000 ft.; seaside of mountains between Maracai and Choroni (n).
416. *Thelypteris* (*Amauropelta*) *oligocarpa* (Humb. & Bonpl. ex Willd.) Ching; YU. 12/12/56 [1/1]; 2,500 ft.; seaside of mountain range between Maracai and Choroni (n).
417. *Polypodium* (*Phlebodium*) *aureum* L.; YU. [2/1]; 3,000 ft.; seaside of mountain range between Maracai and Choroni (n).
418. *Polypodium lasiopus* Klotzsch; YU. 29/1/57 [1/3]; 6,500 ft.; seaside of mountains between Maracai and Choroni (n).
419. *Microgramma tecta* (Kaulf.) Alston; MO, YU. [2/22]; 2,000 ft.; seaside of mountains between Petaquire and the sea (n).
420. *Microgramma lycopodioides* (L.) Copel.; MO, YU. [2/15]; 2,500 ft.; seaside of mountains between Maracai and Choroni (n).
421. *Pleopeltis percussa* (Cav.) Hook. & Grev.; MO, YU. [3/3]; 4,000 ft.; seaside of mountains between Maracai and Choroni (n).
422. *Polypodium sororium* Humb. & Bonpl. ex Willd.; MO, YU. 9/2/57 [1/6]; 8,000 ft.; highest mountains E of Colonia Tovar (n).
423. *Dicranoglossum furcatum* (L.) J. Smith; YU. 9/2/57 [1/2]; 3,000 ft.; seaside of coast range of mountains (n).
424. *Vittaria costata* Kunze; YU. 29/1/57 [1/1]; 5,500 ft.; seaside of mountain range between Maracai and Choroni (n).
425. *Anetium citrifolium* (L.) Splitg.; YU. 29/1/57 [1/2]; 6,000 ft.; seaside of mountain range between Maracai and Choroni (n).
426. *Olfersia cervina* (L.) Kunze; MO, YU—3. 9/2/57 [1/4]; 4,000 ft.; seaside of mountain range between Petaquire and Chichiribichi (n).
427. Not located. 29/1/57 [1/?]; 6,000 ft.; seaside of mountain range between Maracai and Choroni (n).
428. *Elaphoglossum herminieri* (Bory & Fée ex Fée) T. Moore; YU. 29/1/57 [1/1]; 3,500 ft.; seaside of mountain range between Maracai and Choroni (n).
429. *Elaphoglossum lingua* (C. Presl) Brackenr.; YU. 3,500 ft.; seaside of mountain range between Maracai and Choroni (n); 29/1/57 [1/2] (s).
430. *Elaphoglossum* sp.; YU; cited by Eaton (1861) as *Acrostichum apodum* Kaulf. 29/1/57 [1/?]; 3,500 ft.; seaside of mountain range between Maracai and Choroni (n).
431. *Hypolepis stuebelii* Hieron.; MO, YU. [3/4]; 3,000 ft.; seaside of mountain range between Petaquire and the sea, also farther west (n).
432. *Asplenium auriculatum* Sw.; YU. 29/1/57 [1/1]; 6,000 ft.; seaside of mountain range between Maracai and Choroni (n).
433. *Asplenium pteropus* Kaulf.; MO, YU. [2/8]; 5,000 ft.; seaside of mountain range between Petaquire and Choroni (n).
434. *Asplenium cirrhatum* Rich. ex Willd.; YU. 9/2/57 [1/3]; 5,000 ft.; seaside of mountain range between Petaquire and the sea (n).
435. *Diplazium pedatum* Klotzsch; YU. [2/1]; 5,000 ft.; seaside of mountain range between Maracai and Choroni and between Petaquire and the sea (n).

435β. *Diplazium pedatum* Klotzsch; YU. 12/12/56 [1/1] (s).

436. *Diplazium pedatum* Klotzsch; MO, YU. 29/1/57 [1/7]; 6,000 ft.; seaside of mountain range between Maracai and Choroni (n).
437. *Thelypteris* (*Amauropelta*) *diplazioides* (Moritz ex Mett.) Ching; YU. 26/1/57 [1/1]; 100 ft.; near Colombia N of Choroni (n).
438. *Thelypteris* (*Amauropelta*) *balbisii* (Sprengel) Ching; YU. 26/1/57 [1/1]; 200 ft.; near Colombia on the coast (n).
439. *Thelypteris* (*Amauropelta*) sp., aff. *gracilis* (Heward) Proctor; YU. 29/1/57 [1/1]; 3,500 ft.; seaside of mountain range between Maracai and Choroni (n).
440. *Thelypteris* (*Amauropelta*) *pilosula* (Mett.) R. Tryon; YU. 6/1/57 [1/1]; 8,000 ft.; highest mountains E of Colonia Tovar (n).
441. *Thelypteris* (*Cyclosorus*) *hispidula* (Decne.) Reed; YU. [2/1]; 4,000 ft.; a few mi. SW of Colonia Tovar (n).
442. Not located. 25/1/57 [1/?]; 300 ft.; seaside of mountains between Maracai and Choroni (n).
443. *Cyclopeltis semicordata* (Sw.) J. Smith; MO. 25/1/57 [1/?]; 200 ft.; between Choroni and Colombia (n).
444. "*Ctenitis microchlaena*" (Fée) A. R. Smith, comb. ined.; YU. 9/2/57 [1/1]; 5,000 ft.; seaside of mountains between Petaquire and the sea (n).
445. *Thelypteris* (*Goniopteris*) *nephrodioides* (Klotzsch) Proctor; YU. 9/2/57 [1/1]; 3,000 ft.; seaside of mountains between Petaquire and the sea (n).
446. *Thelypteris* (*Goniopteris*) *paucijuga* (Klotzsch) A. R. Smith, vel aff.; YU. 9/2/57 [1/3]; 4,000 ft.;

seaside of mountains between Petaquire and the sea (n).

447. *Ctenitis pulverulenta* (Poiret) Copel.; K, YU—2; cited by Christensen (1920) as *Dryopteris karsteniana* (Klotzsch) Hieron. 9/2/57 [1/3]; 3,000 ft.; seaside of mountains between Petaquire and the sea (n).
448. *Dennstaedtia bipinnata* (Cav.) Maxon; MO, YU—2. [3/5]; 4,000 ft.; seaside of mountains north of Colonia Tovar (n).
449. = 450*β* (n).
450. *Dicranopteris seminuda* (Klotzsch) Maxon; MO, YU—2. [3/20]; 6,500 ft.; high mountains NE of Colonia [Tovar] (n).
450*β*. *Dicranopteris flexuosa* (Schrader) L. Underw.; MO, YU. 9/2/57 [1/6] (s).
451. *Trichomanes* (*Acarpacrium*) *trigonum* Desv.; YU. 28/1/57 [1/1]; 4,500 ft.; seaside of mountain range between Maracai and Choroni (n).
452. *Trichomanes* (*Didymoglossum*) *punctatum* Poiret subsp. *sphenoides* (Kunze) W. Boer; B, G, GH, MO, YU; cited by Wessels Boer (1962). 29/1/57 [1/19]; 4,500 ft.; seaside of mountains between Maracai and Choroni (n).
453. *Trichomanes* (*Lecanium*) *membranaceum* L.; MO, YU. 10/2/57 [1/20]; 3,000 ft.; seaside of mountain range between Petaquire and the sea (n).
454. *Trichomanes* (*Didymoglossum*) *lineolatum* (Bosch) Hook.; B, G, GH, MO, YU; cited by Wessels Boer (1962). 10/2/57 [1/16]; 3,500 ft.; seaside of mountain range between Petaquire and the sea (n).
455. *Trichomanes* (*Microgonium*) *ekmanii* W. Boer; B, G, GH, L, MO, US; cited by Wessels Boer (1962). 13/12/56 [1/?]; 5,500 ft.; seaside of mountains between Maracai and Choroni (n).
456. *Trichomanes* (*Lacosteopsis*) *rupestre* (Raddi) Bosch; YU. 29/1/57 [1/2]; 3,000 ft.; seaside of mountains between Maracai and Choroni (n).
457. *Hymenophyllum* (*Sphaerocionium*) *elegans* Sprengel forma *minor* C. Morton; GH, MO, YU; cited by Morton (1947). 29/1/57 [1/19]; 6,200 ft.; seaside of mountains between Maracai and Choroni (n).
458. *Hymenophyllum* (*Sphaerocionium*) *hirsutum* (L.) Sw. 29/1/57 [1/?]; 6,000 ft.; seaside of mountain ridge between Maracai and Choroni (n).
459. *Trichomanes* (*Lacosteopsis*) *debile* Bosch; MO, YU—2. 10/3/57 [1/14]; 5,000 ft.; seaside of mountains between Valencia and San Estevan (n).
460. *Danaea elliptica* J. E. Smith; MO, YU. 3,500 ft.; seaside of mountain range between Petaquire and Chichiribichi (n); 9/2/57 [1/10] (s).
461. *Selaginella haematodes* (Kunze) Spring in Martius; MO, YU. 9/2/57 [1/16]; 2,500 ft.; seaside of mountain range between Petaquire and Chichiribichi (n).
462. = *313*, not located.
463. *Elaphoglossum ornatum* (Mett.) Christ; K, YU; cited by Mickel in Smith (1985). [2/4]; 3,000 ft.; seaside of mountain range between Agua Blanca and Cumbote (n).
464. *Pleopeltis percussa* (Cav.) Hook. & Grev.; YU. [?/1]; 6,500 ft.; Colonia Tovar (n). On same sheet as *421*.
465. *Grammitis* sp.; YU; cited by Eaton (1861) as *Polypodium truncicola* Klotzsch. [2/?]; 6,000 ft.; seaside of mountains between Valencia and San Estevan and between Agua Blanca and Cumbote (n).
466. *Elaphoglossum* sp.; YU; cited by Eaton (1861) as *Acrostichum perelegans* Fée. 7/3/57 [1/?]; 4,000 ft.; seaside of mountain range between Valencia and Campanero (n).
467. *Grammitis chrysleri* (Copel.) Proctor; YU. 30/1/58 [1/3]; 6,500 ft.; seaside of mountains between Agua Blanca and Cumbote (n).
468. *Adiantum latifolium* Lam.; YU. 7/3/57 [1/2]; 1,000 ft.; between Valencia and San Estevan, seaside of mountain range (n).
469. *Adiantum petiolatum* Desv.; YU. [2/4]; 500–1,000 ft.; near San Estevan a few mi. N of Puerto Cabello (n).
469*β*. *Adiantum* sp.; YU; cited by Eaton (1861) as *A. kaulfussii* Kunze [may be *A. petiolatum* Desv.].
470. = *469β* (n), not located.
471. *Polypodium triseriale* Sw.; YU. 7/5/57 [1/1]; 7,000 ft.; high mountains E of Colonia [Tovar] (n).
472. *Thelypteris* (*Amauropelta*) *pachyrhachis* (Kunze ex Mett.) Ching var. *pachyrhachis*; GH, MO, YU. [2/6]; 4,000 ft.; seaside of mountains between Agua Blanca and Cumbote, and between Valencia and San Estevan (n).
473. *Thelypteris* (*Cyclosorus*) *conspersa* (Schrader) A. R. Smith; YU. [2/3]; 4,000 ft.; Macarao River valley W of Caracas, also seaside of mountains between Valencia and San Estevan (n).
473. *Thelypteris* (*Cyclosorus*) *hispidula*; YU. [?/3].
474. *Thelypteris* (*Goniopteris*) *straminea* (Baker) Reed; YU; this is an ISOTYPE of *Polypodium stramineum* Baker in Hook. & Baker, Syn. Fil. 316. 1867. [1/4]; 2,300 ft.; Piedernales near Güigüe (n).
475. *Thelypteris* (*Cyclosorus*) *hispidula* (Decne.) Reed; YU. 7/3/57 [1/1]; 2,500 ft.; seaside of mountains between Valencia and San Estevan (n).
476. *Thelypteris* (*Steiropteris*) *leprieurii* (Hook.) R. Tryon var. *costalis* (Baker) A. R. Smith; K; this is an ISOTYPE of *Aspidium costale* Mett. ex Kuhn, Linnaea 36: 111. 1869. 7/3/57 [1/?]; 1,500 ft.; seaside of mountains between Valencia and San Estevan (n).
477. *Thelypteris* (*Steiropteris*) *leprieurii* (Hook.) R. Tryon var. *costalis* (Baker) A. R. Smith; YU. 7/3/57 [1/1]; 1,500 ft.; seaside of mountain range between Valencia and San Estevan (n).
478. Not located. 7/3/57 [1/?]; 1,000 ft.; seaside of mountain range between Valencia and San Estevan (n).
479. *Lindsaea stricta* (Sw.) Dryander var. *stricta*; G, GH, GOET, K, MO, PH, YU; cited by Kramer (1957). 7/3/57 [1/12]; 4,000 ft.; seaside of mountain range between Valencia and San Estevan (n).
480. *Cnemidaria spectabilis* (Kunze) R. Tryon var. *spectabilis*; GH, K, MO, YU—2; cited by Stolze (1974). 7/3/57 [1/9]; 4,500 ft.; seaside of mountain range between Valencia and San Estevan (n).
481. *Hymenophyllum* (*Sphaerocionium*) *dependens* C. Morton; GH, US, MO, YU; cited by Morton (1947). 29/1/58 [1/?]; 5,000 ft.; seaside of mountain range between Agua Blanca and Cumbote (n).
482. *Dicranopteris pectinata* (Willd.) L. Underw.; MO, YU. 7/3/57 [1/6]; 6,000 ft.; seaside of mountains between Valencia and San Estevan (n).
483. *Dicranopteris pectinata* (Willd.) L. Underw.; MO, YU. 7/3/57 [1/5]; 5,500 ft.; seaside of mountains between Valencia and San Estevan (n).

484. Not located. 7/3/57 [1/?]; 5,500 ft.; seaside of mountains between Valencia and San Estevan (n).
485. *Schizaea poeppigiana* Sturm in Martius; MO. 27/2/57 [1/?]; 5,800 ft.; a few mi. S of Colonia Tovar (n).
486. = *322*, *Selaginella* (n), not located. 7/3/57 [1/?]; 4,000 ft.; seaside of mountains between Valencia and San Estevan (n).
487. *Selaginella cruciformis* Alston ex Crabbe & Jermy; BM; cited by Alston et al. (1981). 7/3/57 [1/?]; 3,000 ft.; seaside of mountains between Valencia and San Estevan (n).
487?. *Lophosoria quadripinnata* (J. Gmelin) C. Chr.; YU. [?/7].
488. *Polypodium fraxinifolium* Jacq.; YU. 26/3/57 [1/1]; 8,000 ft.; high mountains E of Colonia Tovar (n).
489. *Asplenium serratum* L.; YU. 7/3/57 [1/3]; 3,500 ft.; seaside of mountain range between Valencia and San Estevan (n).
490. Not located. 7/3/57 [1/?]; 4,000 ft.; seaside of mountain range between Valencia and San Estevan (n).
491. *Cyathea barringtonii* A. R. Smith ex Lellinger; YU; cited by Barrington (1978) as *Trichipteris cordata* (Klotzsch) R. Tryon. [2/2]; 6,300 ft.; seaside of mountain range between Maracai and Choroni (n).
492. *Cyathea villosa* Willd.; YU. [2/4]; 5,800 ft.; seaside of mountain range between Agua Blanca and Cumbote, also savannahs S of Colonia [Tovar] (n).
492?. *Cyathea villosa* Willd.; YU.
493. *Selaginella flabellata* (L.) Spring var. *latifrons* A. Braun, Ann. Sci. Nat. Bot., V. 3: 278. 1865; ISOTYPES, BM, MO, YU; cited by Alston et al. (1981). 30/1/58 [1/4]; 3,000 ft.; seaside of mountains between Agua Blanca and Cumbote (n).
494. *Selaginella cavifolia* A. Braun; YU. [2/4]; 6,000 ft.; Colonia Tovar (n).
495. *Elaphoglossum variolatum* Mickel; YU. 4,000 ft.; seaside of mountain range between Agua Blanca and Cumbote (n); 30/1/58 [1/1] (s).
496. *Adiantum* sp.; YU; cited by Eaton (1861) as *A. capillus-veneris* L. 20/2/58 [1/?]; 3,000 ft.; Hacienda Curisal (n).
497. *Diplazium celtidifolium* Kunze; YU. 22/4/58 [1/1]; 4,500 ft.; seaside of mountain range between Petaquire and the sea (n).
498. *Diplazium flavescens* (Mett.) Christ; MO, YU. 22/4/58 [1/?]; 4,000 ft.; seaside of mountain range between Petaquire and the sea (n).
499. *Rumohra adiantiformis* (G. Forster) Ching; YU; cited by Eaton (1861) as *Aspidium coriaceum* Sw. 22/4/58 [1/?]; 5,500 ft.; seaside of mountains between Petaquire and the sea (n).
s.n. *Lindsaea klotzschiana* Moritz in Ettingshausen; YU; originally det. *L. quadrangularis* Raddi.

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H. (*Sphaerocionium*) sp., undescribed?—31, pt
Hypolepis bogotensis Karsten—64, pt; 64β, pt
H. parallelogramma (Kunze) C. Presl—66; ad 66
H. stuebelii Hieron.—431
H. viscosa Karsten—64, pt; 64β, pt
Lastreopsis effusa (Sw.) Tindale subsp. *divergens* (Willd.) Tindale—205
L. exculta (Mett.) Tindale—330
Lindsaea klotzschiana Moritz in Ettingshausen—63α; 63β; 379; 380, pt
L. lancea (L.) Beddome var. *lancea*—378, pt
L. stricta (Sw.) Dryander var. *stricta*—377; 378, pt; 380, pt; 479
Lomariopsis fendleri D. Eaton—335
Lonchitis hirsuta L.—100
Lophosoria quadripinnata (J. Gmelin) C. Chr.—48; 487?
Loxoscaphe theciferum (H.B.K.) T. Moore—62
Lycopodium acerosum Sw.—317
L. alopecuroides L.—315
L. cernuum L.—318; 399; 399β
L. clavatum L.—314; 314β
L. myrsinites Lam.—320
L. cf. *pendulinum* Hook.—347
L. reflexum Lam.—316
L. taxifolium Sw.—319
L. thyoides Humb. & Bonpl. ex Willd.—313; 400
L. sp.—337; 398
Lygodium venustum Sw.—14
Marattia laevis J. E. Smith—3
Microgramma lycopodioides (L.) Copel.—420
M. reptans (Cav.) A. R. Smith—354
M. tecta (Kaulf.) Alston—419
M. vacciniifolia (Langsd. & Fischer) Copel.—248
Nephrolepis occidentalis Kunze—161
N. pendula (Raddi) J. Smith—162; 162β
N. rivularis (Vahl) Mett. ex Krug—370
Niphidium crassifolium (L.) Lellinger—223
N. mortonianum Lellinger—222
Olfersia cervina (L.) Kunze—426
Ophioglossum nudicaule L. f.—342
O. reticulatum L.—312
Osmunda regalis L.—5
Paesia glandulosa (Sw.) Kuhn—94
Pellaea ovata (Desv.) Weath.—89
Phanerophlebia juglandifolia (Humb. & Bonpl. ex Willd.) J. Smith—233
Pityrogramma calomelanos (L.) Link—298
P. chrysoconia (Desv.) Maxon ex Domin—357?
P. tartarea (Cav.) Maxon—299
P. trifoliata (L.) R. Tryon—297
Plagiogyria semicordata (C. Presl) Christ—325
Pleopeltis macrocarpa (Bory ex Willd.) Kaulf.—249; 250
P. percussa (Cav.) Hook. & Grev.—421; 464
×*Pleopodium leucosporum* (Klotzsch) Mickel & Beitel—251
Polybotrya canaliculata Klotzsch—262
P. serratifolia (Fée) Klotzsch—261
Polypodium (*Phlebodium*) *aureum* L.—417
P. bolivari Sota—343
P. buchtienii Christ & Rosenstock—246
P. camptophyllarium Fée var. *lachniferum* (Hieron.) A. M. Evans—221γ
P. consimile Mett. var. *consimile*—220; 220β
P. dispersum A. M. Evans—221, pt
P. dissimile L.—238; 238β
P. eurybasis C. Chr.—221, pt; 221β
P. fraxinifolium Jacq.—234; 235; 236; 488
P. aff. *fraxinifolium* Jacq.—237; 414
P. funckii Mett.—243
P. fuscopetiolatum A. R. Smith—242; 341
P. hygrometricum Splitg.—407
P. lasiopus Klotzsch—244; 418
P. loriceum L.—353
P. moritzianum Link—214
P. plumula Humb. & Bonpl. ex Willd.—221, pt
P. polypodioides (L.) Watt var. *burchellii* (Baker) Weath.—253
P. (*Phlebodium*) *pseudoaureum* Cav.—241
P. remotum Desv.—245
P. sessilifolium Desv.—240; 413
P. sororium Humb. & Bonpl. ex Willd.—422
P. steirolepis C. Chr.—247
P. thyssanolepis A. Braun ex Klotzsch—252

P. triseriale Sw.—352; 415; 471
P. ursipes Moritz ex C. Chr.—254
P. sp.—221δ; 239; 243?
Polystichum muricatum (L.) Fée—172; 174
P. platyphyllum (Willd.) C. Presl—175
P. sp., aff. *polyphyllum* (C. Presl) C. Presl—171
P. sp.—173
Pteridium arachnoideum (Kaulf.) Maxon—104
Pteris altissima Poiret in Lam.—365
P. consanguinea Mett. ex Kuhn—97
P. deflexa Link—101; 102
P. gigantea Willd.—95
P. grandifolia L.—96
P. longifolia L.—105
P. podophylla Sw.—98, pt
P. propinqua Agardh—98, pt; 99
P. quadriaurita Retz.—103; 103β
Rumohra adiantiformis (G. Forster) Ching—499
Saccoloma domingense (Sprengel) C. Chr.—61; 61β
S. elegans Kaulf.—376
S. inaequale (Kunze) Mett.—375
Salpichlaena volubilis (Kaulf.) J. Smith—117, pt
Schizaea elegans (Vahl) Sw.—396
S. poeppigiana Sturm in Martius—485
Selaginella cavifolia A. Braun—322, pt; 323; 494
S. cladorrhizans A. Braun—324, pt
S. cruciformis Alston ex Crabbe & Jermy—487
S. diffusa (C. Presl) Spring—397
S. flabellata (L.) Spring var. *latifrons* A. Braun—493
S. flagellata Spring—324, pt; 403
S. haematodes (Kunze) Spring in Martius—461
S. pallescens (C. Presl) Spring—321; 321β
S. porphyrospora A. Braun—402
S. viticulosa Klotzsch—258, pt; 322, pt
S. sp.—486
Sticherus bifidus (Willd.) Ching—42
S. nudus (Moritz ex Reichardt) Nakai—41
S. pennigera (Martius) Copel.—43
S. rubiginosus (Mett.) Nakai—40
Stigmatopteris nephrodioides (Klotzsch) C. Chr.—198
Tectaria heracleifolia (Willd.) L. Underw.—164; 164β
T. incisa Cav.—165β; 166
T. incisa Cav., vel aff.—165
T. plantaginea (Jacq.) Maxon var. *plantaginea*—412
T. trifoliata (L.) Cav.—165 additional
Thelypteris (*Meniscium*) *arborescens* (Humb. & Bonpl. ex Willd.) C. Morton—232β
T. (*Amauropelta*) *aspidioides* (Willd.) R. Tryon—306; 360
T. (*Goniopteris*) *asterothrix* (Fée) Proctor—201
T. (*Amauropelta*) *balbisii* (Sprengel) Ching—438
T. (*Amauropelta*) *cheilanthoides* (Kunze) Proctor—187, pt
T. (*Amauropelta*) *concinna* (Willd.) Ching—179, pt; 185, pt
T. (*Amauropelta*) *concinna* (Willd.) Ching, vel aff.—176
T. (*Cyclosorus*) *conspersa* (Schrader) A. R. Smith—473, pt
T. (*Steiropteris*) *decussata* (L.) Proctor var. *decussata*—373
T. (*Amauropelta*) *deflexa* (C. Presl) R. Tryon—186
T. (*Amauropelta*) *diplazioides* (Moritz ex Mett.) Ching—159; 437
T. (*Meniscium*) *ensiformis* (C. Chr.) R. Tryon—232, pt
T. (*Steiropteris*) *fendleri* (D. Eaton) Reed—372
T. (*Goniopteris*) *gemmulifera* (Hieron.) A. R. Smith—193; 193γ
T. (*Cyclosorus*) *grandis* A. R. Smith var. *aequatorialis* (C. Chr.) A. R. Smith—188
T. (*Cyclosorus*) *hispidula* (Decne.) Reed—191; 441; 473, pt; 475
T. (*Steiropteris*) *leprieurii* (Hook.) R. Tryon var. *costalis* (Baker) A. R. Smith—476; 477
T. (*Goniopteris*) *nephrodioides* (Klotzsch) Proctor—445
T. (*Amauropelta*) *oligocarpa* (Humb. & Bonpl. ex Willd.) Ching—179, pt; 181, pt; 416
T. (*Amauropelta*) *opposita* (Vahl) Ching—177
T. (*Amauropelta*) *opposita* (Vahl) Ching, vel aff.—182
T. (*Amauropelta*) *pachyrhachis* (Kunze ex Mett.) Ching var. *pachyrhachis*—187, pt; 472
T. (*Cyclosorus*) *patens* (Sw.) Small var. *patens*—189; 192
T. (*Cyclosorus*) *patens* (Sw.) Small var. *scabriuscula* (C. Presl) A. R. Smith—190
T. (*Goniopteris*) *paucijuga* (Klotzsch) A. R. Smith—446
T. (*Goniopteris*) *pennata* (Poiret in Lam.) C. Morton—200
T. (*Amauropelta*) *pilosohispida* (Hook.) Alston—158
T. (*Amauropelta*) *pilosula* (Mett.) R. Tryon—178; 180; 183; 184, pt; 440
T. (*Goniopteris*) *poiteana* (Bory) Proctor—199
T. (*Steiropteris*) *praetervisa* (Kuhn) A. R. Smith—371
T. (*Amauropelta*) *proctorii* A. R. Smith & Lellinger—185, pt
T. (*Amauropelta*) *pteroidea* (Klotzsch) R. Tryon—206
T. (*Amauropelta*) *rudis* (Kunze) Proctor—185, pt; ad 185; 187, pt
T. (*Amauropelta*) *rupestris* (Klotzsch) Reed—307
T. (*Meniscium*) *salzmannii* (Fée) C. Morton—232, pt
T. (*Amauropelta*) *scalaris* (Christ) Alston—181, pt
T. (*Goniopteris*) *straminea* (Baker) Reed—474
T. (*Goniopteris*) *tetragona* (Sw.) Small—196
T. sp., aff. *gracilis* (Heward) Proctor—439
Trichomanes (*Lacosteopsis*) *capillaceum* L.—22; 395
T. (*Achomanes*) *crispum* L.—388
T. (*Lacosteopsis*) *debile* Bosch—459
T. (*Lacosteopsis*) *diaphanum* H.B.K.—16, pt; 17; 18
T. (*Microgonium*) *ekmanii* W. Boer—455
T. (*Didymoglossum*) *lineolatum* (Bosch) Hook.—454
T. (*Lecanium*) *membranaceum* L.—453
T. (*Didymoglossum*) *ovale* (Fourn.) W. Boer—25; ad 25
T. (*Neurophyllum*) *pinnatum* Hedwig—390
T. (*Acarpacrium*) *polypodioides* L.—329
T. (*Didymoglossum*) *punctatum* Poiret subsp. *sphenoides* (Kunze) W. Boer—452
T. (*Didymoglossum*) *pusillum* Sw.—24; ad 24
T. (*Lacosteopsis*) *radicans*—20
T. (*Didymoglossum*) *reptans* Sw.—23
T. (*Pachychaetum*) *rigidum* Sw.—16, pt
T. (*Achomanes*) *robustum* Fourn.—26
T. (*Lacosteopsis*) *rupestre* (Raddi) Bosch—21; 456
T. (*Acarpacrium*) *trigonum* Desv.—451
T. (*Achomanes*) sp., undescribed?—388β; 389
Vittaria costata Kunze—424
V. gardneriana Fée—259β
V. graminifolia Kaulf.—258, pt
V. moritziana Mett.—259, pt
V. remota Fée—260
V. stipitata Kunze—259, pt

NOTES

A NEW *ECHEANDIA* (LILIACEAE) FROM VENEZUELAN GUAYANA

Echeandia bolivarensis Cruden, sp. nov. TYPE: Venezuela. Bolívar: Igneous forested slopes, Serranía de Pijiguao, 160 km SW of Caicara del Orinoco, 6°35′N, 66°45′W, 100–125 m, 12 Sep. 1985, *Steyermark, Holst & Manara* 131761 (holotype, MO, on two sheets, 3472626, 3472627; isotype, UC).

Regio penaria radicum ab cormo 4–5 cm, 4–5 cm longa. Folia basalia 6–10, anguste oblanceolata, marginibus denticulatis-serrulatis, 45–60 cm longa, 11–18 mm lata. Scapus glaber, 4–5 ramosus. Folia caulina 4–5, longiattenuata. Tepala flava. Filamenta squamata, linearia. Antherae librae. Capsula late oblonga.

Storage region of the roots 4–5 cm from the corm, 4–5 cm long. Basal leaves 6–10, ascending, narrowly lanceolate above the base, bases persistent as a fibrous collar, minutely denticulate-serrulate, usually 45–60 cm long and 11–18 mm wide. Scape glabrous, 98–118 cm high, 5-branched. Cauline leaves 4–5, long-attenuate. Tepals yellow, ca. 10 mm long. Filaments minutely to noticeably scaled, linear, 6.5 mm long. Anthers free, 2.4–3 mm long, appearing to dehisce laterally. Ovary 2 mm long. capsule broadly oblong, 10–11 mm long, 6.5–7.5 mm wide. Seeds black, colliculose, 2.5–3 mm across.

Known only from the type locality, this species is easily distinguished from other yellow-flowered South American *Echeandia* species by the combination of scaled filaments, many branches, and the storage organs developing at some distance from the corm. It is unusual for yellow-flowered species to occur at such low elevations.

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SOLANUM TOLIARAEA, A NEW SPECIES FROM MADAGASCAR

Solanum toliaraea D'Arcy & Rakotozafy, sp. nov. TYPE: Madagascar: *D'Arcy & Rakotozafy 15460* (holotype, MO; isotypes, K, P, TAN).

Frutex armatus spinis brevibus validis rectis, foliis rotundis parvis stellato-tomentosis; flores solitari v-geminati, calyce inermi sed in statu fructu accrescenti, echiniformi, acinum tegenti.

Slender, branched shrub or tree to 3 m tall; twigs slender, at first appressed tomentose with reddish hairs, soon puberulent with reduced buff-colored trichomes and deeply furrowed, armed with short, stout-based, nearly straight, puberulent spines. Leaves mostly paired in fasciculate short-shoots, entire, rotund, apically rounded, basally rounded, truncate or cordate, mostly 8–20 mm long, thick, felty with dense short-stalked, stellate hairs, the costa evident, the minor venation obscure; peduncles canaliculate adaxially but often appearing terete because of the dense tomentum, mostly 5–10 mm long, with occasional small straight spines. Inflorescences solitary flowers or paired fascicles from the leafy short-shoots; pedicels resembling the petioles but somewhat longer. Flowers with calyx ca. 4 mm long, lobed about ⅓ way down, the lobes convex, obtuse, tomentose, unarmed; corolla pale purple, mauve, or white, ca. 10 mm long, lobed ⅓ way down, tomentose outside except on the membranaceous inter-lobe fringing areas, glabrous within, the nervature drying conspicuous within; stamens 5, equal, the anthers yellow, slender, 5 mm long, opening by minute terminal pores; ovary glabrous, drying somewhat lobed, the style slender, exserted slightly beyond the stamens, with a few short, gland-tipped simple hairs near the base. Berry green, juicy, 4-lobed, ca. 5 mm diam., entirely but loosely enveloped in the calyx, the spiny, accrescent calyx echinoid, subglobose, ca. 2 cm diam.; seeds (*Descoings 2375*) compressed, dark, 2.5 mm long.

At time of flowering the calyx of this species is devoid of spines, in contrast to its copiously spiny, echinoid condition when in fruit.

Collections of this species were first confused with *Solanum dubium* Fresen of Ethiopia, which has similar spiny accrescent calyces, but that species is herbaceous and has much larger, lobed leaves. The species described here differs from the other two arborescent species of southwestern Madagascar in its accrescent, spiny calyx and in its rotund, concolorous leaves. *Solanum toliaraea* is sympatric, at least in part, with other arborescent solanums, *S. bummeliifolium* Dunal and *S. heineanum* D'Arcy & Keating, which differ in usually spineless calyces and porrect, scutellate hairs.

Solanum toliaraea was seen as scattered individuals in didieriad woodlands of southwestern Madagascar. Most collections were made from plants growing on sand near the coast just north of the major city of Tulear and hence just north of the Tropic of Capricorn.

The name *toliaraea* is derived from the Malagasy spelling for the city of Tulear.

Material seen. MADAGASCAR: TULEAR (Toliary): bush à *Didierea* sur dunes, embouchure de Fiherenana, Belalanda, Nov. 1956, *Bosser 10472* (MO, P); scrub forest on pure shifting sand, 8 km N of Tulear on road to Morombe, 5 Feb. 1975, *Croat 30778* (MO); road to 5 km N of Belalanda, 17 May 1983, *D'Arcy & Rakotozafy 15460* (MO, K, P, TAN); Sable, Manombo, région de Tuléar, *Decary 16214, 18714* (P); route de Manombo sur sable, 7 Jan. 1957, *Descoings 2375* (MO); bush à *Didierea* sur dunes, embouchure de Fiherenana, Belalanda, May 1960, *Keraudren 690* (P); bush à Euphorbiés, route de Monombo, près de la côte, environs de Tuléar, 3 Nov. 1960, *Léandri & Jean de Dieu 3627, 3635, 3804* (P); thorn scrub of *Euphorbia* and *Didierea* on

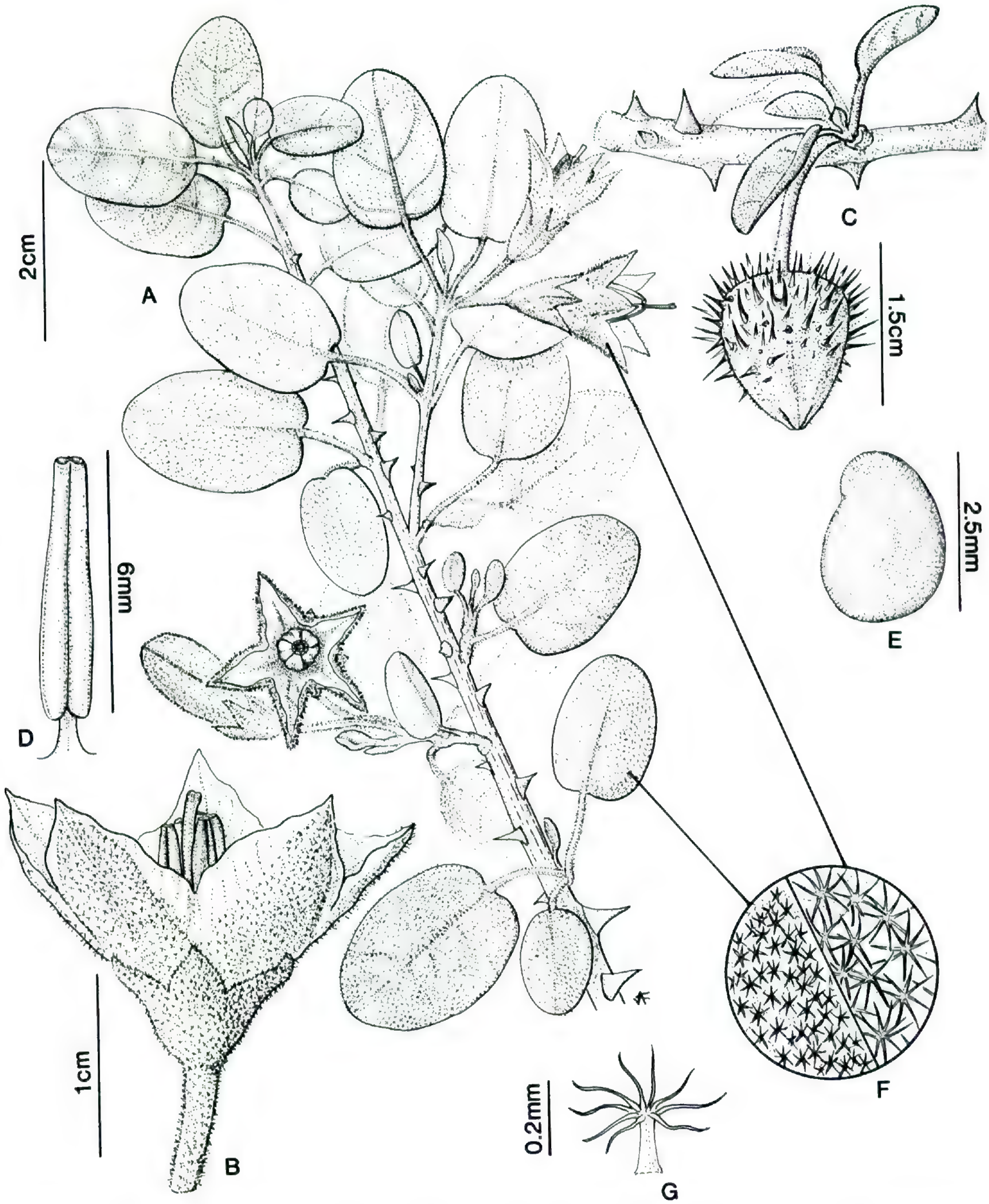

FIGURE 1. *Solanum toliaraea*.—A. Habit.—B. Flower.—C. Fruit.—D. Stamen.—E. Seed.—F. Indument.—G. Trichome from leaf. (E after *Descoings 2375*, other figures after *D'Arcy & Rakotozafy 15460* [MO].)

sand dunes behind littoral, Route Nationale no. 9, 15 km N of Tulear, 12 Nov. 1978, *Lorence 1940* (MO).

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NOTE CONCERNING *FESTUCA HENRIQUESII* (GRAMINEAE) IN NORTHERN PORTUGAL

The species *Festuca henriquesii* Hackel (Gramineae), first described in 1883, is endemic to Portugal. In various floras and subsequent publications, namely Coutinho (1939), Sampaio (1946), Litardière (1952), and Tutin et al. (1980), the location of this species has been given as restricted solely to the Serra da Estrela, a mountain range in northeastern Portugal. Little information is available concerning its ecology, except that specimens have generally been collected from high places in this mountain range.

Recently, however, I recorded this species from a grassland area in the Serra do Gerês, in northern Portugal (Hale, in press). I had believed that this was the first record for the species outside of the Serra da Estrela range. The location, in grazed grassland within an area generally of ericaceous shrubland, is known as "Lagoas" because of two small nearby lakes. The plants were growing on an acid soil over granitic parent material at an altitude of 1,150 m (grid reference X326 071; Carta Militar 31).

Further investigation revealed, however, that this record for the species in the Serra do Gerês was not unique. Besides two records from the Serra da Estrela, three specimens of *F. henriquesii* exist in the Herbarium of the Institute of Botany "Dr. Gonçalo Sampaio" in Porto, collected from the Serra do Gerês and nearby areas (Table 1). Despite the existence of these specimens, however, this species appears not to have been previously reported from these mountain ranges.

It is clear from these records that *Festuca henriquesii* is not restricted to the Serra da Estrela; the range includes the serras of Gerês, Peneda, and Barroso. The species might be a glacial relict restricted to a few mountain ranges and not noticed before outside of the Serra da Estrela; alternatively, its distribution may be expanding. In view of the apparently discontinuous distribution, these other mountain ranges being nearly 200 km from that of Estrela, it is quite possible that the species might turn up in other intervening mountain ranges in the north of Portugal.

TABLE 1. *F. henriquesii* records outside Estrela.

Location	Habitat	Date of Collection
Lamas do Homem, Gerês	Dry ground	6/7/1948
Barca do Homem, Gavieira, Peneda	Grassland	–/7/1961
S. Fins, Montalegre, Barroso	Roadside	11/8/1978
Lagoas, Gerês	Grassland	6/7/1984

I thank the staff of the Herbarium of the Institute of Botany "Dr. Gonçalo Sampaio," Porto, for confirming the identification of the "Lagoas" specimen and for access to the previous records of the species.

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PASSIFLORA CITRINA, A NEW SPECIES IN SECTION *XEROGONA* (PASSIFLORACEAE), FROM MESOAMERICA

The center of diversity for *Passiflora* L. subg. *Plectostemma* Masters sect. *Xerogona* (Raf.) Killip is in northern Central America, where at least six species occur in Guatemala alone. The section is notable in the genus *Passiflora* for its unusual capsular fruit. Killip (1922, 1924, 1927) described five species of this section from Central America and southern Mexico that had been confused with *P. rubra* L. or *P. capsularis* L. Newly described here is the yellow-flowered *P. citrina*, yet another member of this section that has been hidden under misapplication of the name *P. capsularis*.

Passiflora citrina MacDougal, sp. nov. TYPE: Honduras. Comayagua: El Carrizal, 14 km NW of Siguatepec, 900 m, 27 June 1971, *Molina & Molina 26057* (holotype, F; isotypes, EAP, NY, US). Figure 1.

Passiflora pubescens scandens; caulis sub5-angulatus; petioli eglandulosi; folia bilobata vel trilobata, lobis lateralibus acuminatis vel rotundis, lobo centrali obtuso vel obsoleto, marginibus integris, angula inter lobos laterales (30–)35–55(–70)°; bracteae nullae vel raro floribus bractea solitaria, 2–4 mm longa praeditis; flores aurei vel citrini vel viridiflavi, prope bases subcylindrico; coronae filamenta uniseriata, connata per maiorem longitudinem et perianthio adnata; androgynophorum 21–28 mm longum; ovarium dense pubescens; fructus fusiformis vel obovoideus, conspicue 6-carinatus; semina 6–7(8) sulcata.

Small vine, pubescent to hirsutellous throughout with 0.10–1.0(–1.2) mm ± erect, slightly antrorsely inclined or bent trichomes. Stems subpentangular, striate, densely pubescent with 0.2–0.8-mm bent trichomes. Stipules 4–7(–11) × 0.5–0.9 mm, linear-triangular, falcate, the apices not necrescent. Petioles 0.3–1.2(–2.0) cm long, eglandular. Laminas (2–)3–6.5(–9) × (1.5–)3–7(–9.5) cm at fertile nodes, widely obovate (obtriangular to widely oblong) in general outline, rounded to truncate (very shallowly cordate) at the base, entire, adaxially sometimes variegated along the main veins of the lateral lobes, evenly pubescent or often the trichomes in 2 distinct size classes and then the leaf scabrous and lightly hirsutellous, abaxially densely pubescent, 2(–3)-lobed 0.07–0.4(–0.6) the distance to the base, the lateral lobes acuminate to rounded, the central lobe (acute) obtuse to obsolete, the angle between the lateral lobes (30–)35–55(–70)°, the ratio of lateral to central lobe lengths (1.0–)1.2–2.0(–2.5), the ratio of laminar width to length (0.50–)0.6–0.9(–1.1); juvenile leaves variegated, deeply 2-lobed, the lobes acuminate, the angle between the lobes 80–100° or more; laminar nectaries absent. Posture of shoot apex ± straight. Prophyll of vegetative ramifying bud 1, narrowly lanceolate-triangular. Peduncles (solitary) geminate at the nodes, (0.3–)0.7–3.2(–4.3) cm long, uniflorous, ebracteate or rarely with one bract near the apex, 2–4 × 0.2–0.4 mm, linear to linear-triangular. Flowers yellow or bright yellow (to greenish yellow), sometimes drying with reddish brown speckles, inodorous, cylindrical in bud, the ventricose hypanthium 5–9 mm diam., sometimes with some of the trichomes borne on slightly raised bases; floral stipe 1.5–4 mm long; sepals 20–28(–34) × 2.5–5 mm, narrowly oblong-lanceolate or slightly oblanceolate, basally connate 2–6 mm, ecorniculate, strongly 3-veined, the veins raised and hirsutellous; petals 19–28 × 1.7–2.6 mm, narrowly oblong-lanceolate, basally adnate to the sepals; coronal filaments in 1 series, 9–14 mm long, erect, variably connate much of their length and adnate to the perianth, free distally 3–6 mm, pale yellow with yellow tips, not banded; operculum 1.0–2.1 mm long, membranous, only barely plicate near the erose apex; nectary 5(10)–ventricose, an additional annulus absent; limen (disk) ca. 2 mm diam., closely surrounding the base of androgynophore; staminal filaments connate 21–28 mm along the androgynophore, the free portions 4.5–6.0 mm long; anthers 4.4–6.0 mm long; ovary 2.8–4.2(–5.0) × 1.5–2.3 mm, obovoid-ellipsoid, densely pubescent, the trichomes mostly 0.2–0.5 mm; styles 5.0–6.8 mm total length; stigmas ca. 1.3 mm diam. Fruit (2.5–)3–4.3 × 1.2–2.3 cm, fusiform-ellipsoid or slightly obovoid, basally conical

or slightly attenuate, apically conical, acutely 6-carinate with thin 1–2-mm-high ridges, pubescent, reddish, dehiscent?, the stipe 1–8 mm long; arils unknown; nearly mature seeds 3.5–4 × 2.2–2.4 mm, slightly obcampylotropous with the chalazal beak strongly inclined toward the raphe, transversely sulcate with 6–7(–8) sulcae, the ridges continuous, smooth, and rather flat.

Habitat and distribution. *Passiflora citrina* is endemic to the pinehills country of central to western Honduras and adjacent eastern Guatemala. There it has been collected in moist (often open) pinewoods, *Pinus–Liquidambar* forest, or edges of moist mixed forest; it usually is climbing over grasses, tall herbs, and small shrubs in thickets.

Vernacular names. The name "moco" is recorded on an herbarium sheet from Chiquimula, Guatemala. "Calzoncillo," a vernacular name used for several of the bilobed passifloras in Mesoamerica, is recorded from Intibucá, Honduras.

Misapplied names. *Passiflora capsularis* auct., non L.: Killip (1936, 1938), in part; Standley & Williams (1961), in part.

The specific epithet refers to the color of the flowers.

Additional specimens examined. GUATEMALA. CHIQUIMULA: La Cumbre, old road to Quezaltepeque, 1,500 m, 28 Sep. 1971 (fl), *Molina & Molina 26821* (F); Volcán Quezaltepeque, 3–4 mi. NE of Quezaltepeque, 1,500–2,000 m, 8 Nov. 1939 (fl), *Steyermark 31508* (F). HONDURAS. COMAYAGUA: Temagua, 2,000 ft., 5 Aug. 1933 (fl), *Edwards P-640* (F); Trincheras, 20 km N of Siguatepeque, 4,500 ft., 29 July–10 Aug. 1951 (fl, fr), *Howard et al. 637* (MICH, NY); Trincheras on old road, ca. 14°39′N, 87°55′W, 1,050–1,100 m, 1 Nov. 1988, *MacDougal et al. 3048* (BM, MEXU, MO,TEFH); near Cerro Trincheras, km post 127.5 on road between Siguatepeque and Lago Yojoa, 980 m, 11 Nov. 1988, *MacDougal et al. 3469* (BM, MEXU,MO, US, TEFH); Barranco de Trincheras, 1,300 m, 29 Aug. 1955 (fl), *Molina 5826* (F); Barranco de Trincheras, 3 km a Montañuela, 1,200 m, 28 Mar. 1964 (fl), *Molina 13637* (F); 8 mi. W of Siguatepeque, 1,300 m, 7 Sep. 1975 (fl, fr), *Molina & Molina 31167* (F, MO); 24 km S of Lake Yojoa along road to Siguatepeque, 1,400 m, 26 Mar. 1976 (fl), *Pilz & Pilz 1572* (MO); Barranco de Trincheras, 18 km N of Siguatepeque, 1,200 m, 15 Apr. 1951 (fl), *Williams & Molina 17991* (F, US). COPÁN: 5 km al SO de Santa Rosa de Copán, 1,200 m, 29 Mar. 1963 (fl), *Molina 11705* (F, LL, NY, US); 5 km SO de Santa Rosa de Copán, 1,200 m, 29 Mar. 1963 (fl), *Molina 11655* (F, NY). INTIBUCÁ: Los Baños Públicos, alrededores de La Esperanza, 14 Mar. 1973 (fl, fr), *J. R. Martínez & Bejarano 110* (TEFH); Barranco Yamaranquilla, cerca de Yashse, 1,500 m, 12 Apr. 1956 (fl), *Molina 6510* (F, US); El Duraznillo, Cordillera, Opalaca, 2,000 m, 24 May 1964 (fl), *Molina & Molina 14086* (F). OCOTEPEQUE: 17 km NE of Nueva Ocotepeque, 13 Aug. 1970 (fl), *Harmon & Dwyer 3785* (MO); 41 km al NE de Nueva Ocotepeque, camino al San Pedro Sula, 1,490 m, 12 June 1985 (fl), *E. Martínez S. & O. Téllez 12932* (DUKE, MEXU); El Moral on Cordillera Merendón, 1,600 m, 27 Aug. 1968 (fl), *Molina 22263* (F, NY).

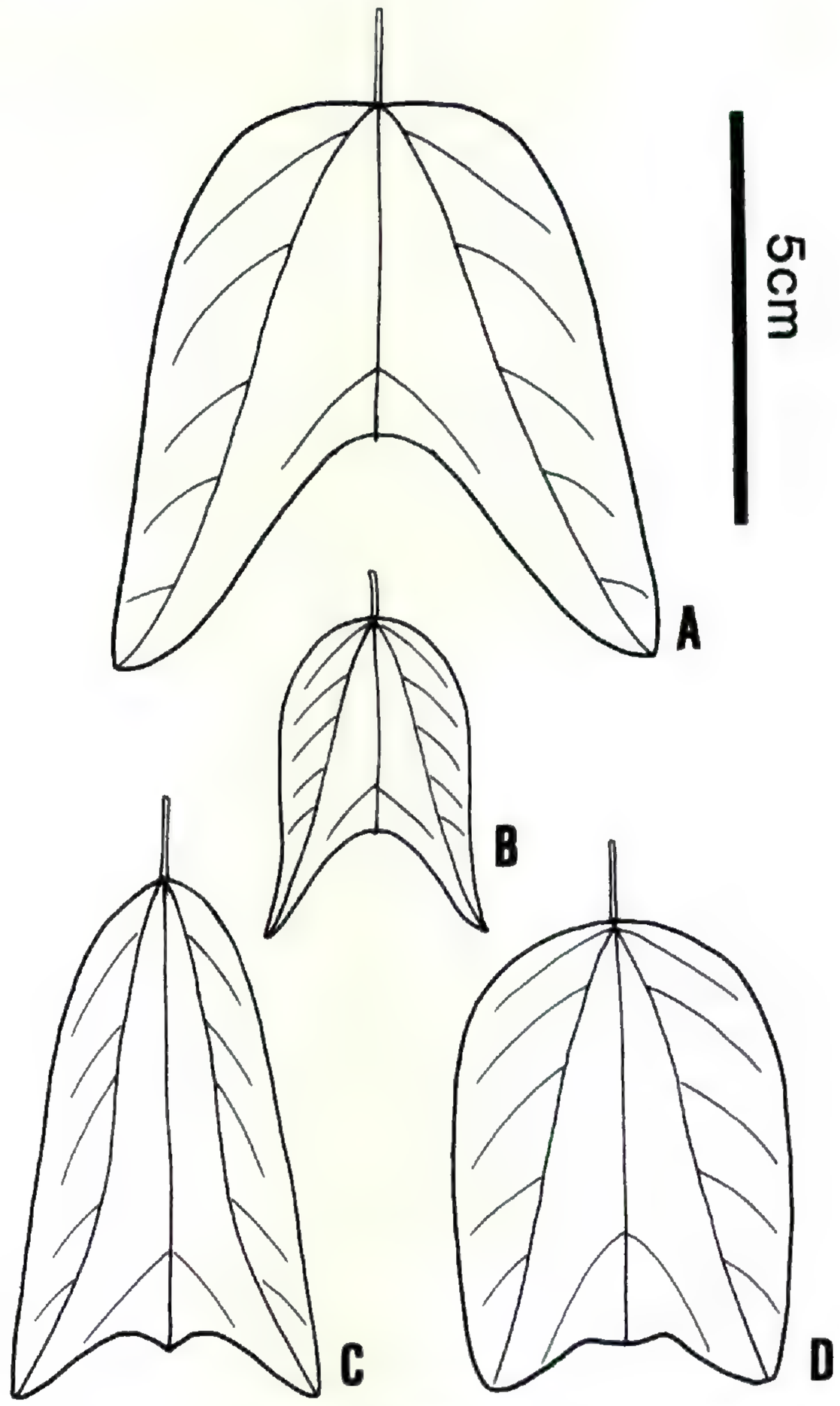

FIGURE 1. Variation in shape of leaves of *Passiflora citrina*.—A. *Molina 5826*.—B. *Molina & Molina 14086*.—C. *Molina & Molina 26057*.—D. *Molina & Molina 31167*.

Passiflora citrina may be referred to subg. *Plectostemma* sect. *Xerogona* because of the subpentangular stem, absence of petiolar or laminar nectaries, absence or near absence of floral bracts, elongate fruits with six keels, and seeds with a transversely grooved sclerotesta having a chalazal beak that is sharply angled towards the raphe. Mature fruits are unknown; however, a fruit that is probably of full size with nearly mature seeds is found on the isotype at NY. On a different collection, *Howard et al. 637*, the collector observed the fruits to be "red," but no fruits are included with the specimens. It is unknown whether the fruit

of this species is six-valvately dehiscent, as is usual in the other members of sect. *Xerogona*.

Passiflora citrina is remarkable for its elongate yellow flowers that are tubular in the basal half. The androgynophore is distinctively long and sets the species apart from all other members of sect. *Xerogona* except *P. sanguinolenta* Masters from southern Ecuador. Though very similar to *P. citrina*, *P. sanguinolenta* has nearly triangular stems, peduncles solitary at the nodes, pink to purplish red flowers that retain a diminutive second series of coronal filaments, and seeds with slightly rugulose ridges. Both species have slightly elongate flowers of similar morphology, flowers that have departed from the usual bowl-shaped hymenopteran-adapted groundplan in sect. *Xerogona* (Lindman, 1906) by reduction and fusion of the coronal filaments and partial connation and adnation of the perianth. In *P. citrina* the sepals are free from each other to within 2–6 mm of their bases, but they are submarginally adnate to the edges of the petals; the petals, in turn, are adnate to the connate portion of the coronal filaments. The net effect is a cylindrical structure formed by the adnation of the basal half of the perianth to the tubular and basally connate coronal filaments. The coronal filaments are free only in the distal 3–6 mm and are usually not visible on herbarium sheets without dissection. In dissected and living specimens, I could detect no trace of a second series of coronal filaments near the operculum.

The derived floral morphology of *P. sanguinolenta* is related to a shift in pollinators: the species is primarily hummingbird pollinated in its native habitat (C. Hofmann, pers. comm.). It is probable that *P. citrina* has also shifted away from pollination by hymenopterans.

The butterfly *Heliconius charitonius* was observed using *MacDougal et al. 3048* as a host plant.

Floral bracts are fundamentally absent in *P. citrina*, but in *Molina 6510* the peduncles occasionally bear a single bract at the apex.

This species was first identified as undescribed while the author was a National Science Foundation Fellow at Duke University, and I gratefully acknowledge the financial support of the NSF, the assistance of the curators from the herbaria cited above, and Donald E. Stone for inspiration and guidance during my doctoral studies. The Jessie Smith Noyes Foundation generously provided postdoctoral support for research on Passifloraceae at the Missouri Botanical Garden.

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A NEW SPECIES OF *STRYPHNODENDRON* (FABACEAE: MIMOSOIDEAE) FROM AMAZONIAN ECUADOR

Stryphnodendron Mart. (Fabaceae: Mimosoideae) is a genus of 25 known species, primarily Brazilian in distribution. It is well represented in Amazonia by forest trees and in the Brazilian cerrado region by shrubby species (Occhioni Martins, 1974, 1981; Occhioni, in prep.). Recent collections by the senior author and associates in eastern Ecuador, in the course of fieldwork for a floristic study of the trees of the region, have revealed a new species of *Stryphnodendron* at the western edge of the Amazon basin and in the adjacent foothills of the Andes.

Stryphnodendron porcatum Neill & Occhioni f., sp. nov. TYPE: Ecuador. Napo: 1 km N of Coca, Tropical Moist Forest, alluvial soil, floodplain near mouth of Río Coca, secondary forest and pasture, 250 m, 00°25′S; 77°00′W, 15 Sep. 1986 (fl, frt), *David Neill & Walter Palacios 7359* (holotype, QCNE; isotypes, MO, RFA, QCA, QAME, AAU, NY, K, GB, US, about 10 additional isotypes to be distributed). Figure 1.

Stryphnodendro guianensi (Aubl.) Benth. subsp. *glanduloso* Forero foliis simile, sed calyce et corollae lobis aureopubescentibus recedit; a speciebus ceteris epicarpii ornamento, ordinatione irregulare cristarum in fructus valvis differt.

Trees attaining 40 m with trunk to 60 cm diam. Outer bark grayish brown, lenticellate. Young branchlets, inflorescence axis, and petioles with minute dense brown scurfy tomentum. Leaves 15–16(–22) cm long; petiole terete, puberulent 3.5–5.0 cm, with a 1-mm verruciform gland about 2.5 cm from its base; rachis villous 11–12(–18) cm, with rounded glands between the distal 5–8 pairs of pinnae. Pinnae 11–13 pairs, opposite or subopposite, 5–6(–9) cm long, with small rounded glands between the pairs of leaflets, excepting the 2–3 basal pairs. Leaflets 10–13-jugate (6–7-jugate in the proximal 1–2 pinnae), alternate, elliptic, 6–10(–14) × 3–4(–5) mm, the apex retuse or slightly emarginate, the base unequal; venation inconspicuous; upper surface glabrous, lustrous; lower surface sparsely and evenly villous, the midrib and margins more densely so, with a dense tuft of villi near the base of the blade; margins slightly revolute and thickened; petiolules 0.5 mm, villous. Inflorescence spicate, cylindric, axillary, solitary or 2 together; peduncle terete, brown-scurfy, 1–1.5 cm long; rachis densely pubescent, 5–8 cm long. Flowers hermaphroditic, or sometimes all staminate, 3.5–4 mm long, bracts conchiform, deciduous. Calyx cupular, 1 mm with 5 deltoid lobes, densely golden pubescent. Corolla narrowly campanulate, 2–2.5 mm; lobes acute, 1 mm; basal half of corolla glabrous or with a few scattered golden hairs, the lobes densely golden pubescent externally. Stamens 10, free; filaments 3–4 mm; anthers elongate, 0.5 mm, with a stipitate deciduous apical gland. Ovary 1.5 mm, short-stipitate, densely white-pilose; style 2 mm, filiform, glabrous or with a few hairs. Legume subligneous, 10–12(–14) × 2–2.5(–3) cm, slightly curved, dark brown with scurfy epidermis, the epicarp ornamented with a pattern of ridges aligned at an angle from the center of each valve trending proximally toward the edges, forming a repeated, irregular chevron-like pattern. Seeds transverse, ellipsoid-oblong, 8–10 × 5 mm, dark brown, surrounded by sweet gelatinous pulp.

Additional specimens examined. ECUADOR. NAPO: Cañón de Los Monos, 15 km al N de Coca, 250 m, 00°20′S, 77°01′W, 5 Apr. 1985 (frt), *Neill, Baker, Palacios & Zaruma 6365* (MO, QAME, RFA); Estación Experimental INIAP-Payamino, 5 km al N de Coca, Reserva Florística El Chuncho, 250 m, 00°25′S, 77°00′W, 8–11 Aug. 1986 (frt), *Neill, Palacios & Zaruma 7227* (MO, QAME, RFA); 2 km al N de Coca, 250 m, 4 Oct. 1987 (flr), *Neill, Palacios, Cerón & Manning 7837* (MO, QAME); Reserva Biológica Jatun Sacha, Río Napo, 8 km río abajo de Misahuallí, 450 m, 01°08′S, 77°30′W, 2 Oct. 1986 (flr.), *Walter Palacios 1369* (MO, QAME, RFA). PASTAZA: 2 km al NE de Mera, 1,100 m, 01°27′S; 78°06′W (sterile), *Neill, Baker, Palacios & Zaruma 6161* (MO, QAME). MORONA-SANTIAGO: Taisha, 500 m, 02°23′S; 77°30′W, Oct. 1975 (fl, frt), *E. L. Little, Jr. et al. 690* (QAME, US); Sucúa, 1,200–1,500 m, 02°34′S, 78°10′W, 7–9 Oct. 1975 (flr, frt), *E. L. Little, Jr. et al. 670* (QAME, US).

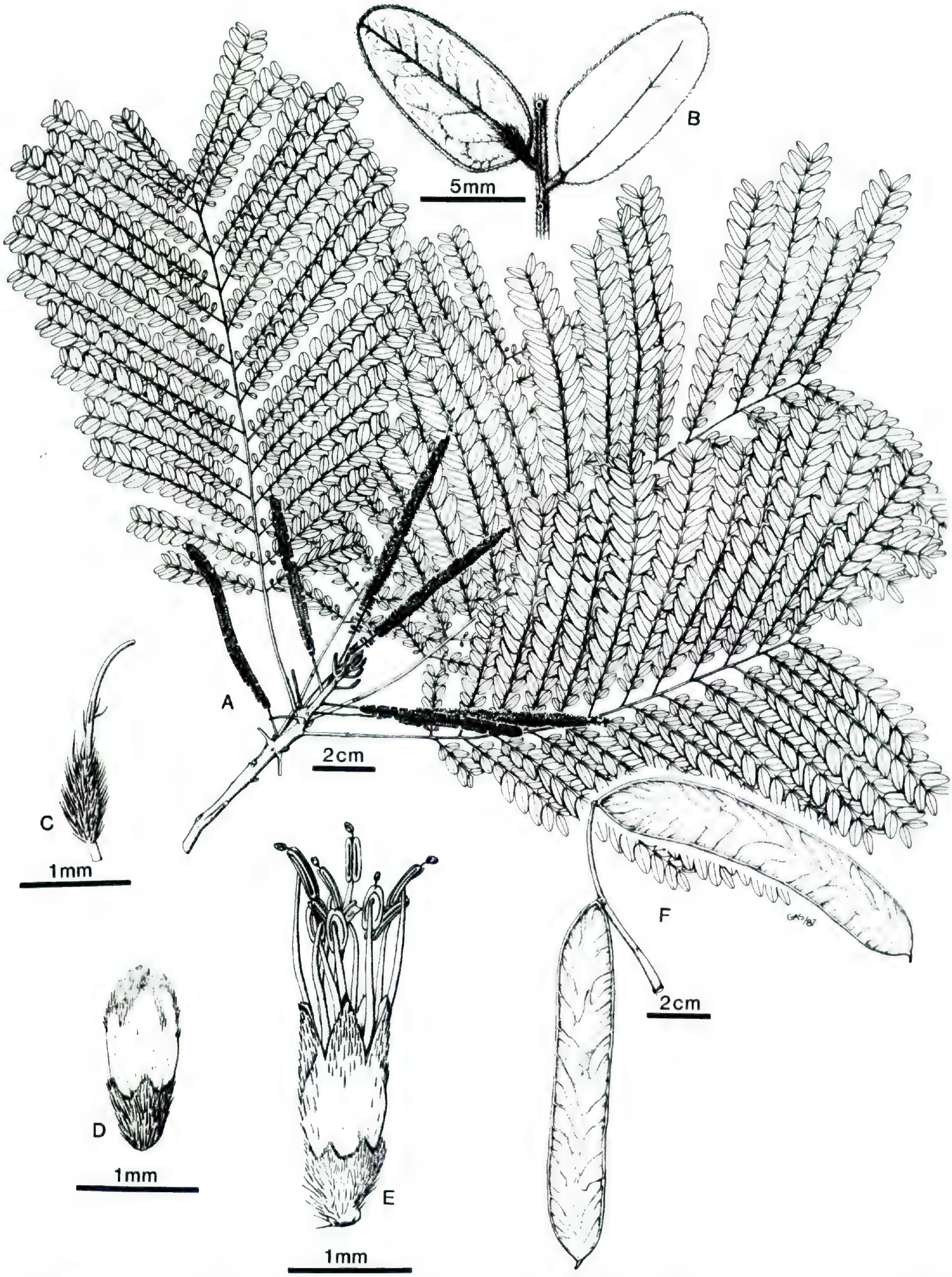

FIGURE 1. *Stryphnodendron porcatum.*—A. Habit.—B. Pair of leaflets, showing upper (right) and lower (left) surfaces, and small glands between each pair of leaflets.—C. Pistil.—D. Flower bud.—E. Open flower.—F. Mature fruits, showing pattern of ridges on epicarp.

Stryphnodendron porcatum is probably most closely allied with *S. guianense* (Aubl.) Benth. subsp. *glandulosum* Forero, known from Peru, Bolivia, and Amazonia in western Brazil, which has similar pubescence of foliage, including the tuft of hairs near the base of the blade, and densely pilose ovary. In *S. guianense* subsp. *glandulosum*, however, the calyx and corolla are short-puberulent externally, whereas in *S. porcatum* the calyx and corolla lobes are densely pubescent with longer, golden hairs, while the corolla tube is nearly glabrous with scattered golden hairs. The typical subspecies of *S. guianense*, which ranges widely in Amazonia and the Guianas, lacks the tuft of hairs at the base of the leaflet blades, and all floral parts are glabrous.

The most distinctive feature of *S. porcatum*, which readily separates it from all other species in the genus, is the striking ornamentation of the legume, an irregular chevron-like pattern of ridges on the surface of the valves. The specific epithet refers to this sculptured surface of the fruits (Latin *porca* = "ridge between two furrows made in plowing"; Stearn, 1966).

Some individuals of *S. porcatum* are evidently female-sterile; the flowers of *Palacios 1369* completely lack pistils.

To our knowledge, this is the first published report of the genus *Stryphnodendron* for Ecuador. No other species are known to occur sympatrically with *S. porcatum* in the Amazon region of the country.

Stryphnodendron porcatum occurs on rich silty alluvial soils of river floodplains, and in Amazonian Ecuador, on upland Oxisol hills up to 1,500 m on the lower slopes of the Andes. In primary forest it attains a height of 40 m with a diameter at breast height of 70 cm. In the region around Coca, Napo Province, Ecuador, *S. porcatum* is also frequent in secondary forests and is often left in pastures after the surrounding forest is cut.

The sweet pulp surrounding the seeds is similar to that of *Prosopis* and *Gleditsia*. Several trees at the INIAP-Payamino agricultural experiment station near Coca stand in experimental pastures established for raising tropical hair sheep. The sheep eat with great relish the *Stryphnodendron* pods that fall to the ground, apparently attracted by the sweet pulp. The new species therefore shows some promise for inclusion in agronomic trials as part of the agroforestry and silvo-pastoral production systems involving sheep, pastures, and forage legumes now being developed for and implemented by settlers in the Napo region of Ecuador.

The support of the U.S. Agency for International Development (USAID) and the Forestry Directorate of the Ecuadorian Ministry of Agriculture, for the research in eastern Ecuador, is gratefully acknowledged. The authors thank Enrique Forero for bringing us together through correspondence, and Alejandro Suárez for preparing the illustration.

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A NEW SPECIES OF *HYBANTHUS* (VIOLACEAE) FROM PANAMA

Hybanthus is a very poorly known genus of 150 species of herbs, trees, and shrubs from the Old and New World. The last synopsis of the genus throughout its range enumerated 32 species in the New World (Melchior, 1925); Morton (1944) provided the most recent synopsis of the Central American species. The new species proposed here, *Hybanthus jefensis*, is clearly distinct from all species in Central America and is not placed within any species presently known from Colombia (Smith & Fernández-Pérez, 1954).

Hybanthus jefensis Todzia, sp. nov. TYPE: Panama. Panamá: Cerro Jefe, near Río Indio, 2,100–2,200 ft., 17 Feb. 1968, *Dwyer 1969* (holotype, MO). Figure 1.

Frutices caulibus juvenibus strigulosis; stipulae anguste triangulares in siccitate chartaceae; folia alterna crenulata glabra in siccitate rubropunctata in pagina inferna; inflorescentiae axillares fasciculatae in brachyblastis, floribus 1–4 in pedicellis 1–2 cm longis; petalum panduratum 0.7–1 cm longum rotundatum ad apicem; capsulae 7–8 mm longae.

Shrubs 1–2.5 m tall; older stems terete, reddish brown, glabrous, sparsely branched; younger stems terete to quadrangular, dark to light brown, strigulose with hairs curving upwards, with leaves erect and ± adpressed to stems; stipules narrowly triangular, 1.5–2 mm long, ca. 0.5 mm broad at base, drying chartaceous, brown. Leaves alternate, elliptic to narrowly obovate, 3–12 cm long, 1–3.8 cm broad; petioles terete, 0.5–1 cm long, glabrous; the blade acute at apex, attenuate at base, smooth, glabrous, drying chartaceous with red dots and reticulations beneath, each side with 5–7 usually obscure, gradually arcuate lateral veins; the margin crenulate with 8–17 glandular teeth on each side. Inflorescences 1–4-flowered, axillary, fasciculate on short shoots ca. 2 mm long; bracts inserted at base of pedicels, lanceolate, 1–2 mm long, acute, drying chartaceous, brown; bracteoles on lower half of pedicels 0.5–1 mm long, lanceolate; pedicels 1–2 cm long, slender, glabrous, articulate above the middle. Flowers white, zygomorphic; sepals 5, lanceolate, 2–2.5 mm long, acute, glabrous; lateral petals 4, 4–5 mm long, falcate, with irregularly crenate margins; anterior petal pandurate, 0.7–1 cm long, with claw 4–5 mm long, sparsely pilose, lip 3–5 mm long, 4–5 mm broad at widest point, rounded at apex, glabrous; stamens 5, sessile, free or connate; filaments very short, the anterior 2 stamens with a subglobose gland dorsally; anthers 1–1.5 mm long, sparsely pilose dorsally and at base; connective appendages ca. 2 mm long, 0.5–1 mm broad, rounded at apex, membranaceous; ovary globose, ca. 1 mm long, glabrous, with 3 locules containing 1–2 ovules each; style 2–3 mm long, curved at apex. Capsules loculicidally and elastically 3-valvate, 7–8 mm long, glabrous, with 3–6 seeds, often with persistent style and sepals; seeds globose to ovoid, 2–3 mm diam., smooth, black.

Distribution, habitat, and phenology. Endemic to the Cerro Jefe region of the Prov. Panamá, Panama, at 650–1,000 m elevation in disturbed and undisturbed premontane wet forest. Flowering and fruiting October, November, December, January, and February.

Representative specimens examined. PANAMA. PANAMÁ: region of Cerro Jefe, ca. 1,000 m, 3 Oct. 1969, *Correa et al. 1598* (MO); between Cerro Azul and Cerro Jefe, 24 Dec. 1967, *Dressler 3270* (MO); between Cerro Jefe and La Eneida, 17 Jan. 1968, *Dwyer et al. 8195* (MO); 6.5 km by road N of Lago Cerro Azul, 650–730 m, 13 Jan. 1974, *Nee 9292* (MO).

This species is distinctive by virtue of its small crenulate leaves with red dots and punctations when dried; axillary inflorescences fasciculate on short shoots ca. 2 mm long; stipules that are chartaceous when dry; and pedicels 1–2 mm long. The anterior petal, one of the most diagnostic characters of the genus, is pandurate, 0.7–1 cm long, and rounded apically. In southern Central America *H. jefensis* appears to be most similar to *H. guanacastensis* Standley from which the new species differs by its chartaceous (vs. indurate) stipules, crenulate (vs. doubly serrate) leaf margins, shorter anterior petals (0.7–1 cm long vs. ca. 1.2 cm long), and smaller capsules (0.7–0.8 cm long vs. 1.5–2 cm long). *Hybanthus jefensis* is probably most closely related to *H. sylvicola* Standley & Steyerm. of southern

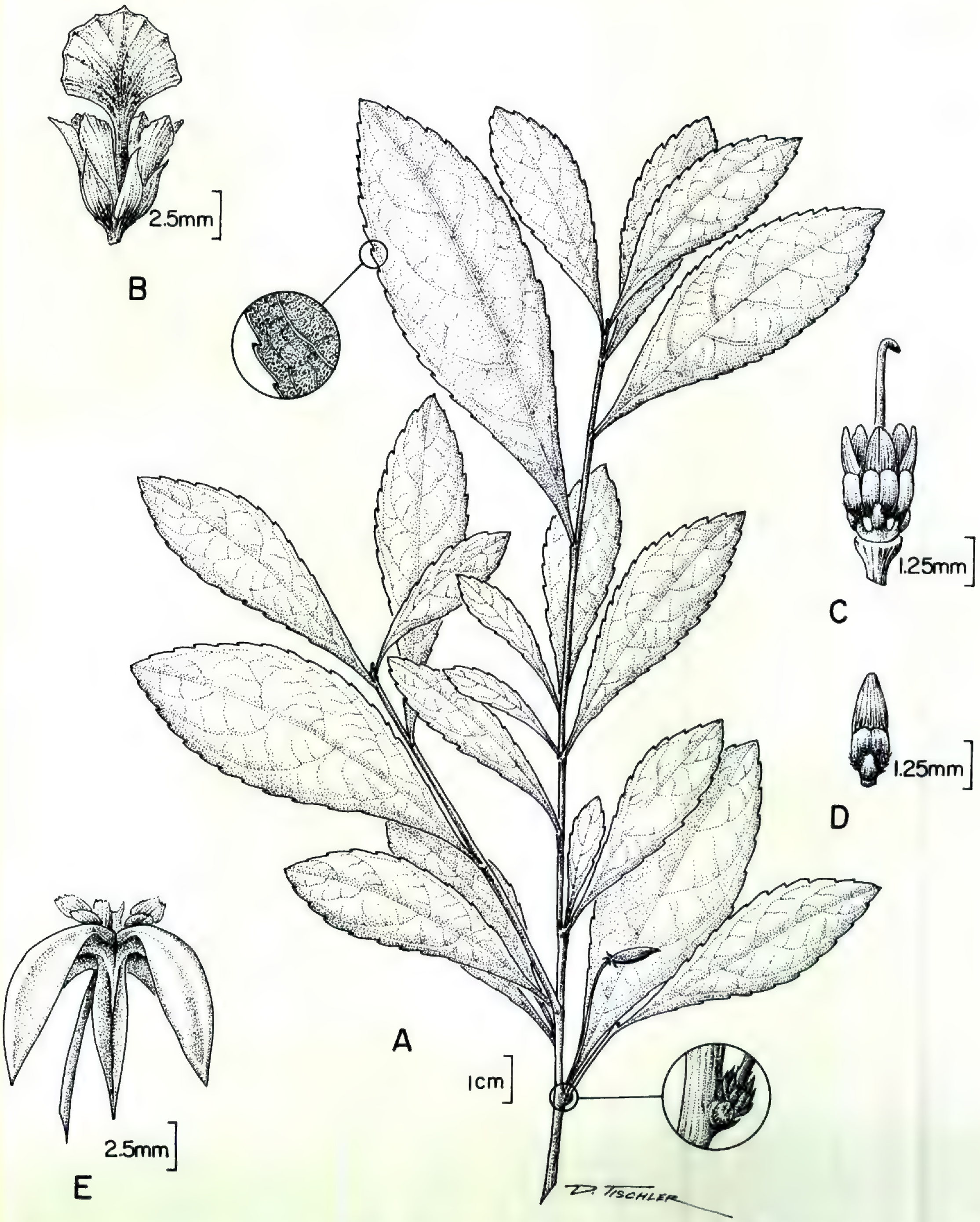

FIGURE 1. *Hybanthus jefensis.*—A. Habit with close-ups of leaf margin and leaf axil showing bracts at base of fascicles.—B. Flower.—C. Close-up of anthers and style with sepals and petals removed.—D. Close-up of an anterior anther. (A–D from *Dwyer 1969.*)—E. Fruit (from *Dwyer 8195*).

Mexico and Guatemala but differs by having strigulose (vs. glabrous) young branches, leaves with (vs. without) red punctations beneath, and lip 0.7–1 cm vs. 1.1–1.3 cm long.

Hybanthus jefensis is yet another endemic to the region of Cerro Jefe in central Panama (Lewis, 1971). In addition to the three *Hybanthus* species reported in the *Flora of Panama* (Robyns, 1967), two other species are presently known from Panama (D'Arcy, 1987; pers. obs).

KEY TO *HYBANTHUS* IN PANAMA

1a. Shrubs or small trees, woody; flowers in fascicles borne on short shoots.
  2a. Shrubs or small trees 1–7 m tall; capsules 0.7–2 cm long.
    3a. Stipules drying white, indurate; leaves sharply serrate, drying uniform in color beneath, without red dots; anterior petal 1.2–4 cm long; capsules 1–2 cm long.
      4a. Anterior petal up to 4 cm long; capsules 1.5–2 cm long; seeds 4–5 mm long ..... *H. prunifolius*
      4b. Anterior petal ca. 1.2 cm long; capsules 1–1.3 cm long; seeds 2–3 mm long ..... *H. guanacastensis*
    3b. Stipules drying brown, chartaceous; leaves crenulate, drying with red dots and reticulations beneath; anterior petal 0.7–1 cm long; capsules 0.7–0.8 cm long ..... *H. jefensis*
  2b. Shrubs less than 1 m tall; capsules 0.3–0.6 cm long ..... *H. galeottii*
1b. Annual or perennial herbs, not woody; flowers solitary, not borne on short shoots.
  5a. Leaves opposite to subopposite at base, elliptic to lanceolate, long-attenuate at apex; plants annual ..... *H. attenuatus*
  5b. Leaves alternate, ovate to oblong-ovate, acute at apex; plants perennial ..... *H. thiemii*

I thank Guy Nesom for providing the Latin description, Doris Lee Tischler for the handsome illustration, and James W. Grimes, George Rogers, and Henk van der Werff for reviewing the manuscript. This work was supported by a Noyes Foundation grant to the Missouri Botanical Garden.

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SMITH, L. B. & A. FERNÁNDEZ-PÉREZ. 1954. Revisio Violacearum Colombiae. Caldasia 6(28): 83–181.

—Carol A. Todzia, *Department of Botany, University of Texas, Austin, Texas 78712, U.S.A.*

BOOK REVIEW

Mora-Osejo, Luis Eduardo. 1987. *Estudios Morfológicos, Autoecológicos y Sistemáticos en Angiospermas*. Academia Colombiana de Ciencias Exactas, Físicas y Naturales, Serie Jorge Alvarez Lleras 1: 1–195. Retail price: $15.00. (Available from Dr. L. E. Mora-Osejo, Academia Colombiana de Ciencias Exactas, Físicas y Naturales, Apartado Aéreo 44763, Bogotá D.E. 1, Colombia.)

Morphological, Autecological and Systematic Studies in Angiosperms is an important addition to the increasing botanical literature of high scientific quality being produced in Latin America. It has been published by the Colombian Academy of Sciences as the first volume of a new series called "Serie Jorge Alvarez Lleras." The actual text is 188 pages long, with 75 figures, including several color photographs, and a bibliography with over 90 citations. The text is divided into two parts. The first part deals with the morphological and autecological studies and includes five chapters (1–5), while the second deals with the systematic studies and is made up of one chapter (6).

The author indicates that one of his objectives is to present to a broader audience the "typological" method, which has been developed in Germany but is not well known among Spanish- and English-speaking phytomorphologists. In the first chapter he discusses the general principles of the typological method, including such concepts as homology, position, continuity, similarity, etc.; the procedures employed in the study of specific problems; the contribution of typology to our understanding of the organization and architecture of the angiosperms; and the relationship of typology with taxonomy and phylogeny. In Chapter 2, the typological theory and its relation to the evolution of the inflorescence is discussed. Chapter 3 deals with new concepts developed by the author on the diversity and evolution of organizational patterns found in the floral meristems in angiosperms, based on his observations of a number of families, including Melastomataceae, Araliaceae, Bignoniaceae, Asteraceae, Cyperaceae, Juncaceae, Poaceae, Bromeliaceae, and Scheuchzeriaceae. Chapters 4 and 5 deal with the author's original typological studies in *Lilaea*, *Triglochin*, and *Scheuchzeria*, which include the study of the architecture of the meristem and its correlation with the reproductive strategies of these plant groups. In Chapter 6, Mora-Osejo gives an example of the applicability of the typological method to the taxonomic study of *Oreobolus* R. Br., a genus of Cyperaceae.

There are several aspects of this publication that I find outstanding, the most important being the thorough discussion of the theory and practice of the typological method. The author explains how this method allows for a comparative analysis of architectural patterns in plants as opposed to a purely descriptive analysis. The method also allows for interpretation of information derived from the detailed analysis of plant structures through the understanding of the interconnections among them. At the same time, it provides valuable tools for understanding adaptations to the environment as well as reproductive strategies in angiosperms.

Aside from its obvious scientific value, the reader is also very favorably impressed by the good quality of the printed product and by the quantity and quality of the illustrations, which include numerous schematic representations, color and black and white photographs, details of plant parts, and more.

The volume is a substantial contribution to our understanding of this important subject, as are most of Professor Mora-Osejo's publications. His study of the biology of the Haloragaceae, published as part of his treatment of the family for the *Flora de Colombia*, is another example of his scientific excellence. It is to be expected that this volume will be given proper consideration by phytomorphologists in the United States and in Latin America. Its contents are well worth careful study. This work is the result of many years of careful research by one of Latin America's most prominent scientists.—Enrique Forero, *Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.*

NOTICES

The 1988 Jesse M. Greenman Award

The 1988 Jesse M. Greenman Award has been won by John H. Wiersema for his publication "A Monograph of *Nymphaea* Subgenus *Hydrocallis* (Nymphaeaceae)," which appeared in Systematic Botany Monographs, volume 16. This monograph is derived from a Ph.D. dissertation submitted to the University of Alabama, under the direction of Dr. Robert R. Haynes. Dr. Wiersema based his classification on numerical taxonomy, scanning electron microscopy of seeds and pollen, chromosome numbers, floral biology, artificial hybridization, flavonoid chemistry, and general morphology. Fourteen species are recognized in the subgenus, which is restricted to the American tropics and subtropics, and one new subspecies is proposed.

This Award is named for Jesse More Greenman (1867–1951), who was curator of the Missouri Botanical Garden Herbarium from 1919 until 1943. A cash prize of $250 is presented each year by the Garden, recognizing the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation that was published during the previous year.

Nominations for papers published during 1988 are now being accepted for the 21st annual award, which will be presented in the summer of 1989. Reprints of such papers should be sent to: Greenman Award Committee, Research Division, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. In order to be considered for the 1989 award, reprints must be received by June 1, 1989.

Reprints

Copies of "The Genus Xyris (Xyridaceae) in Venezuela and Contiguous Northern South America" (Ann. Missouri Bot. Gard. 75: 522–722. 1988) can be obtained by sending $15.00 to: Dr. Robert Kral, Herbarium, Box 1705, Station B, Vanderbilt University, Nashville, Tennessee 37235, U.S.A.

Volume 75, Number 4, pp. 1169–1670 of the Annals of the Missouri Botanical Garden was published on 8 March 1989.

Tropical florulas

Recognizing the utility of floras of restricted tropical areas to workers in a variety of biological disciplines, Missouri Botanical Garden staff members have produced several during the past few years. Available titles are:

La Flora de Jauneche

C. H. Dodson, A. H. Gentry & F. M. Valverde

This is the first in a series of florulas of the life zones of Ecuador. It treats the plants of the Jauneche field station, located in tropical moist forest between Quito and Guayaquil, at an altitude of 50–70 meters. The station occupies 130 hectares and has a known flora of 728 species. All are treated, and each is illustrated with a line drawing of its habit and details of critical features. The book is bilingual: all information is in both English and Spanish.

xxxix + 512 pages, 184 plates, 14 figures; soft bound. Published by Banco Central de Ecuador. 1986. $25.00

Flora of the Río Palenque Science Center

C. H. Dodson & A. H. Gentry

This flora is similar in plan to the Jauneche work, but it treats more species, about 1100. The Río Palenque station occupies 167 hectares at an altitude of 150–220 meters in the tropical rainforest life zone.

xxx + 628 pages, 278 plates, 22 figures; soft bound. Published as Selbyana, vol. 4, 1978. $35.00

Flora of Barro Colorado Island

Thomas B. Croat

About 1350 species of vascular plants are described and many illustrated from Barro Colorado Island, the Smithsonian Institution's 15.6 sq. km reserve in the Panama Canal. "Croat's well-executed effort sets the precedent for the kind of work perquisite to fuller understanding." David Barrington, *Plant Science Bulletin.*

ix + 943 pages, illustrated. Stanford University Press. 1978. $60.00.

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NEW SPECIES AND COMBINATIONS IN TROPICAL AMERICAN *POLYSTICHUM* (DRYOPTERIDACEAE)[1]

David S. Barrington[2]

ABSTRACT

A taxonomic history for the fern genus *Polystichum* in Latin America and an analysis of the important characters at the species level in the genus provide the context for the recognition of new and overlooked taxa. Three new species are described from Latin America, and a new combination is provided for a *Polystichum* species from the southern Andes.

In the course of preparing a treatment of the genus *Polystichum* for the *Flora Mesoamericana*, I have discerned a set of new and neglected species from Central America and the northern Andes, which I report here. The species now included in the genus *Polystichum* have only once been included in a monograph (Mettenius, 1858); there has been no modern monographic work on the genus in the New World. An inquiry into species and speciation phenomena in Costa Rica (Barrington, 1985a, b; Barrington, et al., 1986) has led in turn to an inquiry into the significance of hybrids with respect to species concepts in the ferns (Barrington et al., in press). I report here on the morphological characters important in distinguishing species of Latin American *Polystichum*. This review of characters provides the context for the descriptions of species, which make up the central contribution of this work.

TAXONOMIC HISTORY

The genus *Polystichum* Roth, terrestrial ferns characterized by fastigiate leaves with inequilateral leaf segments and peltate indusia (when present), is prominent and diverse in montane regions

[1] I thank Luis Diego Gómez P. for his energy and support of my fieldwork in the Sierra Talamanca, Steven R. Hill for his critical reading of the Latin descriptions, and Lynn Bohs for her thorough review of the manuscript. Several nomenclatural and taxonomic problems were resolved with Rolla Tryon's help. The curators of the following herbaria supported this project through loan of materials: A, AAU, CR, ENCB, F, GH, MO, NY, UC, US, USNA, YU. The University of Vermont provided support for laboratory and fieldwork through its Institutional Grants BRSG-79 and BSCI85-1.

[2] Pringle Herbarium, Department of Botany, University of Vermont, Burlington, Vermont 05405-0086, U.S.A.

throughout the world. The generic name originates with Roth (1799), but it was K. B. Presl (1836) who first circumscribed the genus as it is now recognized. The most important influence on the taxonomic history of *Polystichum* was the treatment of W. J. Hooker (1862), in which most of the twice-pinnate taxa in the world were combined into one species. As a result, the morphological and taxonomic diversity of species was left unstudied by the otherwise productive taxonomists of the late nineteenth century. Christensen (1906) maintained Hooker's counterproductive species concept in *Polystichum*, which has perpetuated the tendency for taxonomists to ignore the diversity of twice-pinnate species. Christensen did recognize 41 forms, many of which were associated with names whose types represent distinct species.

Latin America and eastern Asia are the two centers of diversity for the genus *Polystichum*. Although the diversity and biology of species are well known in Asia (Tagawa, 1940; Daigobo, 1972), we know little about the genus in the New World tropics. Maxon (1909) was the first to recognize natural species in the American tropics, but his work was confined to the West Indies. Only recently (A. R. Smith, 1981; Stolze, 1981) has similar progress been made in defining the continental species. In the past few years, the extent of the taxonomic problem has become clear with the demonstration of extensive hybridization and allopolyploidy in the American tropics (Barrington, 1985a, b; Barrington et al., 1986). I reviewed the present taxonomic status of the genus *Polystichum* in Latin America (Barrington, 1985c).

Morphology

The analysis leading to the descriptions of the new species provided here and the work on hybridization and polyploidy have revealed the most useful characters for delineating *Polystichum* species in Latin America. Since there has been no previous morphological review for the genus in the Neotropics, I provide an analysis of the important characters for *Polystichum*. I have also commented on ontogenetic and environmentally induced variation, which is unusually confusing in the genus.

Indument

Indument in *Polystichum* consists entirely of scales and scale homologs (squamules and microscales); true hairs, bristles, and spines are absent, at least in Latin American species. The general form, texture, and frequency of scales are important in delineating taxa of *Polystichum*. Particularly important are histological features of the scales: they may be conform (sensu Tryon, 1970) or they may have a margin of cells different in shape and orientation from the scale body. Scale color is important too, although variable with position on the plant and age of the plant. Tagawa (1940) contended that the smallest scales on the abaxial lamina surface (the microscales) are important in defining subgeneric groups in *Polystichum*. In Latin America, variation in microscales is extremely conservative, consistent with Tagawa's contention. Most species have the acicular microscales typical of sect. *Metapolystichum*.

I have followed Smith (1981) in describing the processes that arise from the edges of scales and squamules as cilia, although this is an oversimplification. In fact, scales and squamules bear a continuum of processes from cilia (long and delicate) to setae (short and stiff). I have chosen to call all of these processes cilia and use adjectives to describe their length and stiffness. The kinds and proportions of these cilia on the different scales and squamules are important taxonomic characters in *Polystichum*.

Lamina

The dissection and texture of the lamina provide critical characters for distinguishing species of *Polystichum*, although they are phenotypically and ontogenetically variable. Particularly confusing is the tendency for older plants to have larger, more dissected leaves. Nevertheless, species can be circumscribed within the context of the ontogenetic variation encountered. In addition, the shape, angle of attachment, and revoluteness of leaf segments (pinnae and pinnules) are all important, although phenotypically variable (especially revoluteness). Development of the spinules (extensions of vein tips) varies among species. The complex interaction of ontogeny, environment, and genotype that shapes *Polystichum* leaves perhaps explains the recognition of large, poorly resolved taxa by both Hooker and Christensen.

Sori and Sporangia

The placement of the sorus relative to the vein tips is important in *Polystichum*, even though it is variable across a segment. Indusium presence or absence is an important character, although the indusium is sometimes deciduous in neotropical *Polystichum* species. In addition, the diameter, shape, and histology of the indusium vary among, but usually not within, species. Color is sometimes use-

ful but is variable with age. The design of the perispore is usually constant within species.

Color of the indument is a useful character in *Polystichum*, as in many ferns. The color names used in the descriptions here are the National Bureau of Standards color names as defined in *National Bureau of Standards Special Publication 440* (and its predecessor, *Circular 553*), evaluated by comparison of indument with the ISCC-NBS Color-Name Chart (a supplement to *NBS Special Publication 440*), which is a partial set of color chips representing the color centroid. I standardize color terminology in this way, rather than using the Ridgway-Dade terminology and standardization (Stearn, 1983), because those color names are much less familiar, and the color chips on which they are based are much harder to locate. Indument is variable and systematically useful in all three dimensions of the color centroid (hue, value, and chroma); it is also variable in these dimensions with position on the plant and age of the individual.

Hybridization and Species Definition

Hybrids between the new Costa Rican species described here and several other species were encountered during fieldwork. Several of these hybrids have been described elsewhere (Barrington, 1985a, b). All of them meet two criteria of hybridity: intermediacy and spore irregularity. Since all of the hybrids have irregular spores, they are probably sterile and hence provide evidence of species-level divergence between their progenitors (Barrington et al., in press). This evidence provides a first working hypothesis for species definition in tropical American *Polystichum* and the basis for recognizing the new species described here.

Descriptions of New Species

Polystichum concinnum Lellinger ex Barrington, sp. nov. TYPE: Costa Rica. San José: Villa Mills, S of Pan American Highway about one km E of Hotel La Georgina, ca. 3,100 m, 3 Jan. 1980, *D. S. Barrington 694* (holotype, GH; isotype, VT). Figure 1.

Filix grandis terrestris. Caudex erectus base ascendente. Squamae petiolorum anguste lanceolatae, coriaceae, badiae, pallidomarginatae, cilia proximalia squamarum petiolorum longa tenuiaque, distalia brevia, indurata, saepe processibus recurvatis unciformibus. Lamina 0.4–2.0+ m longa, bipinnata, indumento paginae rhachidis abaxialis constans e squamis lanceolatis umbrinis. Pinnae patentes attenuatae, pinnis medianis circa 7–18 cm longis. Pinnulae crenatae patentes fere planae vix spinulosae circa 0.8 cm longae 0.4 cm latae, squamis minimis acicularibus, pallidibus. Sorus terminalis in ramo acroscopico venae locatus, indusio peltato circa 0.5–0.7 mm diametro.

Plant terrestrial, the spreading-ascendent leaves to 2 m long. Stem erect from an ascendent base, sometimes with weak lateral branches. Petiole with 8 vascular bundles, 2 large adaxial and 6 small abaxial; petiole scales narrow-lanceolate, coriaceous, conform, blackish red to dark reddish brown with sharply delimited narrow lighter borders, the color transition to border abrupt; the proximal cilia frequent, long and delicate, the distal cilia scattered, short, indurate, often with recurved hooklike processes. Petiole squamules unguiculate and deltate, wrinkled, very dark red with deep orange borders, with cilia scattered on the unguiculate squamules to dense on the deltate squamules. Lamina 0.4 to more than 2 m long, chartaceous, acuminate, 2-pinnate, abaxial rachis scales strong brown, ciliate and lanceolate to sparsely ciliate and unguiculate. Pinnae ca. 20–35 on each side of the rachis, attached at right angles to the rachis, attenuate, the median pinnae ca. 7–18 cm long, basal pinnae about $\frac{9}{10}$ as long; pinna-rachis squamules strong brown, sparsely ciliate, lanceolate or rarely unguiculate. Pinnules ca. 10–25 on each side of the pinna rachis, attached at nearly right angles to the pinna rachis, flat, truncate at the base and obtuse to rounded, crenulate (the basal acroscopic pinnules of each pinna often pinnatisect above the auricle), weakly spinulose, about 0.8 cm long and 0.4 cm wide, the basal pinnules of each pinna abruptly shorter than the next distal pinnules; microscales of costules and veins acicular, pale, without glandular cells. Sorus terminal on an acroscopic vein branch, covered by a thin, peltate, casually deciduous indusium ca. 0.5–0.7 mm diam., the indusium flange of cubical to radially elongate, slightly sinuate cells organized into radial files, the indusium-flange margin a single row of narrow, radially elongate cells. Spores with a well-developed cristate perispore.

Distribution. Endemic to high, wet forests of the Sierra Talamanca, Costa Rica and Panamá, 2,000–3,000 m, occasionally to 3,400 m in disturbed areas above treeline.

The affinity of this large, graceful species is with the large group of indusiate and two-pinnate species most diverse in southern Mexico. *Polystichum concinnum* is most similar to two Mexican species, *P. rachichlaena* Fée and *P. erythrosorum* A. R. Smith: all three are large indusiate, flat-leaved, two-pinnate species with crenate pinnules, and they are

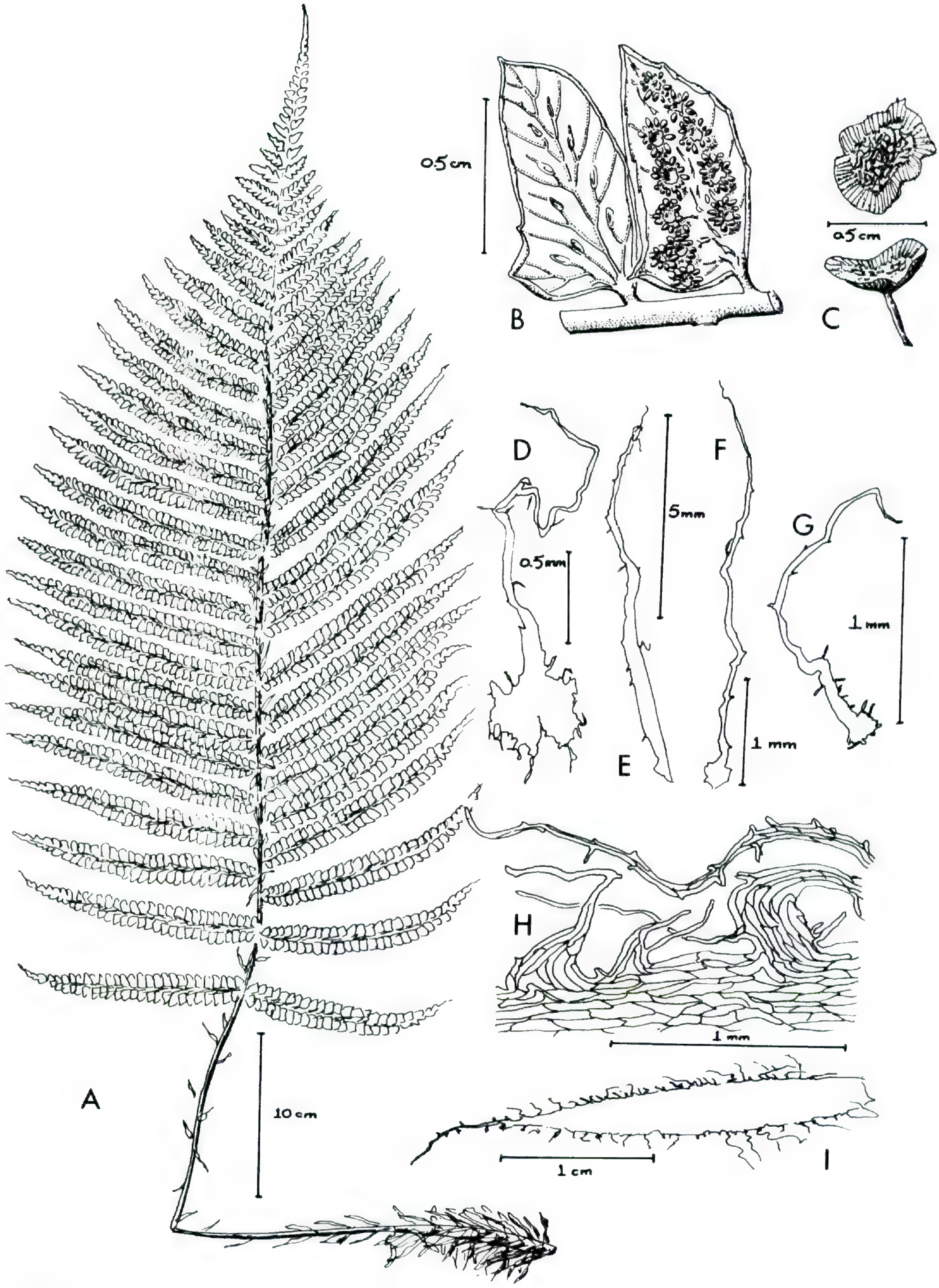

FIGURE 1. *Polystichum concinnum.*—A. Leaf.—B. Two pinnules, the left one with sori removed.—C. Indusium, from above (upper) and side.—D. Rachis scale.—E, F. Rachis squamules.—G. Pinna-rachis squamule.—H. Medial edge of petiole scale (below), petiole scale apex.—I. Petiole scale.

all confined to high-altitude forests. *Polystichum rachichlaena* is notable for the large size (over 1 mm diam.) and persistence of its indusia; it also has petiole scales virtually devoid of cilia. The lamina and sorus of *P. concinnum* are similar to those of *P. erythrosorum*, but the petiole scales of *P. erythrosorum* are broader, marginate, and strongly bicolorous (basally lustrous and black with brownish orange borders). In addition, the long, delicate cilia of *P. concinnum* are lacking in *P. erythrosorum*, and the small distal cilia are not dark and indurated as they are in *P. concinnum*. *Polystichum concinnum* is well represented in herbaria; it has been determined most often as either *Polystichum muricatum* (L.) Fée (which differs in having short petiole-scale cilia) or *Polystichum ordinatum* (Kunze) Liebm. (which differs in having narrow leaf bases and strongly bicolorous petiole scales with thick bases).

David B. Lellinger, of the United States National Herbarium, first distinguished *P. concinnum* and coined its species epithet.

Several chromosome counts of plants from the Talamanca range yielded $n = 41$ pairs at meiosis I.

Additional specimens examined. COSTA RICA. CARTAGO: Villa Mills, 1 km N of Restaurant La Georgina, 30 May 1978, *Barrington 576* (GH, VT). SAN JOSÉ: Cerro Chirripó, SW slopes, along ridge trail from Canaan to summit, 8,500–10,000 ft., 22 & 27 Aug. 1967, *Evans, Lellinger & Bowers 73* (US). PANAMA. CHIRIQUÍ: Cuesta de Las Palmas, southern slope of Cerro de la Horqueta, 1,700–2,100 m, 18 Mar. 1911, *Maxon 5527* (US).

Hybrids. Hybrids between this species and the distinctive *P. speciosissimum* have been collected four times from roadcuts on the Pan-American Highway in the Sierra Talamanca area of Costa Rica (*Barrington 705, 1274, 1516*, VT; *W. D. Stevens 14317*, MO). Hybrids with the following species are discussed under that taxon.

Polystichum talamancanum Barrington, sp. nov. TYPE: Costa Rica. Cartago: Cerro de la Muerte, roadcut 0.4 mi. W of highest point on Pan-American Highway, SE aspect, 3,330 m, 4 Jan. 1980, *D. S. Barrington 708* (holotype, GH; isotypes, CR, VT). Figure 2.

Filix terrestris. Rhizoma repens frondibus fasciculatis. Squamae petiolorum lanceolatae, plerumque papyraceae, luteofuscae, ciliis longis tenuibusque. Lamina foliorum fecundorum 12–70+ cm longa, rigide erecta in locis apricis, indumento paginae rhachidis abaxialis constanti e squamis longilanceolatis croceis. Pinnae ascendentes acuminatae vel breviter attenuatae, pinnae medianae circa 5 8 cm longae. Pinnulae patentes fere (70–80° e rhachidi), revolutissimae in locis apricis crescente, vix spinulosae, circa 0.8 cm longae, 0.4–0.5 cm latae, squamis minimis aicularibus pallidis. Sorus terminalis insidens ramo acroscopico venae, indusio genuino nullo vel spathulato, raro peltato, 0.05–0.07 mm lato.

Plant terrestrial, the rigidly erect leaves to 60 cm long. Rhizome short-creeping, with small lateral branches. Petiole with 2 large adaxial and 6 small abaxial vascular bundles; petiole scales lanceolate, herbaceous or rarely chartaceous, conform except at cilia, medially dark yellow-brown, the border similar or distally moderate olive-brown, the color transition to border gradual; the cilia proximally common, long, arising from broad bases of several cells ± perpendicular to the scale axis, thin and delicate; petiole squamules unguiculate, strong brown, ± flat, with broad and short cilia common at base. Lamina of fertile leaves 12 to 70+ cm long, rigidly erect (spreading-erect in shade), lanceolate, 2-pinnate; abaxial rachis scales narrow-lanceolate, uniformly medium to deep orange-yellow, with short cilia throughout and long cilia distally; abaxial rachis squamules like those of the petiole, deep orange, crumpled, the cilia well developed at squamule base. Pinnae about 40 on each side of the pinna rachis, attached at about a 40° angle to the rachis, acuminate to short-attenuate, the median pinnae ca. 5–8 cm long, basal pinnae ½–9/10 as long; abaxial pinna-rachis squamules deep orange with long cilia at the base and scattered short cilia distally, the larger long-lanceolate, the smaller unguiculate. Pinnules ca. 11–14 on each side of the pinna rachis, attached at about a 70–80° angle to the pinna rachis, strongly revolute in sun (only the sides of the pinnules revolute, not the tips), barely revolute in shade, cuneate at base and acute-tipped, crenulate (the basal acroscopic pinnules of each pinna often pinnatisect above the auricle), with spinules only at auricle and pinnule apex, ca. 0.7–0.9 cm long, 0.4–0.5 cm wide (wider at the well-developed auricle), the basal pinnules of a pinna about the same length as the more distal pinnules; microscales acicular, pale, without glandular cells. Sorus terminal (rarely subterminal) on an acroscopic vein branch, without true indusia or less commonly with a spatulate or rarely reniform to peltate indusium 0.05–0.07 mm diam., the spatulate indusia composed of a narrow proximal portion with cells elongate parallel to the axis and a broader distal portion with cells irregularly placed and shaped. Spores with a well-developed long-cristate perispore.

Distribution. Endemic to the subalpine rain-páramo areas and disturbed sites in the tropical

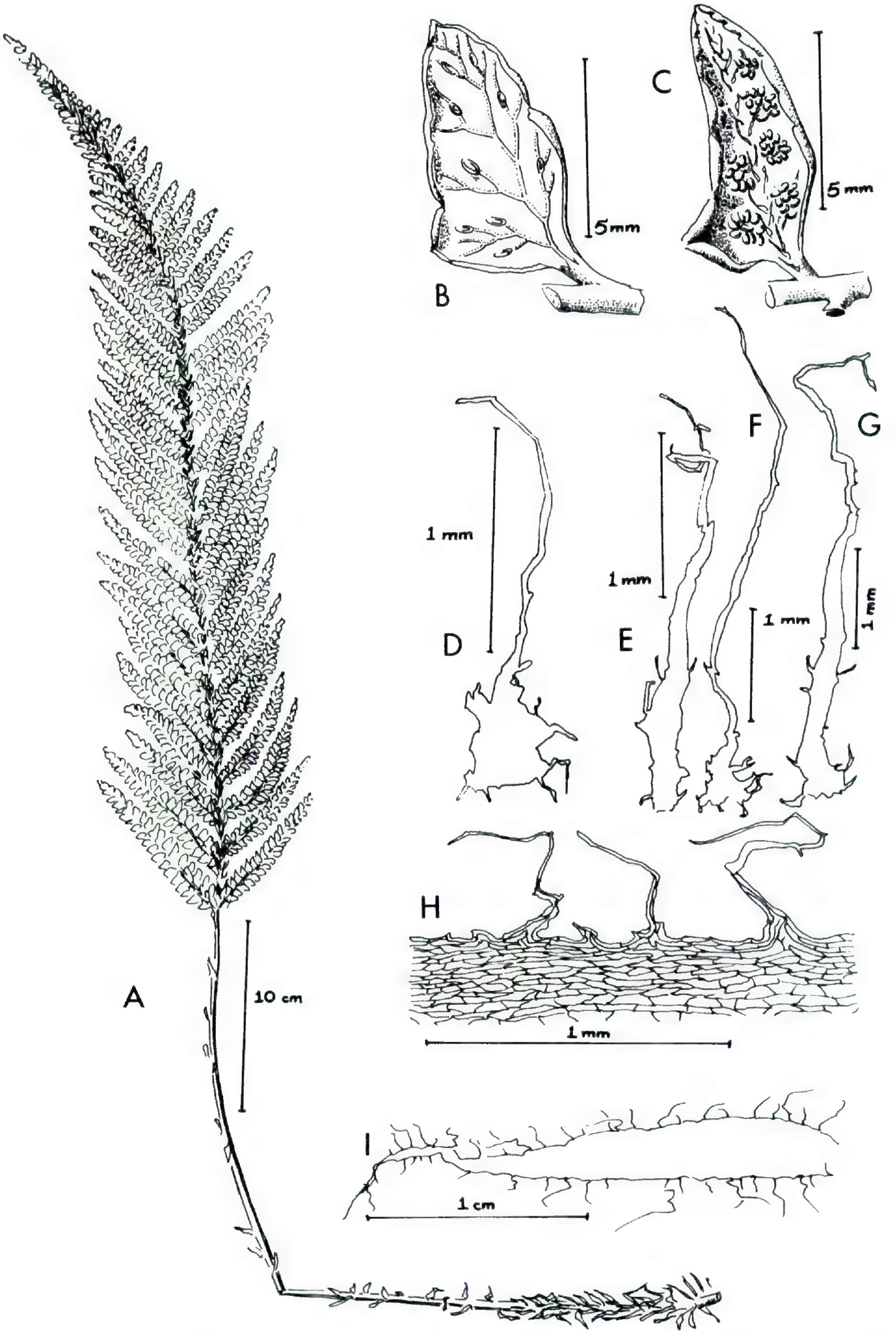

FIGURE 2. *Polystichum talamancanum*.—A. Leaf.—B. Pinnule of plant from shade site, sori removed.—C. Pinnule of plant from sunny site.—D. Petiole squamule.—E, F. Rachis squamules.—G. Pinna-rachis squamule.—H. Medial edge of petiole scale.—I. Petiole scale.

montane rainforest of Costa Rica and western Panamá, 3,000–3,500 m.

Polystichum talamancanum is the allotetraploid derivative of *P. concinnum* (described above) and an unknown diploid species that is also a progenitor of Costa Rican plants of the widespread tetraploid *P. orbiculatum* (Desvaux) Gay (Barrington, 1985b; Barrington et al., 1986, and unpublished data). (*Polystichum orbiculatum* is the

correct name of the widespread Latin American alpine *Polystichum* commonly known as *Polystichum polyphyllum* (Presl) Presl.) *Polystichum talamancanum* is prominent in rock clefts and on roadbanks along the Pan-American Highway above treeline in Costa Rica. It tends to have more patent pinnae and flat pinnules in shade. The indusia are variously developed: some sporophytes never have indusia; others regularly produce spatulate indusia. This variation complicates discrimination of *P. concinnum*, *P. talamancanum*, and their backcross hybrid.

Polystichum talamancanum, endemic to the region above treeline in the Sierra Talamanca, may be confused with *Polystichum orbiculatum* and allied taxa. *Polystichum orbiculatum* in Costa Rica has flaccid petiole scales that are paler and more orange than those of *P. talamancanum* and has long, delicate cilia throughout. In addition, *P. orbiculatum* has apically as well as laterally revolute pinnules, and it is never indusiate, whereas *P. talamancanum* has pinnules that are revolute only laterally and sometimes has indusia.

In the Andes from Venezuela to Peru, an array of plants has been collected from those like *P. orbiculatum* in Costa Rica to plants much like *P. talamancanum*. The Andean plants most like *P. talamancanum* differ from it in lacking indusia and having broader, larger petiole scales with narrow white borders bearing short, stiff cilia; if they are hybrids, their progenitors differ from those of *P. talamancanum* and are best determined as *P. pycnolepis* (Kze. ex Kl.) Mett. The taxonomy and evolution of *P. orbiculatum* and its allies in the Andes is a complex and intriguing problem: the hybrid origin of *P. talamancanum* on the Sierra Talamanca is likely to be one part of a much broader, Andean set of evolutionary events, including the origin of *P. orbiculatum* and other high-altitude *Polystichum* species.

Additional specimens examined. COSTA RICA. CARTAGO: Cerro de la Muerte, Pan-American Highway, 5 km above Millsville (about 8 km above Nivél), Cordillera de Talamanca, 3,400–3,500 m, 25 July 1949, *Holm & Iltis 590* (MO). SAN JOSÉ: Cerro Asunción del Macizo de Buena Vista, 3,325 m, 31 July 1964, *Jiménez M. 2235* (CR). PANAMA. CHIRIQUÍ: summit of Chiriquí Volcano, 3,374 m, 27 Feb. 1918, *Killip 5459* (US).

Hybrids. *Polystichum talamancanum* hybridizes with three species on the Sierra Talamanca in Costa Rica, making recognition of the taxa involved difficult. It hybridizes with its diploid progenitor *P. concinnum* to yield a highly variable triploid backcross, reported by Barrington (1985b) as *P. muricatum* × *P. polyphyllum*. Representative specimens of this hybrid are *Barrington 596*, *719*, and *1278* (all CR, GH, VT), all from Cerro de la Muerte, Costa Rica. In addition, sterile putative hybrids of *P. talamancanum* with *P. orbiculatum* (*Barrington 1283*, CR, GH, VT) and *P. speciosissimum* (*Barrington 1500*, CR, GH, VT) have been collected from disturbed sites above treeline in the Sierra de Talamanca.

Polystichum bulbiferum Barrington, sp. nov.
TYPE: Ecuador. Prov. Zamora-Chinchipe: road Loja–Zamora, km 39, 1,600–1,650 m (79°04′W, 3°59′S), 21 April 1973, *L. Holm-Nielsen, S. Jeppesen, B. Løjtnant & B. Øllgaard 4095* (holotype, AAU). Figure 3.

Filix terrestris. Rhizoma parvum, ascendens. Squamae petiolarum lanceolatae, papyraceae, emarginatae (conformes), umbrinae, ciliis longis tenuibusque. Lamina 0.3–0.4 m longa chartacea, acuminata, pinnata, abaxialiter bulbilo squamato prope apicem praedita; indumentum rhachidis paginae abaxialis constans e squamis parvis filiformibus fuscis. Pinnae patentes, planae, crenatae, falcatae, attenuatae, vix spinulosae; pinnae medianae circa 7 cm longae 1.5 cm latae, indumento rhachidis pinnae constanti e squamulis numerosis filiformibus fuscis sine ciliis, squamis minimis costularum venarumque acicularibus pallidis. Sorus abaxialis, in venis acroscopicis fasciculi venarum.

Plant terrestrial. Stem ca. 0.5 cm long, 1.0 cm diam., erect from an ascendent base. Petiole scales lanceolate, papyraceous, conform, light yellow-brown, petiole-scale cilia long and delicate; petiole squamules narrow-lanceolate, crumpled, pale orange-yellow, with abundant short cilia. Lamina 0.3–0.4 m long, chartaceous, acuminate, 1-pinnate, with a scale-covered bulbil abaxially near the distal end of the rachis; abaxial rachis scales filiform, deep brown, with very sparse short cilia. Pinnae ca. 15 on each side of the rachis and attached to it at right angles, flat, auriculate, falcate-attenuate, crenate (crenulate to entire above), weakly spinulose at auricle and pinna apex; the median pinnae ca. 7 cm long and 1.5 cm wide, the basal pinnae ca. $\frac{9}{10}$ as long; pinna-rachis squamules abundant, dark brown, filiform, without cilia; microscales of costules and veins acicular, pale, without glandular cells. Sorus abaxial on an acroscopic vein branch, indusia absent. Spores with a well-developed folded perispore.

In its leaf dissection and pinna shape, *Polystichum bulbiferum* resembles the Madagascar species *P. kalambatitrense* Tard. and *P. maevaranense* Tard. Among New World polystichums, it is the only one-pinnate species with bulbils attached below the apex of the leaf. In contrast to the Madagascar species, it is exindusiate, as are all of the polystichums endemic to the northern Andes. The detection of a morphologically distinctive species such

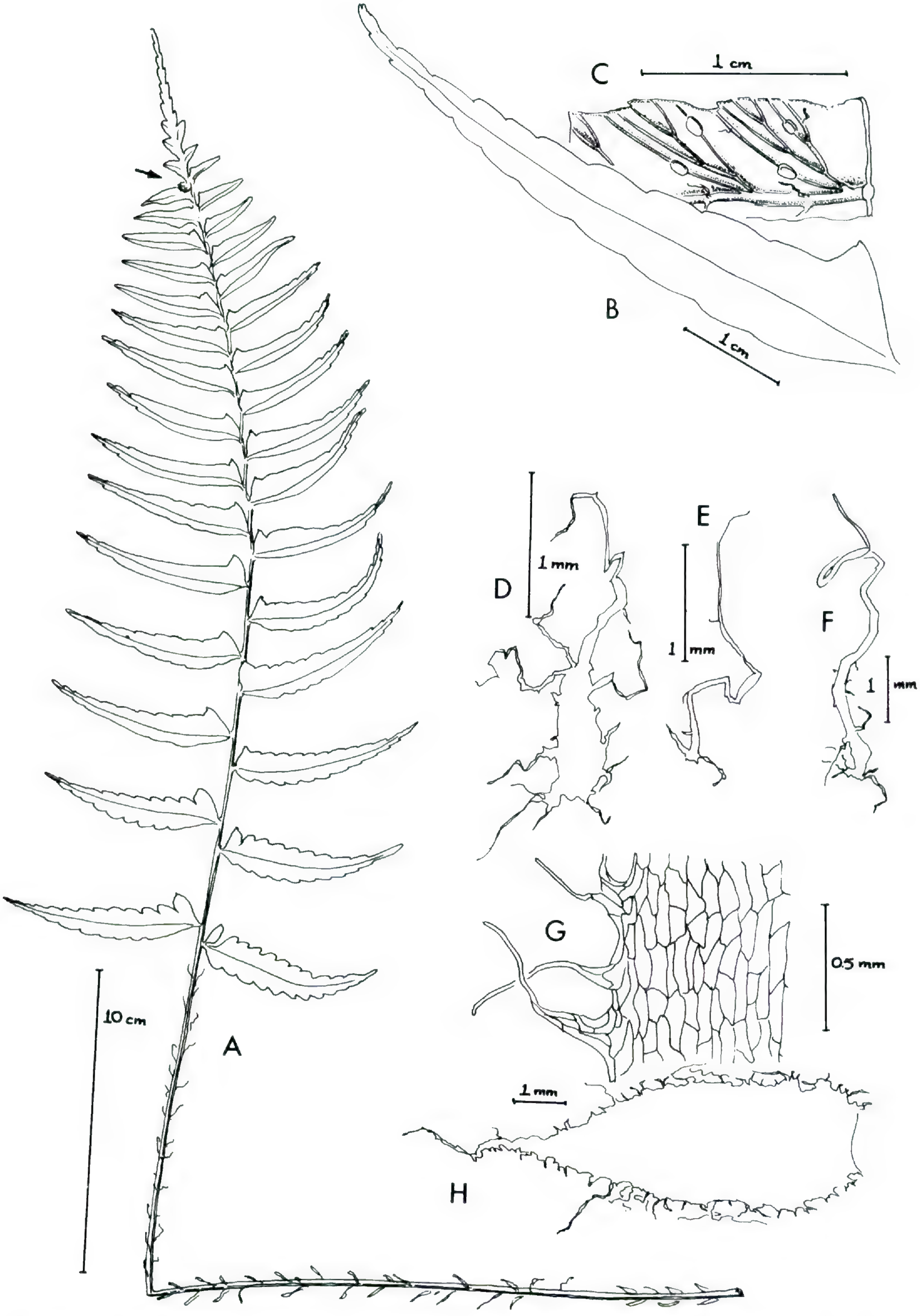

FIGURE 3. *Polystichum bulbiferum.*—A. Leaf with bulbil on rachis (at arrow).—B. Pinna outline.—C. Portion of pinna with sori removed.—D. Petiole squamule.—E, F. Rachis squamules.—G. Medial edge of petiole scale.—H. Petiole scale.

as *P. bulbiferum* only within the last 15 years suggests that major morphological trends in the diversity of the genus in Latin America may still be undocumented by collections, in spite of recent intensive work. This strongly suggests that maintaining substantial collecting programs in tropical forests between 2,000 and 4,000 m is a priority if we are to represent the morphological diversity in this and other genera adapted to the wet montane forests.

Additional specimen examined. ECUADOR. ZAMORA/CHINCHIPE: road between Loja and Zamora, ca. km 29–31, 2–4 km W of Sabanilla, 1,700–1,750 m, 1 Jan. 1979, *Luteyn, Lebrón-Luteyn & McAlpin 6634* (AAU).

NEW COMBINATION

Polystichum subintegerrimum (Hooker & Arnott) Barrington, comb. nov. *Aspidium subintegerrimum* Hooker & Arnott, The Botany of Captain Beechey's Voyage 52. 1832. TYPE: Chile. Bíobío: "Conception" [Concepción], collector unknown (holotype, K).

This distinctive species has black, coriaceous petiole scales, and its two-pinnate leaves have widely spaced pinnae and widely spaced, coriaceous pinnules with auricles pinnatifid only in the basal pinnules of a pinna. It may be well represented in other herbaria besides GH. Some specimens from northern Peru reminiscent of *P. subintegerrimum* have browner petiole scales, more dissected and less coriaceous pinnules, and no indusia. These may be hybrids or a hybrid species including a Peruvian progenitor and *P. subintegerrimum*.

Representative specimens: CHILE. BÍOBÍO: Lonco (Concepción), 22 Sept. 1928, *Espinosa 1, 2, 5* (GH); Concepción, Nov. 1937, *F. Jaffuel 4014* (GH). LA ARAUCANIA (CAUTÍN): Depto. Victoria, along the road to Laguna Malleco, Salto de la Culebra and Laguna Verde, sandy places, 950–1,050 m, 15 Mar. 1939, *J. L. Morrison & R. Wagenknecht 17522* (GH). LOS LAGOS: Chiloe, Fuerte de Ahuí (Ancúd), Jan. 1929, *M. R. Espinosa 7* (GH); Chiloe, Ancúd, Apr. 1868, *R. O. Cunningham s.n.* (GH); Corrál, 6 Oct. 1930, *H. Gunckel 2050* (GH); same locality, 16 Aug. 1930, *H. Gunckel 2082* (GH); Niebla, 13 Dec. 1931, *H. Gunckel 2865* (GH).

Exindusiate specimens: PERU. ANCÁSH: Depto. Yungáy, N side of first lake, Llanganuco, 11,500 ft., 30 July 1960, *S. G. E. Saunders 517* (F); 10 km NE of Yungáy, near Laguna Llanganuco, 3,450 m, 22 Oct. 1965, *Tryon & Tryon 6557* (GH).

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NEW OR NOTEWORTHY ORCHIDS FOR THE VENEZUELAN FLORA. VII. ADDITIONS IN *MAXILLARIA* FROM THE VENEZUELAN GUAYANA[1]

Germán Carnevali[2] *and Ivón Ramírez*[2]

ABSTRACT

Two new *Maxillaria* species from the Venezuelan Guayana, *M. foldatsiana* and *M. santanae*, are described and illustrated. One highly variable species, *M. auyantepuiensis*, is discussed, and a new subspecific taxon is proposed. *Maxillaria tenuis* is noted as a new record for the Venezuelan flora.

Maxillaria Ruiz & Pavón is the largest genus of the subtribe Maxillarinae, with about 400–450 species ranging from Mexico and the West Indies to southern Brazil. The genus reaches its highest development in the Andes, but Middle America, southern Brazil, the Amazonian Basin, and the Guayanas are well represented. The species of *Maxillaria* usually grow in places of heavy rainfall but often can be found in places with a marked dry season. They grow in almost every vegetation association and at any elevation from sea level to near the snow line but are especially common in rainforest or cloud forests at 500–2,000 m. Most members of the genus are epiphytic, but it is not unusual to find lithophytic or even terrestrial species, particularly in open, humid places. The vegetative morphology is very variable, ranging from tiny plants less than 1 cm high to plants 2 m long. They are usually pseudobulbous, sympodial plants, but pseudobulbless, almost monopodial species are not unknown. Rhizomes may be short, making caespitose plants, but many species have long creeping primary stems; these may be appressed to substrate for their entire lengths or only attached at their bases to the host, making erect, ascendent, or pendulous plants.

Maxillaria is characterized generically by solitary flowers originating from the pseudobulb base or from the internodes of the rhizome (the *Camaridium* alliance). The flowers may be minute to very large and showy and are variable in many respects, although the column is always basally produced into a more or less well-developed column-foot to which the labellum is hinged. *Ornithidium* Salisb. has a rigidly attached, unhinged labellum, and thus we feel it should be recognized, even though many authors do not do so. As a member of the subtribe Maxillarinae, all *Maxillaria* species have four dorsiventrally flattened pollinia in two unequal pairs, more or less well-developed, usually semilunate viscidium, and variously sized and shaped stipites or no stipe at all.

In Venezuela there have been recorded about 75 species of *Maxillaria*, of which 47 are known in the Venezuelan Guayana. All major groups within the genus are represented in southern Venezuela. In terms of numbers of species, *Maxillaria* is only surpassed in the Venezuelan Guayana by *Pleurothallis* R. Br. (ca. 57 species) and *Epidendrum* L. (ca. 51 species). The next-largest genus is *Octomeria* R. Br. (ca. 29 species).

A survey of *Maxillaria* species, associated with the Orchidaceae treatment for Steyermark's *Flora of the Venezuelan Guayana* (Carnevali et al., in

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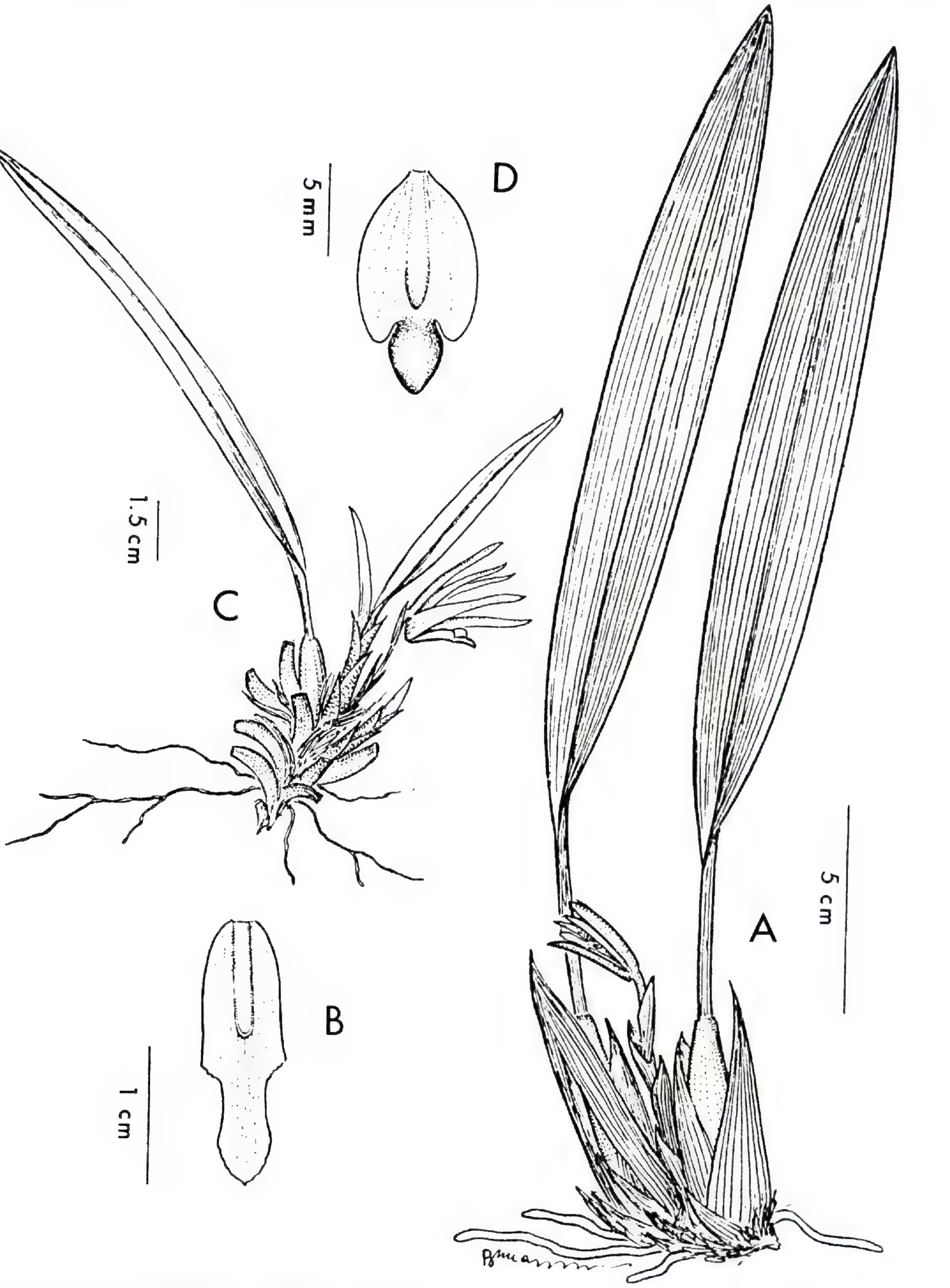

FIGURE 1. A, B. *Maxillaria foldatsiana*.—A. Flowering habit.—B. Labellum, flattened.—C, D. *Maxillaria tenuis*.—C. Flowering habit.—D. Labellum, flattened.

prep.) has revealed: 1) a new subspecies of *M. auyantepuiensis* Fold. and a new species closely related to it, 2) an undescribed taxon in the *Dicrypta* group of the genus, and 3) a new record for the Venezuelan flora, *M. tenuis* C. Schweinf.

THE *MAXILLARIA AUYANTEPUIENSIS* COMPLEX

Our studies of the complex of taxa centered around *M. auyantepuiensis* Fold., which includes *M. desvauxiana* Reichb. f., *M. neophylla* Reichb.

f., and a few others, have revealed a previously undescribed species and a new infraspecific taxon referable to *M. auyantepuiensis*. Here we provide the descriptions of both new taxa.

Maxillaria foldatsiana Carnevali et I. Ramírez, sp. nov. TYPE: Venezuela. Bolívar: Uaipantepui, 1,200 m, *T. Koyama & G. Agostini 7378* (holotype, VEN). Figure 1A, B.

Species haec *M. auyantepuiensi* affinis, sed differt: labello triplo longiore quam latiore (duplo longiore quam latiore in *M. auyantepuiensi*) et lobulo medio conspicue unguiculato (subsessili in *M. auyantepuiensi*).

Apparently epiphytic, erect herbs, 27–30 cm high. Rhizome abbreviated with aggregated pseudobulbs. Pseudobulbs narrowly ovoid, 4.7–5 cm long, 1.3–1.6 cm wide at their broadest, monophyllous, concealed by appressed, scarious sheaths. Leaves coriaceous, erect, narrowly elliptic, acute, basally attenuate into a subcylindric pseudopetiole 4–4.5 cm long, leaf total length 23–24.5 cm, the blade 18.5–20 cm long, 2.3–2.6 cm wide. Inflorescences originating from the pseudobulb base, flowers solitary; peduncle subterete, entirely concealed by 4–5 tubulose, scarious sheaths, 3–5 cm long. Flowers medium-sized for the genus, apparently vertically erect. Perianth segments scarcely open. Floral bracts elliptic, acute, 1.4–1.5 cm long, 0.4–0.5 cm wide. Pedicellate ovary apparently subcylindric, 15–17 mm long. Dorsal sepal narrowly oblong-elliptic, acute, 20–20.5 mm long, 4–4.5 mm wide. Lateral sepals narrowly triangular, acute, 20–21 mm long, basally 3.5–4 mm wide. Petals narrowly elliptic, slightly obovate, acute or narrowly obtuse, 19 mm long, 4–4.5 mm wide. Labellum parallel to the column, in general outline narrowly oblong, 17–18 mm long, 4.5 mm wide at its broadest, slightly pandurate-trilobate above the middle; central lobe elliptic, obtuse-rounded, slightly concave, 7 mm long, 2.5 mm wide, basally attenuate in a short unguiculus about 2 mm long and wide, the narrowly oblong longitudinal callus apically rounded and centrally concave, 7 mm long, 0.8 mm wide. Column straight or slightly recurvate, hemicylindric, ventrally concave, 8 mm long and 2 mm wide at the thickened apical zone. Clinandrium apiculate.

This species is very similar to *M. auyantepuiensis*, from which it differs in its inflorescences longer than the pseudobulb (vs. subequal or shorter), narrowly elliptic floral bracts (vs. widely elliptic), petals to 4.5 mm wide (vs. at least 6 mm in *M. auyantepuiensis*), and conspicuously narrower labellum (in *M. auyantepuiensis* it is approximately twice as long as wide vs. more than three times longer than wide in *M. foldatsiana*). Further, the labellum of *M. foldatsiana* is less trilobulate. As *M. foldatsiana* is only known from the type collection, and the differences between the two species are not deep, we feel that more material may show *M. foldatsiana* to be only a variation of *M. auyantepuiensis*. However, we have studied many specimens of *M. auyantepuiensis* (alive and dried) and have never noticed intergradation in the differential characters, so we think that they are best treated as closely related but distinct species.

This apparently scarce species has been collected only once despite repeated collecting trips to the summits of the tepuis in the last ten years. Perhaps it is endemic to Uaipantepui.

We take great pleasure in naming this species after our friend and colleague Dr. Ernesto Foldats, orchidologist. He was the first to notice the new species as undescribed.

Maxillaria auyantepuiensis is very common in the Gran Sabana, in southeastern Bolívar, Venezuela. Surprisingly, it is seldom collected. This species comprises two infraspecific taxa, one of which has remained undescribed.

Maxillaria auyantepuiensis subsp. *auyantepuiensis* is terrestrial or lithophytic, always growing on sandy soils or on acid sandstone, forming large colonies in more or less open places as scrub or savannalike tepui formations. It is usually exposed to full sun or resides under the light shade of shrubs. Occasionally it reaches the gallery forest margin or even its interior, provided there is enough light and is always over sandstone outcrops or sandy soil. Morphologically, *M. auyantepuiensis* subsp. *auyantepuiensis* is highly variable with fusiform to (rarely) spherical pseudobulbs and sessile to long-petiolate leaves. The sheaths that conceal the pseudobulb do not defibrate but remain intact. The inflorescences vary from shorter than to longer than the pseudobulb and are always conspicuously peduncled. The flowers are held in an upright or suberect posture. The perianth segments are relatively long and narrow with petals 18–19 mm long, 4.3–4.5 mm wide (width/length = 0.38–0.42) the dorsal sepal is 20–21 mm long and 3.5 mm wide (width/length = 0.16–0.17).

Maxillaria auyantepuiensis Fold. subsp. **epiphytica** Carnevali & I. Ramírez, subsp. nov. TYPE: Venezuela. Bolívar: bosque húmedo en las vacinidades del km 119 al sur de El Dorado, 130 m, 12 Jan 1964, *J. A. Steyermark*,

TABLE 1. Characters distinguishing subspecies of *M. auyantepuiensis*.

Characters	Subspecies	
	auyantepuiensis	*epiphytica*
Substrates	Sandy soil or sandstone outcrops	Epiphyte on trees
Habitats	Various tepuilike associations	Rain and cloud forest
Pseudobulb sheaths	Intact	Defibrating
Pseudobulb shapes	Spherical to ellipsoid	Spherical
Leaves	Sessile to long-petiolate	Always long-petiolate
Flowers	Erect to suberect	Spreading horizontally
Petals length × width	18–19 × 4.5 mm	15–16 × 5 mm
Width/length	0.42–0.45	0.30–0.38
Dorsal sepal length × width	20–21 × 3.5 mm	16–17 × 4.5–5 mm
Width/length	0.16–0.17	0.27–0.31

G. C. K. & E. Dunsterville 92993 (holotype, VEN).

Subsp. haec subsp. *auyantepuiensi* vaginis dissolutis, tepalis proportione latioribus differt itemque habitu epiphytico et in silvis pluvialibus incola.

The subspecies are distinguished in Table 1. Both subspecies have been illustrated in Dunsterville & Garay (1965: 181, 498). Plants A, C, and D there depict the variation to be expected in *M. auyantepuiensis* subsp. *auyantepuiensis*. Plant B represents our new *M. auyantepuiensis* subsp. *epiphytica*.

The new subspecies comprises populations of epiphytic plants from rain or cloud forest at variable altitudes from 600 to 1,400 m, with spherical or broadly ellipsoid pseudobulbs that are small in proportion to leaf length and are concealed by defibrating sheaths. These pseudobulbs occur on a short to long, obviously creeping rhizome, which adheres to the bark of the host tree. The leaves are always long-petiolate and very elongate with respect to pseudobulb length. The almost-epedunculate inflorescenses are always shorter than the pseudobulbs, and the flowers are almost held horizontally. The flowers are of proportionately smaller dimensions than in subsp. *auyantepuiensis*, with relatively broader perianth segments (dorsal sepal 16–17 mm long, 4.5–5 mm wide (width/length 0.27–0.31). The labellum is almost identical in the two subspecies.

Maxillaria auyantepuiensis subsp. *epiphytica* is superficially similar to the Ecuadorian species *M. neophylla* Reichb. f., but this has an acute central labellum lobe. The new subspecies also suggests a vegetatively reduced *M. desvauxiana* Reichb. f. from the Amazonian Basin, but their labella are very different, and *M. desvauxiana* does not have defibrating sheaths concealing the pseudobulbs.

The new subspecies has a wider distribution than the typical subspecies and extends beyond the Guayana boundaries. We know of a population in Guatopo, Estado Miranda, of the Coastal Range, represented by *Patrszeck s.n.*, 13 Feb. 1963 (VEN), also a population from Barinitas, Estado Barinas, in the Andean foothills, from which we have living material but no voucher.

The typical subspecies appears to be restricted to the acid sandy soils of the Roraima Formation, and this may explain a limited range in geographic terms even though it appears to be locally abundant in its natural habit.

Paratypes. VENEZUELA. BOLÍVAR: Selva húmeda con árboles de un promedio de 25–30 m de altura en el drenaje del Río Cuyuní, km 140–141.5 al sur de El Dorado, 1,300–1,380 m, 22–28 Dec. 1970, *J. A Steyermark, G. C. K. & E. Dunsterville 104324* (VEN); Cerro Guaiquinima, Río Szczrbanari (Río Carapo), 750 m, 20–25 Jan. 1977, *J. A. Steyermark, G. C. K. & E. Dunsterville 113219* (VEN). MIRANDA: Guatopo, 13 Feb. 1963, *Patcrzck s.n.* (VEN) (Colección en líquido *Dunsterville 252*).

Study of the *Dicrypta* group of the Venezuelan Guayana has revealed an apparently undescribed taxon:

Maxillaria santanae Carnevali & I. Ramírez, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Departamento Atabapo, Cerro Marahuaca, porción central. Bosque con árboles hasta 20 m, aprox. 1,000 m. Floración en cultivo en el orquideario del colector, 11 Nov. 1986, *G. Santana 1* (holotype, VEN). Figure 2.

Species haec *M. crassifoliae* et *M. superfluae* affinis sed species nostra habito conspicue parviore, petalis et labello proportione latioribus et labello unicalloso cinnabarino vel cinnabarino-roseo lobo centrali late triangulari discrepat.

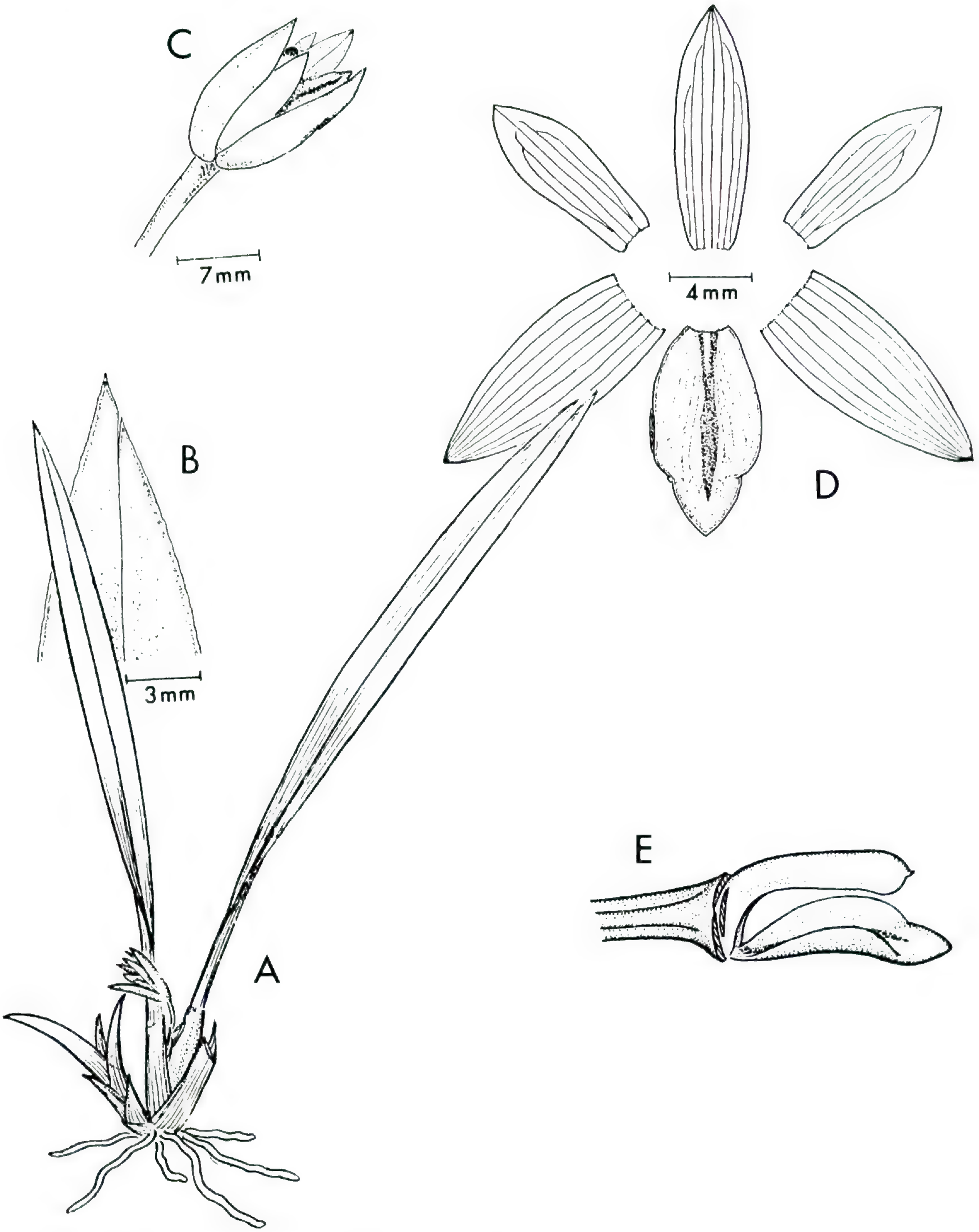

FIGURE 2. *Maxillaria santanae*. —A. Flowering habit. —B. Foliar apex. —C. Lateral view of flower at anthesis. —D. Perianth segments, flattened. —E. Labellum and column.

Small to medium-sized, epiphytic, caespitose, erect herbs, 11–23 cm high. Rhizome short and proportionately thick, entirely concealed by scarious sheaths. Roots proportionately thick and long, pale brown. Pseudobulbs aggregate, ovoid-ellipsoid, ancipital, 2.1–3 cm long, 0.6–1 cm wide, apically unifoliate, clothed with 4–5 sheaths, the innermost 2–4 of these with foliar blades, the blades falling after 2–3 years of growth, leaving the sheaths persisting and becoming grayish brown in fresh or

dry condition. Leaves fleshy-coriaceous, erect or patent-erect, the outer leaves 10–15 cm long from the articulation, the apical leaf 14–21 cm long, 7–10 mm wide when fresh, 5–9 mm wide when dry, basally attenuate and forming a pseudopetiole 1–2.3 cm long, the blade apex acute and deeply oblicuous-bilobulate (one of the halves of the blades 2–4 mm longer than the other). Inflorescences one-flowered, originating from the leaf-sheath axils one at a time. Peduncle subterete, fleshy, 17 mm long, concealed by 3–5 subimbricate, distichous sheaths. Floral bract similar to the peduncle bracts, narrowly triangular, acute, membranose, 6 mm long, 2.5–3 mm wide. Pedicellate ovary subterete, 9–10 mm long, 2.5 mm thick. Flowers medium-sized, campanulate, erect or suberect; perianth segments fleshy, subparallel to the column, greenish yellow, the petals with or without a few small brown-orange dots, the labellum pale orange or rose-lilac with orange-brown basal patches and a salmon-colored, tomentose callus. Sepals elliptic-oblong, acute; the laterals slightly oblicuous, 11–13 mm long, 4–5 mm wide, with a dorsally thickened apex. Petals narrowly obovate-elliptic to narrowly elliptic, subfalcate, acute, 10–10.5 mm long, 2.7–3.2 mm wide. Labellum basally articulate with the column-foot, in overall shape elliptic, subtrilobate about the apical fourth, 9–9.5 mm long, 5–5.5 mm wide between the margins of the lateral lobes; lateral lobes suberect and making a concave labellar disc; central lobe broadly ovate or broadly triangular obtuse, 3.8–4 mm long, 2.8–3.2 mm wide, fleshier than the rest of the labellum and with a central concavity originating where the callus ends, the disc with a thickened, waxy, tomentous longitudinal callus, this 6–7 mm long, 1 mm wide. Column semiterete, slightly thickened, apically arcuate, 6.5–7 mm long; column foot 2–3 mm long. Anther subconic, 2 mm long, obtuse, the basal margins erose.

Paratypes. VENEZUELA. BOLÍVAR: confluencia del Caño Makarupai con el Río Akaruai, unos 10–15 km al SO de la Misión de Wonken, ca. 850 m, en bosque macrotermico medio/medio, caracterizado por una gran abundancia de epífitas debido a los rápidos de la confluencia. Floración en cultivo, Maracay, 2 Jan. 1984, *G. Carnevali 1445* (VEN).

This relatively scarce species has a wide range within the Venezuelan Guayana. One of the authors collected living plants of it in 1982 in the surroundings of Peray-tepui (W of Sta. Elena de Uairén, Gran Sabana, Estado Bolívar), but no voucher was made. The affinities of *M. santanae* lie with all the species of the *Dicrypta* group: M. *crassifolia* Reichb. f.; *M. superflua* Reichb. f., and perhaps *M. bicallosa* (Reichb. f.) Garay, *M. chartacifolia* Ames, and others. This is a difficult group in need of revision—the characters distinguishing the component members are not well defined and seem unreliable. Among the *Dicrypta* group, *M. santanae* can be easily recognized by its small vegetative stature; very narrow leaves; broadly ovate or broadly triangular, obtuse central labellum lobe; and orange-yellow or rose-lilac labellum, which has a callus in the disc and lacks another in the central lobe as is usual in other species of the group.

We are pleased to name this species after Dr. Gustavo Santana, an enthusiastic orchid collector and knowledgeable amateur orchid grower. He collected the living plant from which the holotype specimen was prepared and kindly provided fresh vegetative and floral material for study.

Maxillaria tenuis C. Schweinf., Bot. Mus. Leafl. 11: 289, T. 18, fig. 1, c–d. 1945. TYPE: Perú. Loreto: Mishuyaco, near Iquitos, 100 m, in forest, *Klug 1045* (holotype, US). Figure 1C, D.

Small to medium-sized epiphytic herbs. Rhizome abbreviated. Pseudobulbs cylindric, ellipsoid or oblongoid, apically unifoliate, 1.5–2.3 cm long when mature, 5–7 mm wide, concealed by oblong-ovate, acute, and acuminate sheaths, these verruculous-pustulose without, the innermost bearing leaf blades. Leaves coriaceous, 11–14 cm long, 6–8 mm wide, the blades linear, acute, the base attenuate into a short pseudopetiole 3–15 mm long. Inflorescences erect, 1-flowered, solitary, originating from the base of the young pseudobulbs. Peduncle subterete, 1.5–3.2 cm long, concealed by 2 elliptic, acute, acuminate sheaths, these verruculose without, 8–11 mm long, slightly longer than internodes. Floral bracts almost identical to the last peduncle bract, 9–11 mm long, about 6 mm wide. Pedicellate ovary subterete, longitudinally sulcate, verruculose, 11–12 mm long. Flowers medium-sized but large for the plant, with white tepals and a yellow and white labellum having purple nerves. Perianth segments subcoriaceous, parallel to the column. Dorsal sepal very narrowly elliptic, acute and acuminate, concave basally, 18–27 mm long, 3–4 mm wide. Lateral sepals narrowly oblong to linear-lanceolate, acuminate, slightly oblicuous, 18–27 mm long, 4 mm wide basally, decurrent on the column-foot and forming with it a short mentum. Petals linear-lanceolate, acuminate, 16–23 mm long, 2–2.3 mm wide. Labellum fleshier than the other perianth segments, broadly elliptic to elliptic-ovate overall, trilobate near the apical third, 9.5–10 mm long

between the apices of the extended lateral lobes, 5–6 mm wide; lateral lobes erect and narrow, ending in a free ovate-rounded portion about 1 mm long with the apical margins minutely erose; central lobe very fleshy, 3.5–4 mm long, 2.5–3 mm wide, triangular ovate, acute or obtusate, minutely apiculate subapically, the ventral face rugulous-papillose and longitudinally sulcate. Disc along its entire length with an oblongoid callus, 5–6 mm long, with an apically rounded surface. Column proportionately short, about 4.5 mm long, semiterete, basally produced into foot about 2 mm long.

Additional specimen examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: surroundings of San Carlos de Río Negro, on the road to Solano, 100–120 m, Dec. 1986, *H. L. Clark 8098* (VEN).

Distribution. Known from the rain forests between 80 and 200 m in the Amazonian Basin of Peru, Brazil, and Venezuela.

This is the first record of this species for Venezuela. Since the Venezuelan material shows a few differences with the other known populations, here we offer a complete description with the full range of variation. *Maxillaria tenuis* seems to be rather variable. The type material from Iquitos, Amazonian Peru (*Klug 1045*, US), has sepals about three times longer than labellum (27 : 9.5 mm) and a triangular-ovate central labellar lobe. The second collection known, collected in Amazonian Brazil (*G. A. Black 48-2676*, IAN; *G. A. Black 48-2747*, IAN), has a very narrow central lobe (half the width of the type material) and an apparently bilobated labellar callus. Based on this Brazilian material, a var. *amazonica* Pabst was described (Pabst, 1955). All persons experienced with *Maxillaria* herbarium material know how difficult it is to rehydrate and reconstruct labella in these species, especially the central lobe and calluses, so we wonder if the narrower central lobe and bilobated callus are not artifacts. Provided they are not, we would think that var. *amazonica* could stand as a good variety or subspecies, even though in Pabst & Dungs (1975) they seem to have rejected Pabst's variety without explanation. The third population of the species to be sampled is the one we report here, which seems to depart from the type and from Brazilian material in having shorter sepals, less than two times longer than labellum (18 : 10 mm). The labellum is identical with that of the type material. By orchid standards this seems to be a good difference for the recognition of at least a subspecies, but we feel that the evidence is too scanty, as is the known material, and further material could bridge the gap between the three known populations of this extremely variable species.

Maxillaria tenuis is a well-marked species, especially its vegetative morphology: oblongoid, elongate pseudobulbs, linear leaves, and verrucose-pustulose sheaths. San Carlos de Río Negro is only a hundred meters away from Colombia, across the Río Negro, so we would expect to find *M. tenuis* also in Colombia.

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CONTRIBUCION AL GENERO *MIMOSA* (MIMOSACEAE)[1]

Renée H. Fortunato[2]

Abstract

A taxonomic revision of four species of the genus *Mimosa* L. from Austroamerica is presented. *Mimosa pauperioides* (Burk.) Fortun., stat. nov. is proposed as a species, and its affinity and taxonomic position are discussed. Synonyms of *M. balansae* M. Mich. and *M. niederleinii* Burk. are given. *Mimosa petraea* Chodat et Hassl. is restricted to the Paraguayan territory. All these taxa are briefly described and their geographic distributions are given.

Como parte de la revisión que se esta realizando del geńero *Mimosa* L. para la Argentina, Bolivia, Paraguay, y Uruguay, se da a conocer el estudio taxonómico de cuatro especies presentes en el área. Estas especies pertenecen a la sección *Mimosa* (Bentham, 1842, 1875) por presentar flores haplostémonas.

Dentro de dicha sección, según ciertos caracteres exomorfológicos (hábito, presencia de acúleos, número de pinnas, número de folíolos) se agruparía a *M. pauperioides* y *M. balansae* en la serie *Pectinatae* Benth. y a *M. niederleinii* y *M. petraea* en la serie *Pedunculosae* Benth.

En el sistema de clasificación de Bentham, la ubicación taxonómica de muchas de las especies de *Mimosa* en cada serie es dudosa. A través del estudio biosistemático que se esta efectuando en el género para Austroamerica se espera poder seleccionar los caracteres de valor taxonómico.

1. Mimosa pauperiodes (Burk.) Fortun., stat. nov. *M. balansae* M. Mich. var. *pauperioides* Burk., Darwiniana 8: 146, fig. 22. 1948. TIPO: Argentina. Corrientes: 4 Dec. 1941, *Birabén 5027* (holotipo, LP). Iconografía: A. Burkart in N. Troncoso & N. Bacigalupo, Col. Ci. INTA 6(3): 503, fig. 224, e–i. 1987.

Sufrútice prostrado; tallos estrigosos, delgados, aculeados, a veces inermes; acúleos 1–2 de 0.5–3 mm long., infraestipulares o internodales (generalmente ramas aculeadas e inermes en la misma planta). Pinna uniyugada de 1.5–5 cm long.; folíolos 4–18-yugados de 2–9 mm long. × 0.6–2 mm lat., angostamente elípticos, asimetricos en la base, pubescencia combinada de pelos estrigosos y sedosos en ambas caras, a veces solo estrigosos en la cara abaxial. Inflorescencia con pedúnculos 1–2 por axila de hasta 11 cm long., mayores que las hojas. Flores rosadas; cáliz hialino; corola de 2.5–3 mm long., glabra, 4-lobulada, lóbulos pubérulos en el ápice. Craspedio subtoruloso, hispido y pubérulo en replo y artejos.

Distribución. Común en los suelos arenosos del estado de Rio Grande do Sul en Brasil y en las provincias argentinas de Entre Rios y Corrientes.

Material selecto examinado. ARGENTINA. CORRIENTES: Dep. Curuzú Cuatiá: 12 km del acceso N a Curuzú Cuatiá, *Cristóbal et al. 1961* (CTES). Dep. Empedrado: ruta 12 y Río Empedrado, *Schinini 12099* (CTES). Dep. Mercedes: *L. R. Parodi 6232* (BA, SI); *Millán 347* (BA); Mercedes, *Krapovickas et al. 20333* (CTES, SI); Justino Solari, *Ibarrola 2587* (SI); ruta 14, km 37, SW de Carlos Pellegrini, *Schinini 7767* (CTES, SI); Ayo. Pay Ubre Grande y camino a Itá Corá, *Tressens et al. 2269* (CTES); camino a la feria, orillas del Ayo. Las Garzas, *P. Rodrigo 608* (LP). Dep. San Martín: Arrocera Drews, 8 km N de Carlos Pellegrini, *Krapovickas et al. 29215* (CTES). ENTRE RIOS: Dep. Federación: ruta 14, km 513, *Burkart et al. 29331* (SI); ruta 14 al N de Federación, *Troncoso et al. 2493* (SI); Santa Ana, *Burkart 26234* (SI); *A. L. Cabrera et al. 19353* (LP). Dep. Concordia: *L. R. Parodi 3962* (SI); ruta 14, km 15 al N de Concordia, *Fabris et J. Hunziker 7252* (LP); Ayuí, *Troncoso et al. 3403* (SI). BRASIL. RIO GRANDE DO SUL: Porto Alegre, *Freitas Xavier 17* (SI).

Mimosa balansae var. *pauperioides* fue diferenciada (Burkart, 1948) de *M. balansae* var.

[1] Se agradece a la Lic. Maria Mercedes Arbo por la lectura crítica del manuscrito y a la Fundación Robert Bass por la beca otorgada para consultar la importante colección depositada en el Field Museum of Natural History, Chicago, Illinois, U.S.A. Asimismo, se hace extensivo el agradecimiento a los curadores de los herbarios aquí citados, por el préstamo de los ejemplares.

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balansae por presentar folíolos más angostos y el nervio medio prominente. En el material estudiado se observó que además de los caracteres citados por Burkart, también se podía diferenciar a *M. balansae* var. *balansae* por poseer inflorescencias mayores que las hojas, y tallos inermes o con 1–2 acúleos internodales y/o infraestipulares. Todas estas diferencias se mantienen constantes, e inclusive son más importantes que las existentes entre *M. balansae* y otras especies afines. Por lo aquí descrito, se propone considerar a *M. pauperioides* como especie independiente de *M. balansae*.

En los ejemplares inermes es facil confundir a *M. pauperioides* con *M. petraea*. Ambas presentan afinidad en el tipo de hábito y número y forma de los folíolos; no obstante se diferencian por el largo del pedúnculo, pubescencia, y tamaño de los folíolos.

Según Bentham (1842, 1875), la serie *Pectinatae* Benth. se caracteriza por agrupar sufrútices pequeños o raro arbustos, generalmente con acúleos infraestipulares o internodales, pinna uniyugada, folíolos multiyugados (a veces hasta 6–8-yugados), pedúnculos 1(2) axilares o formando racimos compuestos apicales (desarrollo posterior de las hojas), racimos globosos, flores 4-meras, y craspedio setoso a hispido. A su vez, la serie *Pedunculosae* Benth. se diferencia de *Pectinatae* casi únicamente por incluir especies inermes. En el estudio de ambos grupos supraespecificos, se ha observado que la presencia de acúleos es un caracter variable en muchas especies del género, como ocurre con *M. pauperioides*. Este taxon solo presenta algunas ramas con uno o dos acúleos pequeños, y a veces es una planta totalmente inerme. Si se siguiera el criterio de Bentham, erróneamente se consideraría a los ejemplares aculeados en la serie *Pectinatae* y a los inermes en *Pedunculosae*. Por otro lado, esta especie es más afín a *M. petraea* de la serie *Pedunculosae*. Como se ha señalado, en su mayoría, los caracteres diferenciales descriptos por Bentham para las series del género *Mimosa* no responden a un patrón estable.

2. Mimosa balansae M. Mich., Mém. Soc. Phys. Nat. Genève 28(7): 52, fig. 18. 1883. TIPO: Paraguay: Trinidad, Mar. 1875, *Balansa 1479* (lectotipo, G, selecionado aquí; isolectotipo, F); *Balansa 1479a* (sintipo, G, fragmento F; fotografía n° serie F (ex B†)—1397, F, G, SI); Villa Concepción, in pratis, *Balansa 1835* (sintipo n.v.). Iconografía: A. Burkart in N. Troncoso & N. Bacigalupo, Col. Ci. INTA 6(3): 501, fig. 224, a–d. 1987.

Mimosa balansae M. Mich. var. *robusta* Chodat et Hassl., Bull. Herb. Boissier ser. II. 4: 488. 1904. TIPO: Paraguay: in campis San Bernardino, Nov. 1898/99, *Hassler 3507* (holotipo, G; isotipo, F).

Mimosa balansae M. Mich. var. *rojasiana* Hassl., Repert. Spec. Nov. 8: 557. 1910. TIPO: Paraguay. Gran Chaco: ad ripam occidentalem flum, lat. S23°20′, 23°30′, Oct.? 1903, *Hassler 2355* (holotipo, G).

Sufrútice de ± 15–80 cm alt., erecto a prostrado, robusto a ± grácil; tallos con pubescencia pubérula y estrigosa, ± patente, esparcida a densa, raro glabros; acúleos 2–5 mm long., rectos a recurvos, infraestipulares, presentes en ternos o variando su número de 1–6 (a veces 1 o 2(3) internodales), raro sin acúleos. Pinnas uniyugadas; folíolos (3–)8–25-yugados, 5–15 mm long. × 2–4.5 mm lat., elípticos a angostamente elípticos, estrigosos y pubérulos en ambás caras, hasta completamente glabros en el epifilo, nervio medio subcentral, poco visible en la cara abaxial (solo a veces en la base y/o en el ápice), borde estrigoso-pubérulo, no formando un margen nerviforme. Inflorescencia racemosa; pedúnculos 1–2 por axila, menores que las hojas. Cáliz 0.25–0.5 mm long., hialino, truncado a brevemente ciliado en el borde; corola 2–3.5 mm long., membranácea, glabra, lóbulos pubérulos en el ápice. Craspedio 1–2 cm long. × 0.4–0.5 cm lat., subtoruloso, pubescente.

Distribución. Crece preferentemente en espartillares. Su distribución se extiende desde Bolivia, Paraguay hasta Uruguay, S de Brasil y NE Argentino.

Material selecto examinado. ARGENTINA. CORRIENTES: Dep. Berón de Astrada: *Ibarrola 3969* (LIL); 46 km W de Itá Ibaté, Valencia, *Schinini 14029* (CTES). Dep. Capital: 15 km E de Corrientes, camino a San Luis del Palmar, ruta 5, *Quarín 3247* (CTES); 16 km ENE de Corrientes, ruta 12 Ea. Las Mercedes, *Quarín 3366* (CTES); Molina Punta, *Krapovickas & Cristóbal 11754* (CTES, SI); *Schinini 14134* (CTES, F); Perichón, *Schinini & Martínez Crovetto 12252* (CTES). Dep. Empedrado: Ea. Las Tres Marias, *Pedersen 3063* (LP). Dep. General Paz: Campo Navarro, ruta 5, 81 km SE de Corrientes, *Anzótegui 336* (CTES). Dep. Mercedes: Ea. Itá Caabo, *Pedersen 5355* (LP); Jofré, *Ibarrola 2698* (LIL). Dep. Monte Caseros: Monte Caseros y empalme con ruta 14 a Curuzú Cuatía, *Nicora 4630* (SI); en pajonal inundable, prox. a la Laguna del Yacaré, *Nicora 4778* (SI). Dep. Paso de los Libres: *Meyer 2773* (LIL); ruta 127 y Ayo. Ayuí, *Schinini et al. 17246* (CTES). Dep. Saladas: Ea. Rinesi, *Pedersen 6627* (LP). Dep. San Cosme: Vivero Forestal, paso de la Patria, *Carnevali 2897* (SI); San Cosme, *Clos 5929* (BAB); ruta 12, entre Corrientes y Paso de la Patria, *Nicora & Cámara Hernández* (BAA 272, CTES). ENTRE RÍOS: Dep. Concordia, Estación Agronómica, *Burkart 967* (SI). Dep. Federación: Barra del Mocoretá, *Troncoso et al. 1311* (SI). FORMOSA: Dep. Patiño, Estanislao del Campo, por ruta 81

a 17 km hacia el N, *Cabral, Molina & Fortunato 1194* (BAB); *Insfrán 1175* (BAB). Dep. Pilcomayo: Clorinda a Formosa, *Morel 1685* (LIL); km 5, ruta 11, Laguna Blanca, *Morel 2263* (CTES, LIL); al SE de Pto. Porteño, a 2 km, *Morel 2350* (CTES, LIL); Clorinda, *Morel 1150* (CTES). Sin dep.: común en el campo Guaycalec, *Jörgensen 3212* (MO, SI). Sin loc., *Jörgensen 3218* (MO). MISIONES: Dep. Candelaria, *Meyer 18956* (LIL); Yabebyry, *Montes 654* (CTES). Dep. Concepción: entre Concepción de la Sierra y San Javier, *A. L. Cabrera et al. 28318* (SI). Sin dep.: Cerro Corá, *Martínez Crovetto 9496* (BAB). BRASIL. RIO GRANDE DO SUL: Uruguaiana, Barra do Quarai, *Rambo 4247* (SI). MATO GROSSO: Campo Grande, *Nienstedt 401* (RB). PARAGUAY. ALTO PARAGUAY: Palmas Chicas, Chaco paraguayo, *Rojas 7783* (SI); Puesto Casado, *Rojas 2139, 3042* (SI); Olimpo, *Arenas 339* (SI). AMAMBAY: 20 km S de Bella Vista, *Krapovickas & Schinini 32671* (CTES). CENTRAL: Jardín Botánico, pradera entre gramineas, *Rojas 9896* (SI); campos bajos entre Luque y Trinidad, *Hassler 1687* (SI); Yaguarón, orillas del Ayo. Yaguarón, *Krapovickas et al. 12291* (CTES, SI); Trinidad to Asunción, *Osten 9168* (G); Ipacaraí, *Rojas 14278* (BAF, SI). CONCEPCIÓN: San Salvador, Alto Paraguay, Ea. Arrecife, *Rojas 3036* (SI). CORDILLERA: Cordillera de Altos, *Fiebrig 1005* (F, G); San Bernardino, *Osten 9169* (G). GUAIRA: Azucarera de Tebicuary, Ayo. Ihaca, *Schinini 5864* (G, SI). PARAGUARI: Paraguari, Jardín de la Iglesia, *M. Sanchez 19* (BAB). SAN PEDRO: 228.5 km S de San Estanislao, 24°40′S, 56°21′W, *Fortunato et al. 807* (BAB, PY); Distrito Lima, *Pedersen 9440* (SI). Sin loc.: Pto. Yataybá, *Daguerre* (BA 28/924); Hiaty, *Jörgensen 3624* (BAB, F, LP, SI); Central Paraguay, *Morong 1500* (MO). URUGUAY. PAYSANDU: Chapicuy, Río Uruguay, *Rosengurtt B-3659* (SI); orilla del Río Uruguay, Santa Sofia, *Rosengurtt B-3659 ½* (SI). SALTO: prox. Salto Grande, *Osten 5373* (SI).

Se ha observado en el campo y en el material de herbario que *M. balansae* forma un complejo donde los caracteres descriptos (hábito, pubescencia, número de acúleos, largo de la pinna, y número y largo de folíolos) aparecen combinados en los diferentes ejemplares. Esta variabilidad imposibilita realizar una división infraespecífica natural de la especie, por ello se considera que los epítetos varietales *robusta* y *rojasiana* son solo probables formas ecológicas que presenta el complejo citado.

Mimosa balansae var. *rojasiana* fue descripta por Hassler con folíolos glabrescentes en la cara adaxial. Al estudiar el material típico se pudo observar que los folíolos son pubescentes en ambas caras.

De los tres sintipos citados por Micheli en la descripción original de *M. balansae*, se han podido estudiar *Balansa 1479* y *1479a* (G, F). En esta nota se selecciona y se propone como lectotipo a *Balansa 1479* depositado en el herbario G por ser un ejemplar más completo (fl, fr, y tres hojas de herbario) que *Balansa 1479a*.

3. Mimosa niederleinii Burk., Darwiniana 7: 523. 1947. TIPO: Argentina. Misiones: Varana, 23 Ago. 1887, *Niederlein 1107* (holotipo, SI). Iconografia: A. Burkart, Darwiniana 8: 162, fig. 26. 1948.

Mimosa niederleinii Burk. var. *riograndensis* Burk., Darwiniana 7: 526, fig. 4. TIPO: Brasil. Rio Grande do Sul: Estrela, Mar. 1899, *Dutra 382* (holotipo, HB; isotipo, SI).

Arbusto o sufrútice de ± 0.5–1.5 m alt., ascendente; tallos ramificados, estrigosos y pubérulos, inermes. Estipulas 3–5 mm long. × 0.5 mm lat., subuladas a lanceoladas; pecíolo 0.4–1.5 cm long., pubescente; estipelas 2–3 mm long. × 0.25–0.5 mm lat., subuladas a lineares; pinna uniyugada 3–5 cm long.; folíolos 18–55-yugados, 4–8 mm long. × 0.5–2 mm lat., oblongos, asimétricos en la base, papiráceos a subcoriáceos, discoloros, cara adaxial glabra, brillante, cara abaxial pubérula, levemente estrigosa o hirsuta, raro glabra a subglabra, con 1–2(–3) nervios, nervio medio central a subcentral, prominente, borde ciliado, formando un margen nerviforme (o no marginado). Inflorescencia en racimos espiciformes 1.5–3.2 cm long., axilares. Flores rosadas; bráctea 0.5–1 mm long. × 0.25 mm lat., 1-nervia; cáliz ± 1 mm long., 2-partido a ± 4-dentado, escarioso, blanquecino, lacerado en el ápice, pubérulo en la base; corola 1.5–2 mm long., 4-lobulada, con pubescencia retrorso-estrigosa. Craspedio 1–2 cm long. × 0.3–0.5 cm lat., recto a subtoruloso, 3–4-articulado, artéjos 5–7 mm long., subcuadrados, estrigoso-pubérulos.

Distribución. Vive preferentemente en campos húmedos y modificados del planalto brasileño. Es dudosa su presencia en el territorio argentino, siendo citada para la provincia de Misiones, unicamente sobre la base del ejemplar tipo.

Material selecto examinado. BRASIL. PARANÁ: Bocaiuva do Sul, campina dos Tavares, *Hatschbach 3498* (HB, MBM, SI); Piriquara, Nova Tirol, margens do corrego, 930 m, *Hatschbach 24207* (MBM); Piraquara, Mananciais da Serra, *Oliveira 791* (F); km 168, Municipio Jaguariaira, *Kummrow 438* (RB); Rio Potinga, *Kummrow 402* (LP). SANTA CATARINA: Lajes, Rio Caveiras, Estrada da Rodagem Federal, km 8 S de Lajes, *Smith et al. 11316* (SI). RIO GRANDE DO SUL: Costa do Cadeia, Triunfo, *Sobral 1648* (F); Taquara, Caracol, *Rambo 28704* (SI); Osorio, Fazenda do Ayo. prox. Osorio, *Rambo 46755* (SI); Caracol, prox. Canela, *Rambo 52807* (SI).

En 1947, Burkart describió para Rio Grande do Sul a *M. niederleinii* var. *riograndensis*; posteriormente, en 1979 la citó para el Estado de Santa Catarina. Según él, esta variedad se diferenciaba por presentar folíolos pubérulos en la cara abaxial y pinnas 24–54-yugadas, mientras que la var. *niederleinii* se caracterizaba por poseer folíolos con la cara abaxial pubérula y estrigosa y pinnas

19–32-yugadas. El material tipo consultado de *M. niederleinii* var. *riograndensis* posee la mayoría de los folíolos con pubescencia pubérula, pero, también, se pueden observar algunos pelos estrigosos mezclados, como ocurre en la variedad típica. Con respecto al número de folíolos por pinna, es conveniente señalar, que el material tipo de *M. niederleinii* es un ejemplar pobre y las pinnas no poseen completos los pares do folíolos. Por otro lado, en el material brasileño, se han observado varios ejemplares con pinnas 30–50-yugadas pero con pubescencia pubérula y estrigosa en la cara abaxial de los folíolos. Ante la variabilidad observada en los únicos caracteres diferenciales, se propone en esta nota considerar en la sinonimia de *M. niederleinii* a la var. *riograndensis*.

La cita de *M. niederleinii* para la Argentina fue realizada sobre la base del ejemplar tipo coleccionado en Varana (?), Misiones, por Niederlein en la expedición de la Comisíon Nacional de Límites. En 1948, Burkart señala que dicha localidad pertenece a la parte centro-oriental de la provincia de Misiones, en la region de Fracrán. A pesar de la especificación posterior, desde 1887 hasta el momento, no se ha encontrado nuevamente material de esta especie en la Argentina, en cambio sí es común hallar ejemplares recientemente coleccionados en el SE brasileño; existe la posibilidad que el material citado fuera coleccionado en el estado de Rio Grande do Sul y no en el territorio argentino.

Esta especie posee una variedad en el Edo. de Santa Catarina, Brasil: *M. niederleinii* var. *pseudolepidota* Burk. Esta variedad presenta tallos, pecíolos, pedúnculos, y craspedio con pubescencia densa, estrigosa o setulosa, y ramificada.

4. Mimosa petraea Chodat et Hassl., Bull. Herb. Boissier ser. II 4: 548. 1904. TIPO: Paraguay: in glareoris prox. Chololó in valle fluminis, Y-acá, Dec. 1900, *Hassler 6619* (holotipo, G; isotipo, F; fotografía n° serie F(G)—28277, MO, F, SI).

Sufrútice pequeño 10–30 cm alt., inerme; tallos con pubescencia estrigosa o estrigosa y pubérula, a veces con pequeñas glándulas caedizas. Estípulas 2.5–5 mm long. × 0.5 mm lat., lanceoladas a linear-triangulares, 3-nervias, glabras, ciliadas en el margen. Pecíolo 1–3 mm long.; pinnas uniyugadas 15–30 mm long.; estipelas 0.25–0.5 mm long., lineares, pilosas; folíolos 12–28-yugados 2–3.5(–4.5) mm long. × 0.75–1 mm lat., oblongos a triangulares, con 1–(2) nervios visibles en la cara abaxial, nervio medio subcentral, cara adaxial glabra, cara abaxial ± pubérula, a veces con algunos pelos estrigosos (pubescencia estrigosa, más abundante en los folíolos inferiores de la pinna). Inflorescencia axilar; pedúnculo 1(2) en la axila de las hojas superiores, 5–10 mm long., menores o iguales que las hojas; racimos globosos a subovoides de ± 4 mm long. × 4 mm lat. (sin filamentos); bráctea 2–3 mm long. × 0.5–0.75 mm lat., lanceolada, aquillada, mayores que las flores, glabra a pubérula en el ápice, 1-nervia, margen con glándulas caedizas y ciliado en el ⅓ apical, caediza; botón floral ovoide; cáliz de ± 0.5 mm long., membranáceo, glabro, ciliado en el borde; corola de 1.5–2 mm long., 4-lobulada, turbinada, lóbulos de 0.75–1 mm long., 1-nervios, glabros a levemente pubérulos; filamentos estaminales libres hasta la base. Craspedio 12–17 mm long. × 4–5 mm lat., levemente toruloso, comprimido, estrigoso y pubérulo, 3–4-seminado, artejos de 4–5 mm long.; replo ± 0.5 mm lat. Semilla ± 2.5 mm long. × 2.5 mm lat. (inmadura).

Distribución. Vive en lomadas con rocas aflorantes en las serranías de Paraguay central.

Material adicional examinado. PARAGUAY. CORDILLERA: Itacurubí, *Schinini 3207* (CTES, F). PARAGUARI: Piraretá-Piribeby, *Schinini 2594* (CTES, F, SI); links vom Piribebuy und sublich von Tobati: Serranía nordlich von Fal des Y-agui-guazu, *Fiebrig 840* (F, LIL).

En 1948 y 1952, Burkart citó a esta especie para la Argentina sobre la base del ejemplar: "Misiones, Bonpland, *P. Jörgensen 325*, IX-1909 (BAB 34712)". En el material estudiado solo se pudo encontrar un ejemplar de herbario que si bien posee los mismos datos citados en la exsiccata por Burkart, no coincide en la fecha de colección. En la etiqueta del material se lee XI-1909 y no IX-1909. Esta diferencia probablemente se deba a un error de impresión. Por otro lado, el ejemplar *Jörgensen 325* (BAB 34712) no pertenece a *M. petraea*, sino a una forma más pequeña y pubescente de *M. oligophylla* M. Mich. Al revisar todo el material depositado en el herbario del Depto. de Botánica Agricola, INTA, Castelar (BAB), se pudo comprobar que existen más ejemplares de *P. Jörgensen 325*, los cuales corresponden a distintos números de BAB y a diferentes especies de *Mimosa*, por ej., BAB 30213, 30214, 30224 = *M. oligophylla*; BAB 32116, 32117, 32118 = *M. paupera* Benth., etc. A pesar de la mezcla existente entre el material y el número de BAB, ninguno de los ejemplares vistos pertenece a *M. petraea*. Salvo por la cita de Burkart (1948), hasta el momento no se ha encontrado esta especie en la Argentina, por lo que se cirscunscribe su distribución geográfica al territorio paraguayo. No se descarta que en

el futuro pueda ser coleccionada en las provincias del NE.

En el material examinado de *M. petraea* (Burkart, 1948), fue citado otro ejemplar: "Paraguay, *P. Jörgensen 4450*," el cual tampoco corresponde a la variedad típica, sino a *M. petraea* var. *hirtula* Burk. Dicho ejemplar, al igual que el tipo y demás especímenes estudiados de var. *hirtula* se diferencian de var. *petraea* por ser un sufrútice erecto a procumbente en la base con pinnas 1–6.5 cm long., y generalmente inflorescencias mayores a iguales que las hojas.

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A REVISION OF MESOAMERICAN *PSYCHOTRIA* SUBGENUS *PSYCHOTRIA* (RUBIACEAE), PART II: SPECIES 17–47[1]

Clement W. Hamilton[2]

GROUP 3. THE *GRACILIFLORA* GROUP

Shrub or sometimes small tree; young stems glabrous or sometimes ferrugineous-pubescent; stipules sheathing or not, triangular or ovate or lanceolate, *the apex often bifid or biaristate* (Fig. 2f), uniform in color, glabrous or less commonly fringed or ferrugineous-puberulent, caducous. *Leaf* blades usually elliptic, sometimes narrowly so, or oblanceolate or slightly obovate, *drying reddish or greenish gray, brown, or black*; secondary veins 3–14(–16) pairs, diverging (45°–)55°–90°(–100°), *eucamptodromous or brochidodromous*, with collector vein only in *P. jimenezii*, the axils with domatia (Fig. 4b) or not (with tufts of hair only occasionally in *P. bakeri*); tertiary veins orthogonal reticulate (sometimes percurrent in *P. marginata*). *Inflorescences* panicles of cymes or rarely (*P. bakeri* and sometimes *P. parvifolia*) of glomerules, *usually pedunculate*; *secondary axes usually in 1 pair per rank*, if more than 1 pair then size-differentiated, *often delicate* or diffuse in structure and *diverging at right angles* (Fig. 7h); bracts rarely conspicuously enlarged (to 6 mm long in *P. jimenezii*). *Corolla* tubes (1.5–)2–4(–5) mm long (Fig. 8), the lobes usually without apical extensions (sometimes with blunt protuberances in *P. graciliflora*). *Fruit* when dry usually ellipsoid to spherical (obloid in *P. philacra*); persistent calyx a beak or not evident; *seed dorsal surface with 3–5* (6–8 in *P. parvifolia*) *usually deep longitudinal furrows* (Fig. 10d), the ventral surface with 2 deep or broad longitudinal furrows (plus several irregular furrows in both surfaces in *P. philacra*; ventral surface often concave in *P. graciliflora* [Fig. 10c]).

The most commonly encountered species in the group, *Psychotria marginata* (distribution, Fig. 20), does not obviously closely resemble any other species. *Psychotria graciliflora* (Fig. 21), the other widespread species, is the centerpiece of the morphologically cohesive *P. graciliflora* complex, which includes also *P. bakeri* (Los Santos, Panama), *P. laselvensis* (Costa Rica), *P. liesneri* (eastern Panamá Province), *P. orosiana* (Costa Rica and Panama), *P. parvifolia* (Costa Rica and western Panama), and *P. philacra* (eastern Darién Province; see Fig. 22). *Psychotria jimenezii*, a Costa Rican species (Fig. 23), is unique in the group in having a collector vein, inflorescence bracts as long as 4–6 mm, and seed dorsal surface with usually only three longitudinal furrows, but it too may belong to the *P. graciliflora* complex.

Of the nine species in the group, six appear distylous. All six show between-morph asymmetry in floral part lengths: *Psychotria graciliflora*, *P. jimenezii*, *P. laselvensis*, *P. marginata*, and *P. parvifolia* have longer-exserted parts in pins than in thrums, and in *P. orosiana* pin reproductive organs are longer at both levels. The only positively derived state is seen in *P. liesneri*, which is long-homostylous. Available flowering material of *P. bakeri* and *P. philacra* is insufficient to determine their breeding systems.

17. Psychotria bakeri Dwyer, Ann. Missouri Bot. Gard. 67: 347. 1980. TYPE: Panama. Los Santos: Loma Prieta, Cerro Grande, 720–840 m, 8 June 1967 (fl), *Lewis et al. 2249* (holotype, MO; isotypes, F, GH). Figure 22.

Shrub to 1.5 m; young stems glabrous, the bark smooth; stipules sheathing, the sheath 2.5 mm long, biaristate with extensions 2–3 mm long, glabrous, caducous, leaving a red-brown ridge. *Leaves* petiolate; petioles 3–5 mm long, glabrous, flat above; blades membranous, narrow-elliptic, the apex acute, the base attenuate, (3–)4.5–7 × 1–1.6 cm, glabrous above and below, drying pale red-brown; secondary veins 6–7 pairs, diverging 45°–55°, brochidodromous, arcuate near margin, not elevated, glabrous, the axils occasionally with minute

[1] Part I: Introduction and Species 1–16 appears in the preceding issue of the *Annals of the Missouri Botanical Garden*, Volume 76: 67–111.

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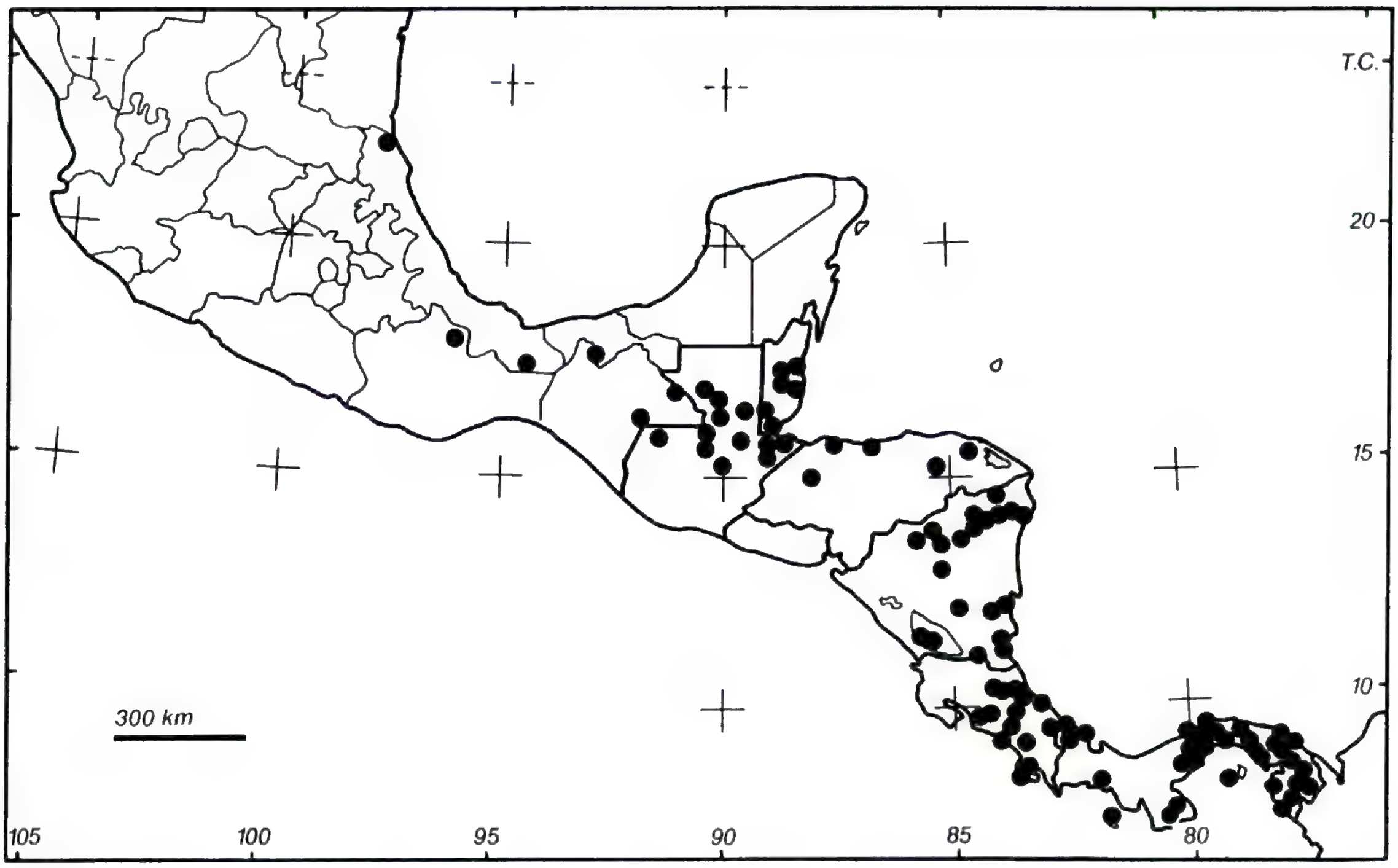

FIGURE 20. Distribution of *Psychotria marginata* in Mesoamerica.

tufts of white hairs; tertiary veins inconspicuous. *Inflorescences* terminal or pseudoaxillary, panicles of glomerules; panicle branched to 2–3 degrees; main axis 1.5–3.5 cm long, the peduncle 1–3 cm long; secondary axes in 1 rank, the first-rank axes 2, 0.4–0.8 cm long; cymes branched to 2 degrees; bracts and bracteoles linear to triangular, often cleft, 1–2 mm long, puberulent within, the margins ciliate. *Flowers* sessile; calyx cup-shaped, the tube 1 mm long, the lobes 5, triangular, 0.5–0.7 ×

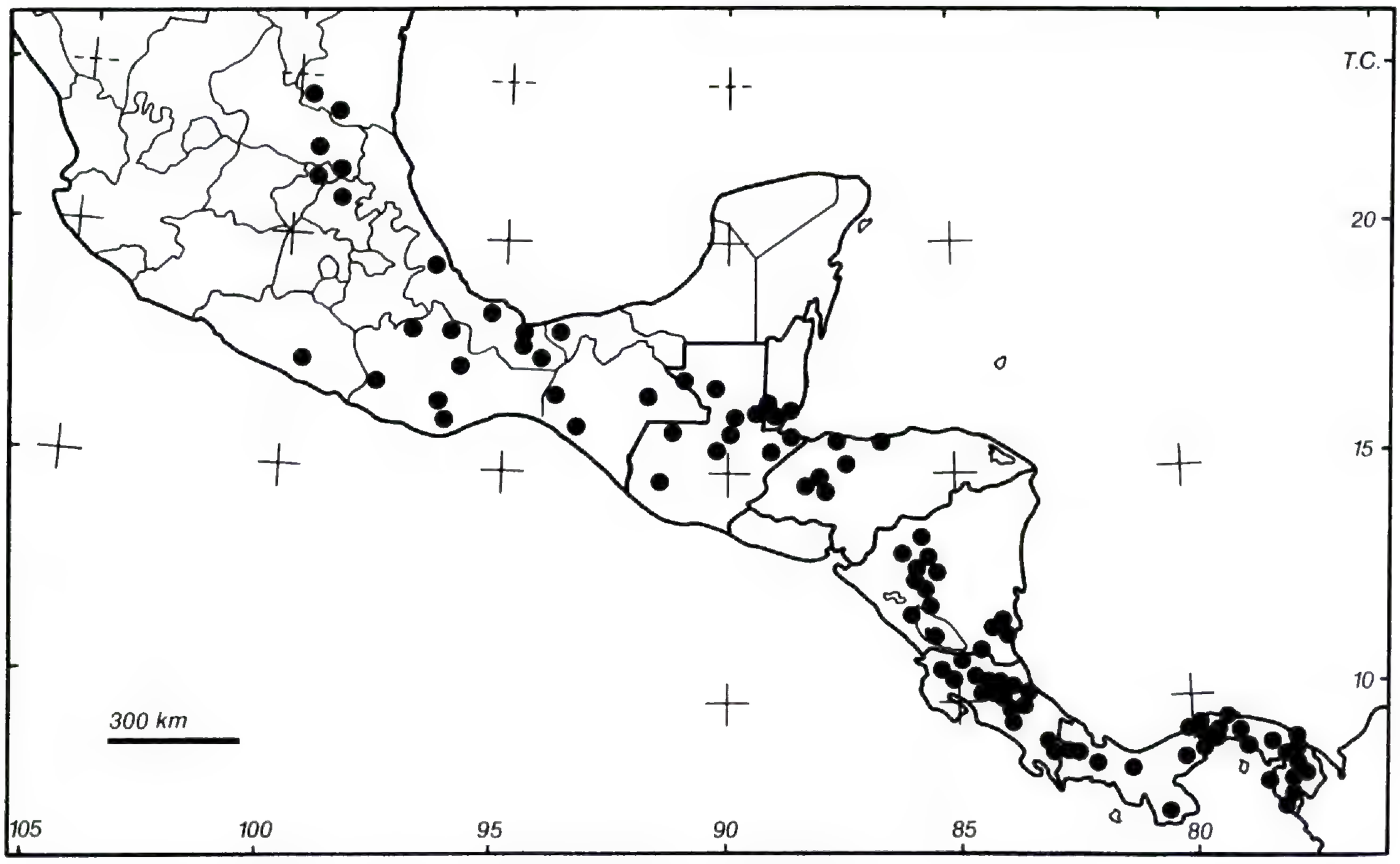

FIGURE 21. Distribution of *Psychotria graciliflora* in Mesoamerica.

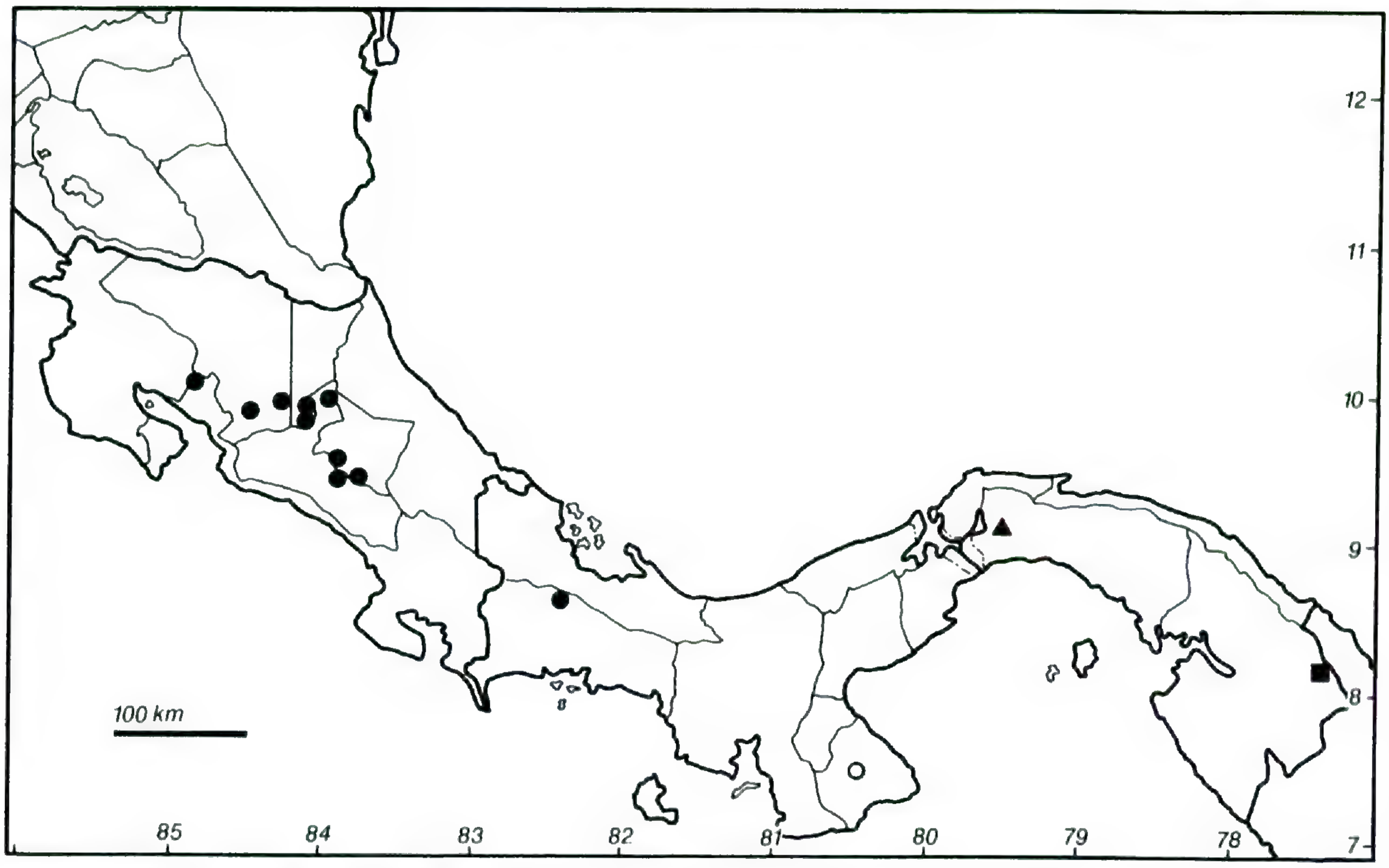

FIGURE 22. Distributions of *Psychotria bakeri* (open circle), *P. liesneri* (triangle), *P. parvifolia* (solid circles), and *P. philacra* (square).

0.6 mm, glabrous; corolla white, the tube cylindrical, 1.5–3 × 1–1.5 mm, white pubescent in throat, the lobes 5, narrow triangular, 1–2 × 1 mm; stamens 5, the filaments not seen in pins, 1.5 mm long in thrums, the anthers 1 mm long; style not seen in pins, 1 mm long in thrums, the branches linear. *Fruit* not seen.

Distribution (Fig. 22). Known only from the type collection from Los Santos, Panama at around 800 m elevation in premontane wet forest with tropical-equatorial climate. It was collected in flower on June 8.

Psychotria bakeri may be recognized by its small narrow-elliptic (usually 4.5–7 × 1–1.6 cm) leaves with acute apex and small (1.5–3.5 cm long) panicles of glomerules. Only the thrum morph has been seen, but one collection does not suffice to suggest thrum-monomorphy.

18. Psychotria graciliflora Bentham in Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 35. 1853. *Mapouria graciliflora* (Benth.) Oerst., Amér. Centr. p. 17, t. 14., fig. 6. 1863. *Uragoga graciliflora* (Benth.) Kuntze, Revis. Gen. Pl. 2: 960. 1891. TYPE: Costa Rica. Alajuela: nr. Naranjo, ca. 1,350 m, (fl), *Oersted s.n.* (holotype, C, n.v., photo, F neg. no. 22832; isotypes, K, US). Figures 10c, 21.

Psychotria oaxacana Standley, Contr. U.S. Natl. Herb. 23: 1391. 1926. TYPE: Mexico. Oaxaca: nr. Sto. Domingo, 480 m, 18 June 1895 (fl), *E. W. Nelson 2688* (holotype, US).

Psychotria vallensis Dwyer, Ann. Missouri Bot. Gard. 67: 438. 1980. TYPE: Panama. Coclé: La Mesa nr. chicken farm, 3 Jan. 1974 (fl, fr), *Dwyer 11867* (lectotype designated herein, MO—2163005A; isolectotypes, F, GH, MO—2 sheets).

Shrub 1–3 m tall; young stems glabrous, the bark gray, smooth to shallowly furrowed; stipules ovate, biaristate with often puberulent extensions 3–4(–6) × 1–1.5 mm, glabrous, caducous, leaving a pale ridge with red-brown fringe. *Leaves* subsessile to petiolate; petioles 1–7 mm long, glabrous, flat above; blades membranous, elliptic, the apex acuminate or sometimes acute, the base attenuate to narrowly cuneate, (2–)3–8(–11.5) × (0.9–)1.3–3(–3.5) cm, glabrous above and below, drying gray-green to deep red-brown; secondary veins (4)5–8(9) pairs, diverging (67°–)70°–80°(–95°), eucamptodromous to brochidodromous, constantly arcuate, barely elevated below, glabrous, the axils lacking domatia or hairs; tertiary veins inconspicuous to evident, the intersecondaries often evident, orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, delicate spreading panicles of cymes; panicle branched to 3 degrees; main axis 3–5 cm long, the peduncle 2.5–3.5 cm long; secondary axes in (2–)3 ranks, the first-rank axes 2, 0.8–1.5 cm long, the second-rank axes 2, 0.2–0.6 cm

long, the third-rank axes 2, 0.1–0.2 cm long; cymes branched to 1–2 degrees; bracts triangular to linear, conspicuous, 1–3 mm long, glabrous, sometimes fringed; bracteoles irregular, 0.5–1 mm long, fringed. *Flowers* sessile to pedicellate, the pedicels to 1.5 mm long; calyx cup-shaped, the tube 0.3–0.5 mm long, the lobes 5, barely evident to triangular to linear, to 1 mm long, puberulent outside; corolla white, the tube cylindrical, 2–2.5 × 1 mm, white pubescent in throat, the lobes 5, linear often with blunt protuberance near apex, 1–2 × 0.5–1 mm; stamens 5, the filaments 2–2.5 mm long in pins, 3–3.5 mm long in thrums, the anthers 1 mm long; style 4–5 mm long in pins, 2.5 mm long in thrums, the branches linear. *Fruit* when dry ellipsoid to spherical, 4–5 mm long, 3–4 mm diam., maturing red, drying red-brown to black; persistent calyx a beak to 1 mm long; seed dorsal surface with 4 longitudinal furrows, the ventral surface concave or with 2 broad shallow longitudinal furrows (Fig. 10c).

Distribution (Fig. 21). Widespread from Mexico through Panama, missing only in El Salvador. It is noteworthy that such a common and widespread species in Central America is rare at best in South America and apparently absent from the Antilles. *Psychotria graciliflora* has the greatest elevation range of any species of the subgenus, ranging 0–2,500 m, and occurs in tropical moist to lower montane rainforest with equatorial and tropical climate. It has been collected in flower January–August, primarily March–July, and in fruit throughout the year, primarily August–February.

Selected specimens examined. MEXICO. CHIAPAS: Mpio. Cintalapa, 16 km NW of Rizo de Oro along a logging rd. to Colonia Figueroa, 1,600 m, 27 Apr. 1972 (fl), *Breedlove 24913* (MEXU); 8 Jan. 1973 (fr), *Breedlove & Smith 31291* (MEXU); Mpio. Ocosingo, adjacent to Laguna Ocotal Grande, 800 m, 6 Feb. 1973 (fr), *Breedlove 33059* (MEXU, MO); SE side of Cerro Tres Picos and ridges nr. summit, 2,100–2,500 m, 28 Mar. 1973 (fl), *Breedlove 34380* (MEXU); Villa Corzo, E base of Cerro Tres Picos nr. Cerro Bola along a logging rd. SW of Colonia Agronomos Mexicanos, 1,500 m, 10 Dec. 1972 (fr), *Breedlove & Thorne 30180* (MEXU). GUERRERO: Mpio. Atoyac, 19 km NE of Atoyac, nr. Santiago La Unión, 770 m, 3 Nov. 1979 (fr), *Koch et al. 79293* (MEXU). HIDALGO: Mpio. Xochicoatlán, Malila, 1,450 m, 16 May 1969 (fl), *Puig 4604* (ENCB, MEXU). OAXACA: Dto. Putla, 10 km al NE de Putla, carr. a Huajuapán, 990 m, 20 June 1982 (fl), *Cedillo & Torres 1481* (ENCB, MEXU); Pluma Hidalgo, N of Pochutla, July 1943 (fr), *Leyva s.n.* (US); Dto. Villa Alta, forest between Los Llanos de Ozumazui and Río Chiquito, 17°35′N, 95°55′W, 500 m, 1 May 1939 (fl), *Schultes & Reko 732* (F); Tuxtepec, Chiltepec, 14 Sep. 1961 (fr), *Sousa 936* (MEXU—2 sheets); Dto. Miahuatlán, 16 km al SE de piedra larga, camino al Progreso, 23 Sep. 1982 (fr), *Torres & Cedillo 1397* (ENCB, MEXU); Dto. Teotitlán, "Río Uluapan" 8 km al E de San Bartolomé Ayantla, carr. Huajuapán–Jalapa de Díaz, 880 m, 20 July 1982 (fl, fr), *Torres et al. 845* (ENCB, MEXU). QUERETARO: Mpio. de Tancoyol, La Parada, 1,300 m, 16 Apr. 1969 (fl), *Puig 4500* (ENCB). SAN LUIS POTOSÍ: Las Canoas, hills, 21 Aug. 1891 (fr), *Pringle 5041* (GH); Mpio. de Xilitla, ejido de Xilitlilla, 1,000 m, 5 May 1959 (fl), *Rzedowski 10577* (ENCB, MEXU). TABASCO: Mpio. Heroica Cárdenas, km 21 de la carret. Cárdenas–Coatzacoalcos, 19 May 1981 (fl), *Magaña & Curiel 201* (ENCB, MEXU). TAMAULIPAS: nr. Gómez Farías, Rancho del Cielo, 1,260 m, 1 May 1967 (fl), *Gómez-Pompa 2019* (MEXU); Jaumave, 1930 (fr), *Viereck 680* (US). VERACRUZ: Mpio. Catemaco, cerro al NE de Coyame, lado NE de Lago Catemaco, 700 m, 14 Dec. 1971 (fr), *Beaman 5310* (ENCB, F, MEXU); Atoyac, 13 May 1937 (fl), *Matuda 1414* (A, F, K, MEXU, MO, NY); Río Vista, Río Coatzacoalcos, nr. Jesús Carranza, 20 m, 9 Aug. 1971 (fr), *Nevling & Gómez-Pompa 2564* (ENCB—2 sheets, GH, MEXU); Mpio. Hidalgotitlán, Río Soloxuchil, 17°16′N, 94°37′W, 152 m, 2 Apr. 1974 (fl), *M. Vázquez et al. 312* (ENCB, F, MEXU); Mpio. Minatitlán, orilla de Río Uxpanapa, un poco arriba del poblado de Uxpanapa, 120 m, 26 May 1981 (fl), *Wendt et al. 3322* (ENCB, MEXU). GUATEMALA. ALTA VERAPAZ: Sebol, 6 km E of San Luis Road, between Achiote and Sebol, 23 Apr. 1964 (fl), *Contreras 4485* (MO); 10 km N of Cobán, 1,200 m, 4 Jan. 1973 (fr), *L. O. Williams et al. 42086* (F). HUEHUETENANGO: between Ixcan and Río Ixcan, Sierra de los Cuchumatanes, 150–200 m, 23 July 1942 (early fr), *Steyermark 49271* (NY). IZABAL: Puerto Barrios, 28 May 1909 (fl), *Deam 6036* (GH, US); vic. Quiriguá, 75–225 m, 15–31 May 1922 (fl), *Standley 24291* (GH, NY, US). PETÉN: San Diego, Río de la Pasión, 16 Apr. 1935 (fl), *M. Aguilar H. 499* (F, GH, K, MO, NY); La Cumbre, on km 138/139 on San Luis–Cadenas road, in second growth, 19 Sep. 1966 (fr), *Contreras 6145* (MO); low forest between Finca Yalpemech and Chinajá, 50–100 m, 28 Mar. 1942 (fl), *Steyermark 45431* (F); along Río Santa Isabel, between mouth of Río Sebol and El Porvenir, 100 m, 21 Apr. 1942 (fl), *Steyermark 45863* (A, GH). QUEZALTENANGO: Finca Pireneos, below Santa María de Jesús, 1,350–1,380 m, 11 Mar. 1939 (st), *Standley 68196* (A). BELIZE. TOLEDO: Columbia Forest Station, 24 June 1972 (fl), *Dwyer 9903* (DUKE, NY); 16 km from Punta Gorda, rd. to San Antonio, 31 July 1980 (early fr), *Dwyer 15141* (MO—3 sheets); Golden Stream, upper reach, 4 May 1944 (fl), *Gentle 4581* (DUKE—2 sheets, MO). HONDURAS. ATLANTIDA: nr. Tela, Triunfo, 0 m, 28 Dec. 1927 (fr), *Standley 53755* (A, US); foothills back of La Ceiba, 25 June 1938 (fr), *Yuncker et al. 8019* (GH, K, MO, NY, US). COMAYAGUA: Pito Solo, Lake Yojoa, 600 m, 24 Aug. 1932 (fr), *Edwards 469* (A, US). CORTÉS: along Río Lindo, nr. Lake Yojoa, 490 m, 8 Aug. 1948 (early fr), *L. O. Williams & A. Molina R. 14562* (GH). SANTA BARBARA: Montaña Santa Barbara above Sauce nr. Lake Yojoa, 1,000 m, 7 Aug. 1948 (fl), *L. O. Williams & A. Molina R. 14487* (GH). YORO: Subirana, 1,100 m, Oct. 1937 (fr), *Hagen & Hagen 1114* (NY). NICARAGUA. BOACO: Cerro Alegre, San José de los Remates, 12°36′N, 85°44′W, 1,100–1,180 m, 11 Feb. 1983 (fr), *P. P. Moreno 20232* (MO). CHONTALES: Cerro Oluma, ca. 3 km SE de Cuapa, 12°18′N, 85°20′W, 700–740 m, 3 Jan. 1984 (fr), *Grijalva et al. 3376* (MO). GRANADA: Volcán Mombacho, lado N, Plan de las Flores, 1,100 m, 5 June 1975 (fl), *Atwood 306* (MO). JINOTEGA: Volcán de Yalí, 1,500 m, 31 May 1975 (fl), *Atwood 275* (MO); "Filas el Portal" NE del Cerro Kilambé, 13°37′N,

85°40′W, 600–900 m, 26 Mar. 1981 (bud), *P. P. Moreno & Sandino 7599* (MO); Macizos de Peñas Blancas, above Río El Gusaneras, 13°15′N, 85°41′W, 1,200–1,400 m, 13–18 Jan. 1979 (fr), *W. D. Stevens 11638* (MO). MATAGALPA: al NW del Cerro Musún, 800–1,200 m, 14 May 1980 (fl), *Araquistain & P. P. Moreno 2490* (MO); La Galia, N of Sta. María de Ostuma, 1,600 m, 12 Mar. 1967 (fr), *A. Molina R. 20580* (F, NY, US); ridge along rd. between La Danta and La Luna, 12°40′N, 85°43′W, 960–1,000 m, 30 July 1978 (fl), *W. D. Stevens 9597* (MO). RÍO SAN JUAN: nr. Caño Chontaleño, 20 km NE of El Castillo, 200 m, 18–21 Apr. 1978 (fl), *Neill & Vincelli 3483* (MO). RIVAS: Isla de Ometepe, N slope of Volcán Maderas on trail from Balgue to Laguna Maderas, 11°27′N, 85°32′W, 23 Jan. 1981 (fr), *W. Hahn 482* (MO). ZELAYA: rd. between Nueva Guinea and Verdún, 11°39′N, 84°26′W, 240 m, 17 Aug. 1983 (early fr), *J. Miller & Sandino 1104* (MO); Río Punta Gorda, Atlanta, desembocadura del Caño el Guineo, 11°33′N, 84°02′W, 10 m, 11 Nov. 1981 (fr), *P. P. Moreno & Sandino 12858* (MO); Caño Costa Riquita, S of rd. between Colonia Nueva León and Colonia Naciones Unidas, 11°43′N, 84°18′W, 150–180 m, 6–7 Nov. 1977 (early fr), *W. D. Stevens 4953* (MO). COSTA RICA. ALAJUELA: rd. from Canas to Upala, 13.8 km N of Bijagua, 100–150 m, 26 June 1976 (early fr), *Croat 36449* (CR, MO); vic. San Rafael de Guatuso, on Río Frío, 10°43′N, 84°48′W, 80–100 m, 4 Aug. 1949 (fl, early fr), *Holm & Iltis 861* (NY); 12 km NNW of San Ramón on rd. to San Lorenzo, 10°10′N, 84°29′W, 1,100 m, 25 Apr. 1983 (fl), *Liesner & Judziewicz 14914* (CR, MO); 13 km W of Fortuna, rd. to Arenal Dam, 10°29′N, 84°43′W, 500–550 m, 29 Apr. 1983 (fl), *Liesner et al. 15230* (CR, MO); San Carlos, Villa Quesada, 850 m, 12 Mar. 1940 (fl), *A. Smith 2612* (F, GH, MO); Alfaro Ruiz, San Luis, 1,500 m, 20 Apr. 1940 (fl), *A. Smith 2647* (F, NY); vic. Fraijanes, 1,500–1,700 m, 12–13 Feb. 1926 (fr), *Standley & Torres 47600* (US). CARTAGO: along Camino Raiz de Hule, SE of Platanillo (Tsipiri), 1,200–1,400 m, 1 July 1976 (fl), *Croat 36785* (CR, MO); 10 km S of Cartago, 1 km S of Palo Verde, 9°46′N, 83°57′W, 1,450 m, 21 Apr. 1983 (fl), *Liesner & Judziewicz 14537* (CR, MO); N of Muñeco, Río Sombrero, ca. 1,400 m, 25 June 1972 (fl), *Primack et al. 196* (DUKE); Cerro de La Carpintera, 1,500–1,850 m, Feb. 1924 (fr), *Standley 35521* (US). GUANACASTE: Parque Nacional Rincón de la Vieja, SE slopes of Volcán Sta. María, 10°47′N, 85°18′W, 900–1,200 m, 27–28 Jan. 1983 (fl, early fr), *Davidse et al. 23455* (CR, MO); 3 km N of Río Naranjo, W of Tenorio Volcano, 550 m, 3 June 1972 (fl), *Lent 2589* (DUKE, MO). HEREDIA: Finca La Selva, OTS field station, Río Puerto Viejo, 100 m, 5 Feb. 1981 (fr), *Folsom 8756* (DUKE); 1 May 1981 (fl), *Folsom 9957* (DUKE); Vara Blanca de Sarapiquí, 1,500–1,750 m, July–Sep. 1937 (fl), *Skutch 3137* (GH, K, MO, NY, US). LIMÓN: llanuras de Sta. Clara, 300 m, Apr. 1896 (fl), *Donnell-Smith 6602* (GH, K, NY, US—2 sheets); drenajes de los Ríos Parismina y Reventazon, 0 m, 3 Oct. 1951 (fr), *Shank & Molina 4283* (GH, US); vic. Guapiles, 300–500 m, 12–13 Mar. 1924 (fl), *Standley 37279* (US). PUNTARENAS: San Vito de Java, Finca Las Cruces, 1,300 m, 22 May 1971 (fl), *Burch 4587* (MO, NY); Cañas Gordas, Finca Loma Linda, 8°44′N, 82°55′W, 1,140 m, 25 Feb. 1973 (fl), *Busey 627* (F, GH, MO); Río Negro between La Unión and Cortu, 8 Aug. 1974 (early fr), *Croat 26543* (GH, MO); Río Burú, upper slopes of Cerro Burú, 9°01′N, 82°52′W, 1,800 m, 19 Aug. 1983 (early fr), *Davidse et al. 23772* (CR, MO). SAN JOSÉ: La Hondura, 1,300–1,700 m, 16 Mar. 1924 (st), *Standley 37831* (US); La Palma, 1,600 m, 17 Mar. 1924 (fl), *Standley 38200* (US); between Volcán Barba and Irazú ca. 5 mi. NE of San Vicente, ca. 1,450 m, 15 Jan. 1968 (fr), *Wilbur & Stone 9665* (CR, DUKE, MO). PANAMA. CANAL AREA: Coco Solo, 11 Oct. 1972 (fr), *Gentry 6475* (MO); vic. Fort Sherman, 15 Jan. 1924 (fr), *Standley 31070* (US); Gamboa, 14 July 1966 (fl), *Tyson et al. 4562* (DUKE, GH, MO). CHIRIQUÍ: Palo Santo, 3 mi. N of Volcán, 19 Feb. 1971 (fr), *Croat 13594* (F, MO); along Río Colorado, 8°50′N, 82°43′W, 1,200–1,400 m, 17 Mar. 1983 (fl, fr), *Hamilton & Stockwell 3424* (CR, MO); 11 July 1983 (fl, early fr), *Hamilton & Krager 3784* (CR, MO); 7.5 mi. from bridge over Río Chiriquí Viejo on rd. to Río Sereño, 1,350 m, 7 Apr. 1979 (fl), *Hammel et al. 6863* (MO); Finca Ojo de Aqua, 8°51′N, 82°46′W, 1,300 m, 14 Oct. 1981 (early fr), *Knapp 1580* (DUKE, MO); ridge 7 mi. N of Los Planes de Hornito, IRHE Fortuna Hydroelectric Project, 8°45′N, 82°12′W, 1,000 m, 13 Mar. 1982 (fl, fr), *Knapp et al. 4178* (MO). COCLÉ: Cerro Pilón, 900–1,173 m, 16 Mar. 1973 (fl), *Liesner 767* (GH, MO, NY); Cerro Pilón, 5 km NE of El Valle, 800–1,045 m, 13 June 1975 (early fr), *Mori 6551* (MO, US). COLÓN: along Río Boquerón above manganese mine, 9°20′N, 79°35′W, 100–200 m, 13 Dec. 1981 (fr), *Knapp & Sytsma 2444* (MO); between France Field and Cativa, 9 Jan. 1924 (st), *Standley 30178* (US). DARIÉN: El Real, Apr. 1966 (fr), *Bristan 83* (GH, MO); Río Mortí, 250 m, 18 Sep. 1967 (early fr), *Duke 14184* (MO, NY); SE of Río Chico, ca. 10 km upstream from Nazareht, 8°15′N, 77°35′W, 500 m, 21 Dec. 1980 (fr), *W. Hahn 163* (MO); E slope of Cerro Sapo, 450 m, 2 Feb. 1978 (fr), *Hammel 1256* (MO); trail SE of Manené to Río Coasi, 24 Dec. 1980 (fr), *Hartman 12211* (MO); vic. Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, 4 July 1959 (fl), *Stern et al. 921* (GH, MO, US); 10 km NE of Jaqué, headwaters of Río Pavarando, 420 m, 31 Jan. 1981 (fr), *Sytsma & D'Arcy 3390* (ENCB, MO); 3 mi. N of Santa Fe, 15 July 1966 (fl), *Tyson et al. 4634* (DUKE, MO). LOS SANTOS: ca. 10 km SW of El Cortezo, 450–600 m, 28 Oct. 1979 (early fr), *Hammel 5428* (MO). PANAMÁ: Río La Maestra, 0–25 m, 4 Dec. 1936 (fr), *Allen 25* (A, F, GH, MO); 5 mi. N of Cerro Azul on rd. to Cerro Jefe, 720 m, 13 Nov. 1965 (fr), *Blum et al. 1699* (SCZ); Majé, trail ca. 5 mi. up Río Majé, 200 m, 10 Nov. 1970 (fr), *Foster & Kennedy 2010* (DUKE, F, MO); Las Cumbres, 26 Nov. 1974 (fr), *J. Gómez 7* (MO); Río Ipetí, S of Pan-Am. Hwy., 9°03′N, 78°25′W, ca. 100 m, 17 Sep. 1982 (early fr), *Hamilton & D'Arcy 1335* (MO); Nuevo Arraiján, 1 km de la carret. Panamericana, 22 Sep. 1974 (fr), *J. Rodríquez 2* (MO). SAN BLAS: Río Kwadi, ca. 6 air miles SW of Mulatupu, ca. 100 m, 20 Sep. 1967 (early fr), *Duke 14214* (MO, NY). VERAGUAS: "Cerro Tute" ridge up from former Escuela Agricola, Santa Fe, 8°35′N, 81°05′W, 800–1,100 m, 15 July 1983 (early fr), *Hamilton & Krager 3949* (MO); Cerro Tute, ca. 10 km NW of Santa Fe, 750–1,000 m, 18 May 1975 (fl), *Mori 6237* (MO—2 sheets).

Types of *P. oaxacana* and *P. vallensis* have morphologies well within the normal range of *P. graciliflora* and are therefore included.

Psychotria graciliflora may be recognized by its fairly small (usually 3–8 × 1.3–3 cm) glabrous

leaves drying grayish or red-brown and with few (usually 5–8) secondary veins diverging usually 70°–80°, its small (main axis 3–5 cm long) delicate inflorescences and its small (4–5 × 3–4 mm) ellipsoid to spherical fruits often drying black. Leaves in Honduras and Nicaragua are at the upper end of the spectrum in terms of size and number of secondary veins, whereas Costa Rican specimens generally have the smallest leaves with the fewest secondaries. Calyx lobes are generally barely evident to triangular, but in Darién and eastern Panamá provinces the lobes are linear.

The exserted style in the pin morph is noticeably longer than the exserted stamens in the thrum (4–5 vs. 2.5–3 mm).

19. Psychotria jimenezii Standley, J. Wash. Acad. Sci. 15: 288. 1925. TYPE: Costa Rica. San José: La Hondura, ca. 1,400 m, 16 Mar. 1924 (fl), *Standley 37892* (holotype, US). Figure 23.

Psychotria wendlandiana Oersted ex Standley, J. Wash. Acad. Sci. 18: 9. 1928. TYPE: Costa Rica. San Miguel, 13 May 1857 (fl), *Wendland 781* (holotype, C, n.v., fragment, F, photo, F. neg. no. 22857; isotype, US).

Treelet or shrub, 2–5(–7) m tall; young stems ferrugineous-pubescent, the bark smooth; stipules lanceolate to ovate, shortly bifid, 6–9 × 3–5 mm, glabrous, often ciliate, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 0.3–2(–3.2) cm long, puberulent, terete; blades membranous, elliptic, the apex acuminate, the base attenuate to cuneate to cordate, (7–)8–15 × (2–)2.5–5(–5.5) cm, glabrous above, puberulent on midvein below, drying red-brown, paler below; secondary veins (11–)12–14(–16) pairs, diverging (60°–)75°–100°, brochidodromous with collector vein undulating near margin, constantly arcuate, prominulous below, glabrous, the axils lacking domatia or hairs; tertiary veins inconspicuous to evident, orthogonal reticulate, the intersecondaries often evident. *Inflorescences* terminal or pseudoaxillary, panicles of cymes; panicle branched to 4 degrees; main axis 6–7.5 cm long, the peduncle rarely lacking or 2.5–5 cm long; secondary axes in 3(–4) ranks, the first-rank axes (2)4(6), the longest pair 1.5–2.5(–4), the medium pair when present 0.5–1.6 cm long, the shortest pair when present reduced to 0.3 cm long, the second-rank axes 2 or 4, the longer pair 0.6–2.2 cm long, the shorter pair when present 0.2–1 cm long, the third-rank axes 2 or 4, the longer pair 0.4–0.8 cm long, the shorter pair when present 0.2–0.6 cm long; cymes branched to 2 degrees; bracts lanceolate, 4–6 mm long, ciliate; bracteoles triangular, often split, to 1 mm long. *Flowers* subsessile, the pedicels to 0.5 mm long; calyx cup-shaped, the tube 0.5 mm long, the lobes 5, triangular, barely evident to 0.2 mm long, glabrous, often ciliate; corolla cream, the tube cylindrical, 2–2.5 × 1.2 mm, white pubescent in throat, the lobes 5, lanceolate to ovate, 1–1.2 × 0.7 mm; stamens 5, the filaments 2 mm long in pins, 3 mm long in thrums, the anthers 0.7 mm long; style 3.5–4 mm long in pins, 2 mm long in thrums, the branches linear. *Fruit* when dry ellipsoid to spherical, 3.5–5(–6) mm long, 3.5–4.5 mm diam., maturing red, drying red-brown, sometimes sparsely puberulent; persistent calyx a beak 0.3–0.5 mm long; seed dorsal surface with 3(–4) deep longitudinal furrows, the ventral surface with 2 longitudinal furrows.

Distribution (Fig. 23). Found in an east–west band across northern Costa Rica from eastern Guanacaste to Cartago and western Limón, at elevations of 200–1,600 m, mostly above 1,000 m, in tropical wet to premontane rainforest with equatorial-mountainous climate. It has been collected in flower February–May and in fruit August–March.

Selected specimens examined. COSTA RICA. ALAJUELA: nr. Qda. Guillermina, N side Volcán Arenal, 10°29′N, 84°42′W, 500 m, 21 Apr. 1973 (fl), *Lent et al. 3412* (DUKE, F, NY); Guadalupe de Zarcero, 1,625 m, 30 May 1938 (fl), *A. Smith 699* (F—2 sheets, GH, MO, NY); Villa Quesada, 600 m, 15 May 1939 (fl, fr), *A. Smith 1793* (MO, NY, US); 2 km N of Bijagua, rd. to San Miguel, 2 Feb. 1976 (fr), *J. Utley & K. Utley 2923* (CR, DUKE). GUANACASTE: 30 km E of Pan-American Hwy. on rd. to Upala, 180 m, 25 Aug. 1980 (fr), *Kress et al. 9594* (DUKE); Los Ayotes, Tilarán, 600–700 m, 21 Jan. 1926 (fr), *Standley & Valerio 45411* (F, US). LIMÓN: below La Palma, upper Río La Hondura on trail to Guapiles, 10°03′N, 83°58′W, 1,100–1,200 m, 16 Dec. 1966 (fr), *Burger 3909* (CR—2 sheets, F—2 sheets, NY). PUNTARENAS: Monteverde, 1,500 m, 14 Apr. 1981 (fl), *Haber 447* (MO). SAN JOSÉ: above Río Hondura at Baja La Hondura, 1,150 m, 31 Dec. 1974 (fr), *J. Taylor 17883* (NY, US); San Rafael nr. Heredia, 1,118 m, 13 Feb. 1890 (fl), *Tonduz 1974* (US).

Psychotria jimenezii may be recognized by its ferrugineous-pubescent aspect, elliptic leaves often with cordate bases, secondary veins usually 12–14 diverging 75°–100° with undulating collector vein, and inflorescences with secondary axes usually in two unequal pairs per rank in usually three ranks.

The exserted pistil in the pin morph is longer than the exserted stamens in the thrum morph (3.5–4 vs. ca. 3.3 mm).

20. Psychotria laselvensis C. Hamilton, Phytologia 64: 228. 1988. TYPE: Costa Rica. He-

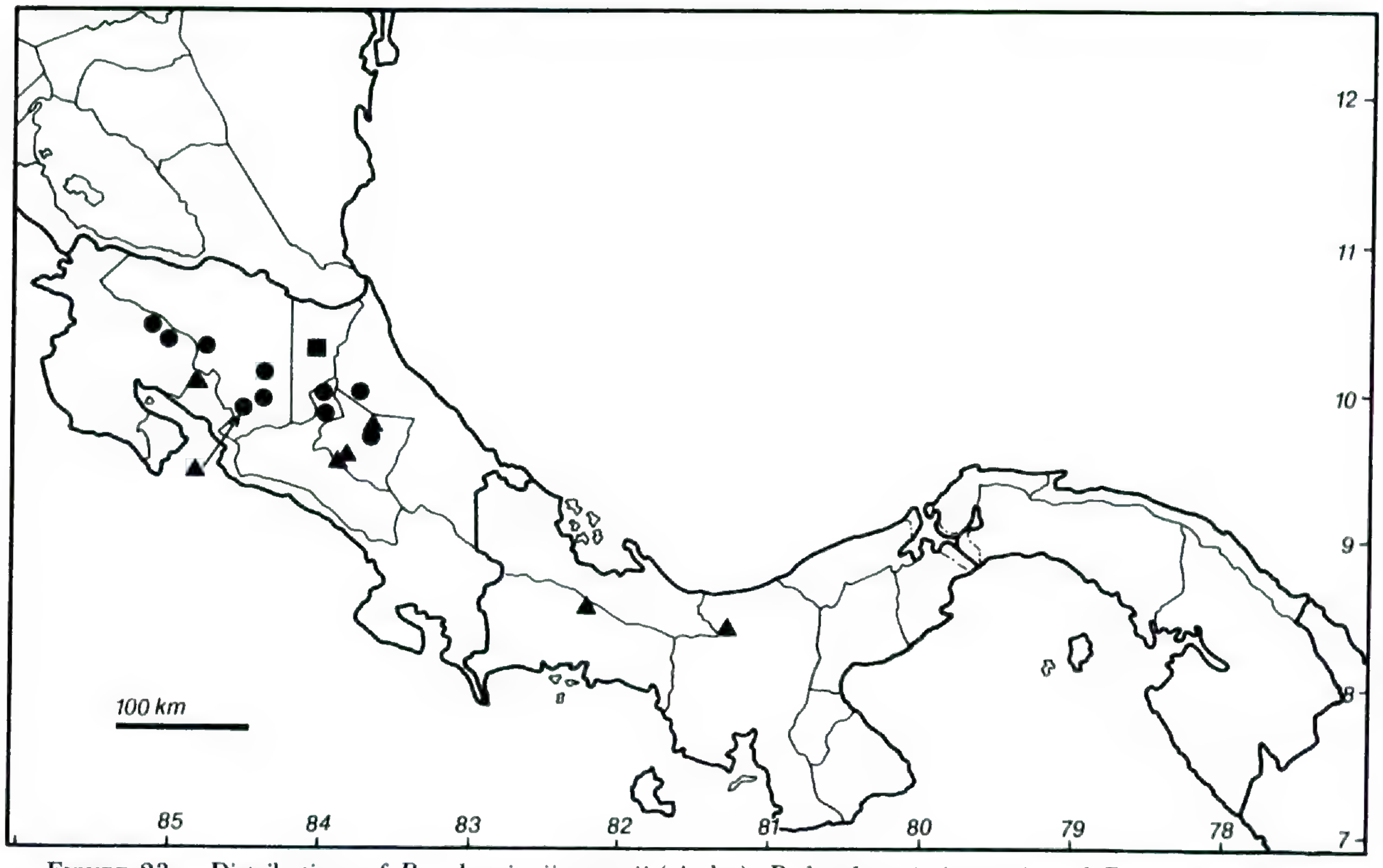

FIGURE 23. Distributions of *Psychotria jimenezii* (circles), *P. laselvensis* (square), and *P. orosiana* (triangles).

redia: Finca La Selva, OTS field station, Río Puerto Viejo just E of its junction with Río Sarapiquí, ca. 100 m, 19 May 1980 (fl), *Hammel 8706* (holotype, DUKE; isotype, CR). Figure 23.

Shrub 1.5–4 m tall; young stems glabrous, the bark smooth; stipules triangular, 3–4 × 3 mm, glabrous, caducous, leaving a pale ridge with red-brown fringe. *Leaves* subsessile to petiolate; petioles 1–7 mm long, glabrous, grooved above; blades membranous to chartaceous, elliptic, the apex acuminate, the base caudate to subcordate, (5–)7.5–13(–16) × (1.5–)2.5–5 cm, glabrous above and below, drying red-black; secondary veins (8–)10–13 pairs, diverging (65°–)80°–85°, brochidodromous, constantly arcuate, prominulous below, glabrous, the axils often with domatia below; tertiary veins evident, reticulate. *Inflorescences* terminal, spreading panicles of cymes; panicle branched to 4 degrees; main axis 6.5–15 cm long, the peduncle 4–9 cm long; secondary axes in 4–5 ranks, the first-rank axes 2 or 4, the longer pair 1.8–4.2 cm long, the shorter pair when present 0.5–0.7 cm long, the second-rank axes 2 or 4, the longer pair 0.6–1.8 cm long, the shorter pair when present 0.2 cm long, the third-rank axes 2, 0.3–0.9 cm long, the fourth-rank axes 2, 0.1–0.4 cm long, the fifth-rank axes 2, 0.2 cm long; cymes branched to 1 degree; bracts lanceolate to triangular, 2–3 mm long, glabrous; bracteoles lanceolate, 0.5–1 mm long, glabrous. *Flowers* pedicellate, the pedicels ca. 0.5 mm long; calyx cup-shaped, the tube 0.3 mm long, the lobes 5, triangular, barely evident, minutely ciliate; corolla white, the tube cylindrical, 2.5–3 × 1.2 mm, white pubescent in throat, the lobes 5, lanceolate, 2 × 1 mm; stamens 5, the filaments 2 mm long in pins, 3–3.5 mm long in thrums, the anthers 1–1.2 mm long; style 5–5.5 mm long in pins, 2.5–3 mm long in thrums, the branches linear, recurved. *Fruit* not seen.

Distribution (Fig. 23). Known only from the type locality, the Organization for Tropical Studies field station at Finca La Selva, Río Puerto Viejo, Heredia, Costa Rica, at ca. 100 m elevation in tropical wet forest with equatorial climate. *Psychotria laselvensis* has been collected in flower February–May and with immature fruit in July.

Additional specimens examined. COSTA RICA. HEREDIA: Finca La Selva, OTS field station, Río Puerto Viejo, 100 m, 1 May 1981 (fl), *Folsom 9958* (CR, DUKE); 4 May 1981 (fl), *Folsom 10004* (DUKE); 18 Feb. 1980 (fl), *Hammel 7778* (DUKE); 1 July 1981 (early fr), *Hammel 10938* (DUKE); 27 Mar. 1982 (fl), *Hammel 11491* (DUKE).

Psychotria laselvensis may be recognized by its resemblance to *P. graciliflora* and *P. orosiana* and its generally larger inflorescences and leaves. It differs from *P. orosiana* in having leaf blades

to 13(–16) cm (vs. 10.5 cm) long, more secondary veins (usually 10–13 vs. 7–9), inflorescence secondary axes commonly 4 (vs. 2) in the first rank, and usually shorter corolla tubes (2.5–3 vs. 2.5–5 mm). These three closely related species—*P. graciliflora*, *P. orosiana*, and *P. laselvensis*—form a continuum with regard to many quantitative characters, but their recognition as species is straightforward.

The exserted pistil in the pin morph is conspicuously longer than the exserted stamens in the thrum (5–5.5 vs. 3.5–4 mm).

21. Psychotria liesneri Dwyer, Ann. Missouri Bot. Gard. 67: 387. 1980. TYPE: PANAMA. PANAMÁ: NE of town of Cerro Azul, 20 km by road from Interamerican Hwy., 10 Dec. 1974 (fr), *Mori & Kallunki 3658* (holotype, MO). Figure 22.

Shrub 2–3 m tall; young stems minutely puberulent, the bark pale, irregularly fissured longitudinally; stipules sheathing, triangular-ovate, 2–2.5 × 1.5 mm, puberulent, red-brown ciliate, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 2–4 mm long, minutely puberulent, flat and furrowed above; blades membranous to subcoriaceous, elliptic, the apex long-acuminate, the base attenuate, the margin inrolled, (4–)4.5–6(–6.7) × (1–)1.5–2.2 cm, glabrous above, puberulent on midvein below, drying dark green-brown to red-brown; secondary veins 8–10 pairs, diverging 70°–80°, brochidodromous, straight then arcuate near margin, prominulous below, glabrous, the axils usually with often minutely ciliate domatia; tertiary veins inconspicuous, orthogonal reticulate. *Inflorescences* terminal, panicles of cymes; panicle branched to 2–3 degrees; main axis 1.5–3 cm long, the peduncle 1–1.5 cm long; secondary axes in (1–)2(–3) ranks, the first-rank axes 2, 0.3–1 cm long, the second-rank axes 2, 0.2–0.5 cm long, the third-rank axes 2, 0.2 cm long; bracts triangular, ca. 0.7 mm long, puberulent, ciliate; bracteoles triangular, to 0.5 mm long, puberulent, ciliate. *Flowers* sessile to subpedicellate, the pedicels to 0.5 mm long; calyx cup-shaped, the tube 0.3 mm long, the lobes 5, triangular, 0.3 × 0.7 mm, puberulent; corolla green-white, the tube cylindrical, 1.5 × 1 mm, white pubescent in throat, the lobes 5, lanceolate, 0.8 × 0.7 mm; stamens 5, the filaments 1.3–1.5 mm long in pins, not seen in thrums, the anthers 0.5 mm long; style 2.2 mm long in pins, not seen in thrums, the branches lanceolate. *Fruit* spherical when dry, (4–)5 mm long, (4–)5 mm diam., maturing red, drying black; persistent calyx inconspicuous; seed dorsal surface with 5–6 longitudinal furrows, the ventral surface with 2 longitudinal furrows.

Distribution (Fig. 22). Known only from the type region, Cerro Jefe, Cerro Azul, and Goofy Lake (Lago Cerro Azul), eastern Panamá province, Panama, at 600–700 m elevation in premontane wet forest with equatorial-mountainous to tropical-equatorial climate. It has been collected in bud in November, in flower in February, with immature fruit in September, and in fruit in November–December.

Additional specimens examined. PANAMA. PANAMÁ: Cerro Jefe, nr. Río Indio, 630–660 m, 17 Feb. 1968 (fl), *Duke 15237* (MO—2 sheets); 8 mi. S of Goofy Lake toward Cerro Jefe, 26 Nov. 1966 (bud), *Dwyer 7083* (GH, MO); 26 Nov. 1966 (fr), *Dwyer 7098* (GH, MO, US); Cerro Jefe, ca. 1 mi. upstream from Frizzel's Finca Indio, 9 Sep. 1970 (early fr), *Foster & Kennedy 1851* (DUKE, F, MO, PMA); Cerro Azul, Feb. 1968 (fl), *Gómez-Pompa et al. 3436* (MEXU).

Psychotria liesneri may be recognized by its small elliptic (usually 4.5–6 × 1.5–2.2 cm) often subcoriaceous leaves with inrolled margins, brochidodromous secondary venation, and small (1.5–3 cm long) inflorescences with secondary veins usually in 2 ranks.

In both flowering collections, the negligible separation between style and stamens suggests that the species is long-homostylous instead of distylous.

22. Psychotria marginata Swartz, Prodr., 43. 1788. *Uragoga marginata* (Sw.) Kuntze, Revis. Gen. Pl. 2: 961. 1891. *Myrstiphyllum marginatum* (Sw.) Hitchc., Annual Rep. Missouri Bot. Gard. 4: 95. 1893. TYPE: Jamaicae australis: (fl), *Swartz s.n.* (holotype, S, n.v., photo, A; isotype, B–Willdenow 4068). Cf. also Swartz, Fl. Ind. Occid. 400. 1797. Figures 4b, 7h, 8, 20.

Psychotria nicaraguensis Bentham in Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 34. 1853. *Uragoga nicaraguensis* (Benth.) Kuntze, Revis. Gen. Pl. 2: 957. 1891. TYPE: Nicaragua. San Juan, (fr), *Oersted 11634* (holotype, C, n.v., photos, GH, NY, US; isotype, K).

Shrub 1–3(–4) m tall; young stems glabrous, the bark smooth; stipules sheathing, lanceolate, 9–13 × 2.5–4 mm, glabrous, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 0.5–2(–2.5) cm long, glabrous, flat or grooved above; blades membranous, oblanceolate, the apex long-acuminate, the base attenuate, (8–)12–18(–20) × (3–)4–6.5(–7.5) cm, glabrous

above and below, the margin often ciliate, drying red-gray to sometimes dull red-brown; secondary veins (9–)12–14(–16) pairs, diverging (55°–)65°–75°, eucamptodromous, constantly arcuate, elevated below, glabrous, the axils usually with domatia along midvein below (Fig. 4b); tertiary veins evident to inconspicuous, orthogonal reticulate to percurrent. *Inflorescences* terminal or pseudoaxillary, diffuse panicles of cymes (Fig. 7h); panicle branched to 5 degrees; main axis (7–)10–15 cm long, the peduncle 4–7 cm long; secondary axes in (4–)5–6 ranks, the first-rank axes 2(4), the longer pair 2–8 cm long, the shorter pair when present 0.5 cm long, the second-rank axes 2, (0.5–)1.5–5.5 cm long, the third-rank axes 2, (0.4–)0.7–2.5 cm long, the fourth-rank axes 2, (0.2–)0.4–1 cm long, the fifth-rank axes 2, 0.2–0.7 cm long, the sixth-rank axes 2, 0.3 cm long; cymes branched to 1–2 degrees; bracts triangular, 1.5 mm long, glabrous; bracteoles lanceolate, 0.3 mm long, glabrous. *Flowers* pedicellate, the pedicels 1–2.5 mm long; calyx cup-shaped, the tube 0.3–0.5 mm long, the lobes 5, not evident to triangular, to 0.2 mm long, often puberulent without; corolla pale yellow, the tube cylindrical, 2–2.5 × 1–1.2 mm, short white pubescent in throat, the lobes 5, lanceolate, 1–1.5 × 0.7 mm, stamens 5, the filaments 1.5–1.8 mm long in pins, 3 mm long in thrums, the anthers 0.8–1 mm long; style 4–4.5 mm long in pins, 2–2.5 mm long in thrums, the branches linear, recurved (Fig. 8). *Fruit* when dry spherical to slightly ellipsoid, 3.5–4 mm long, 3.5–4 mm diam., maturing red, drying black; persistent calyx inconspicuous or sometimes a beak to 0.7 mm long; seed dorsal surface with 4–5 deep longitudinal furrows, the ventral surface with 2 deep longitudinal furrows.

Distribution (Fig. 20). Widespread from Mexico through Panama, at elevations of 0–1,000 m, usually below 500 m, in tropical moist to premontane rainforest with equatorial to tropical climate. *Psychotria marginata* occurs also in Cuba, Jamaica, Colombia, Venezuela, Ecuador, and Peru. It has been collected in flower throughout the year, primarily September–April, and in fruit throughout the year.

Selected specimens examined. MEXICO. CHIAPAS: Mpio. Las Margaritas, low ridges at confluence of Río Ixcán with Río Lacantum (Río Jataté), 300 m, 14 Mar. 1973 (fr), *Breedlove & McClintock 34065* (ENCB); Centro Arqueológico Bonampak, Mpio. Ocosingo, 350 m, 23 Nov. 1981 (fr), *Meave et al. B-8* (MO). OAXACA: km 5 carret. Tuxtepec–Pueblo Viejo a 500 m a la derecha, 15 June 1964 (fl), *Chavelas & Pérez 4* (MEXU, SLPM). TABASCO: Teapa, (fl), *Linden s.n.* (F ex P). VERACRUZ: Mpio. Hidalgotitlán, 6 km E del campamento Hermanos Cedillo, 17°00′N, 94°35′W, 110 m, 13 Mar. 1974 (fl), *B. Dorantes 2537* (MEXU—2 sheets); 4 mi. S of Tampico Alto, MEX 180, 18 July 1971 (early fr), *Dwyer et al. 97* (MO). GUATEMALA. ALTA VERAPAZ: Chahal, 200 m from airfield on village rd., in corozal, 2 Oct. 1968 (fl), *Contreras 7793* (F); vic. Laguna Sapalá (Chajvovuch), 2 km SW of Sibicté, 280 m, 11 Mar. 1942 (fl, fr), *Steyermark 44914* (A, F); Cubilgüitz, 350 m, Mar. 1904 (fl), *Tuerckheim 8533* (F, GH, K, US—2 sheets). BAJA VERAPAZ: Unión Barrios, E of km 154, 7 June 1975 (fr), *Lundell & Contreras 19383* (LL). HUEHUETENANGO: between Ixcan and Río Ixcan, Sierra de los Cuchumatanes, 150–200 m, 23 July 1942 (fr), *Steyermark 49228* (F, GH). IZABAL: Puerto Méndez, on Toquela Rd., 8 Sep. 1980 (fr), *Contreras 10227* (MO); vic. Quirguá, 75–225 m, 15–31 May 1922 (fl, fr), *Standley 24534* (F, GH, MO, NY, US); nr. Puerto Barrios, 0 m, 25 Apr.–6 May 1939 (fl), *Standley 72549* (F, NY). PETÉN: San Diego, Río de la Pasión, 11 Apr. 1935 (fl), *M. Aguilar H. 509* (F, GH, K, MO, NY—2 sheets); La Cumbre, km 135 of Cadenas Road, bordering Chacte River, 2 Oct. 1966 (fr), *Contreras 6312* (DUKE, F); San Luis, km 51–52 of rd., 10 July 1959 (fr), *Lundell 16270* (DUKE); forest between Finca Yalpemech along Río San Diego and San Diego on Río Cancuen, 50–150 m, 25 Mar. 1942 (fr), *Steyermark 45376* (F, NY). BELIZE. BELIZE: Burrel Boom, vic. 2nd Ferry, 2 Aug. 1979 (fr), *Dwyer 14943* (MO). CAYO: Cocquericot, 16 Mar. 1931 (fl), *Bartlett 12043* (F, K, NY), Humming Bird Hwy., 35 mi. section, high ridge, 18 Oct. 1955 (fr), *Gentle 8908* (F, GH, US). STANN CREEK: S of Lynam Agricultural College, nr. Stann Creek, 23 Mar. 1967 (fl), *Dwyer et al. 558* (MO—2 sheets); Stann Creek Railway, back of quarry, 1 Feb. 1939 (fl), *Gentle 2685* (A, F, K—2 sheets, NY, US); Middlesex, 60 m, 15 July 1929 (early fr), *Schipp 245* (A, F, K, MO, NY, US); 2 June 1939 (fr), *Gentle 2818* (A, F, K, NY, US); along North Branch SE of Humming Bird Gap, 75 m, 18 Nov. 1976 (fl), *Proctor 36591* (MO). TOLEDO: vic. San José Mayan Indian village, 10 km N of Columbia Forest Station, 13 June 1973 (fr), *Croat 24386* (DUKE, F, MO—2 sheets); Columbia Forest Station entrance, 11 June 1973 (fr), *Dwyer 11095* (MO—4 sheets); Temash River, high ridge, 28 Feb. 1945 (fl), *Gentle 5241* (DUKE, F, NY). HONDURAS. ATLANTIDA: Lancetilla Valley, 16 km SE of Tela, forest preserve, 10–150 m, 3 Aug. 1977 (fr), *Croat 42608* (MO, US); Montaña Lancetilla, 100 m, 17 Mar. 1962 (fl), *A. Molina R. 10309* (F); mountain Nombre de Dios between Saladito and San Francisco, 200 m, 26 Apr. 1967 (early fr), *A. Molina R. 20864* (F); vic. La Ceiba, slopes of Mt. Cangrejal, 16 July 1938 (fr), *Yuncker et al. 8457* (F, GH, K, MO, NY, US). CORTÉS: nr. Agua Azul, Lake Yojoa, 650 m, 14 Apr. 1951 (fl, fr), *L. O. Williams & Molina 17929* (F, GH, US). GRACIAS A DIOS: Qda. Tiro, Río Platano, 15°43′N, 84°50′W, 4 Apr. 1981 (fr), *Saunders 1215* (F, MO). OLANCHO: 30 km NE Culmí, Mata de Maíz, O de Montaña Punta de Piedra, 700 m, 1–4 May 1975 (fr), *C. Nelson & Vargas 2738* (MO). NICARAGUA. CHONTALES: nr. Sto. Domingo, 9 Apr. 1961 (fl, fr), *Bunting & Licht 1145* (DUKE, F, NY, US). JINOTEGA: Comarca Sta. Cruz, el Calvario, al SW del Cerro Kilambe, 13°34′N, 85°40′W, 900–1,000 m, 27 Mar. 1981 (fr), *P. P. Moreno 7713* (MO); Salto Kayaska, Río Bocay, 13°51′N, 85°22′W, 190–340 m, 7 Mar. 1980 (fr), *W. D. Stevens et al. 16530* (MO). MATAGALPA: 4 km al E de Río Blanco, "Wana Wana," carret. Tuma, 12°55′N, 85°11′W, 280–300 m, 5 May

1984 (fr), *P. P. Moreno 24101* (MO). RÍO SAN JUAN: Río Sabalos, 11°02′N, 84°28′W, 50 m, 19 Feb. 1984 (early fr), *P. P. Moreno 23117* (MO). RIVAS: Isla Ometepe, faldas del lado N del Volcán Maderas, 11°27′N, 85°30′W, 900–1,200 m, 19 Jan. 1983 (early fr), *P. P. Moreno 19687* (MO); Isla Ometepe, Volcán Concepción, 11°33′N, 85°38′W, 600–900 m, 13 Feb. 1984 (fr), *Robleto 218* (MO). ZELAYA: region of Braggman's Bluff (Puerto Cabezas), 1928 (fl), *Englesing 185* (F, K, US); Cerro Waylawás (Peñas Blancas), ca. 5 km al S de Wany, 13°30′N, 84°45′W, 28 Oct. 1982 (fl), *Grijalva & Burgos 1651* (MO); area de la Bahía de Bluefields, Río Escondido, entre Sta. Martha y La Finca, Ginney Point, 0–30 m, 19 Mar. 1949 (fr), *A. Molina R. 1885* (F, GH); Caño Montecristo, desembocadura del Caño El Consuelo, 11°35′N, 83°51′W, 10 m, 7 Feb. 1982 (fr), *P. P. Moreno 15072* (MO); El Guásimo, camino a El Dos, NE de Siuna, 13°48′N, 84°39′W, 360–380 m, 25 Feb. 1983 (early fr), *P. P. Moreno & Robleto 20743* (MO); Monkey Point, 1 km al S sobre la playa, 11°35′N, 83°39′W, 0–5 m, 22 Oct. 1981 (fl), *P. P. Moreno & Sandino 12195* (MO); Colonia Kururia, 14°41′N, 84°04′W, 0–50 m, 3 Mar. 1979 (fr); *Pipoly 4000* (MO); Río Prínzapolka, 2 km S of Waní, 13°42′N, 84°50′W, 0–100 m, 16 Mar. 1979 (fr), *Pipoly 4749* (MO); carret. Matagalpa–Waslala, Río Las Carpas y Río Babasca, 13°15′N, 85°32′W, 540–580 m, 4 Mar. 1982 (fl), *Sandino 2427* (MO); 5 km N de colonia Jacinto Baca Jérez, 11°54′N, 84°24′W, 160 m, 20 Oct. 1984 (fr), *Sandino 4667* (MO); ca. 14.5 km W of Río Wawa ferry on rd. from Puerto Cabezas to Rosita, at Caño Kauhru Tingni, 14°06′N, 83°40′W, 10 m, 2 May 1978 (early fr), *W. D. Stevens 8638* (MO); rd. from Constancia to Laguna Siempreviva, 13°58′N, 84°40′W, 290–360 m, 21 Feb. 1979 (fr), *W. D. Stevens 12409* (MO); vic. Neptune Mining Company, NE Bonanza, 14°01′N, 84°35′W, 200–350 m, 25 Feb. 1979 (fr), *W. D. Stevens 12985* (MO); ca. 6 km upriver from Barra de Punta Gorda, S side, 11°30′N, 83°49′W, 8–10 m, 30 Sep. 1981 (fl), *W. D. Stevens 20736* (MO). COSTA RICA. CARTAGO: Río Turrialba, 500 m, Mar. 1894 (fl, early fr), *Donnell-Smith 4832* (GH, K, US—2 sheets); Atirro, 600 m, Apr. 1896 (fl, fr), *Donnell-Smith 6598* (GH, K, US). HEREDIA: Finca La Selva, OTS field station, Río Puerto Viejo, 100 m, 17 May 1982 (fr), *Hammel 12295* (DUKE); 17 Nov. 1982 (fl), *McDowell 779* (CR, DUKE). LIMÓN: vic. Limón, 0–100 m, 3–7 Sep. 1971 (fr), *Burger & Burger 8488* (CR, F, MO, NY); La Palma, Sixaola, 1 Mar. 1924 (fl, fr), *Dunlap 473* (F, NY); Río Santa Clara, Guapiles, 400 m, 18 Sep. 1964 (fl, fr), *A. Jiménez M. 2366* (CR, F, GH, NY); 4 km NW of El Carmen, 10°13′N, 83°28′W, 10 m, 17 Mar. 1973 (fl, fr), *Lent 3282* (CR, F, NY); Río Reventazón below Cairo, Finca Montecristo, 25 m, 18–19 Feb. 1926 (fr), *Standley & Valerio 48555* (US); Sipurio, Mar. 1894 (fl), *Tonduz 8667* (US). PUNTARENAS: 4 mi. W of Rincón de Osa, 8°42′N, 83°31′W, 30 m, 4–7 June 1968 (fr), *Burger & Stolze 5441* (CR, F, MO, NY); Río Barú, nr. Dominical, 9°17′N, 83°52′W, 0–20 m, 20 Feb. 1977 (fr), *Burger et al. 10654* (CR, F, MO); Corcovado National Park, 28 Nov. 1978 (fr), *Janzen 11545* (MO); Río Volcán, 48 km SE of San Isidro El General, 300 m, 1 Mar. 1966 (fr), *A. Molina R. et al. 18192* (CR, F). SAN JOSÉ: Lado de Vargas, Tabarcia, Mora, 920 m, 22 Apr. 1963 (fr), *A. Jiménez M. 661* (CR, F, NY); entre Pedernal y Candelarita, 900 m, 29 May 1966 (fr), *A. Jiménez M. 3965* (F, GH, NY); vic. El General, 850 m, Aug. 1936 (fl), *Skutch 2873* (GH, K, MO, NY, US). PANAMA. BOCAS DEL TORO: above Qda. Huron on Cerro Bonyik, 150–360 m, 13 Apr. 1968 (fl), *Kirkbride & Duke 591* (F, MO, NY); Almirante, just N of Dos Milla, 20 Aug. 1964 (fl), *McDaniel 5129* (MO); vic. Chiriquí Lagoon, Old Bank Island, 6 Feb. 1941 (fr), *Wedel 2011* (GH, MO, NY, US). CANAL AREA: Barro Colorado Island, 3 May 1969 (fl, fr), *Foster 791* (DUKE, F); 20 Dec. 1931 (fl), *Wetmore & Abbe 3* (A, F, GH, MO); Cerro Galera, just W of Thatcher Bridge, 8°55′N, 79°35′W, 100 m, 15 Feb. 1983 (early fr), *Hamilton & Palmer 2963* (CR, MO); Fort Sherman and nearby, 9°20′N, 80°00′W, 0–100 m, 16 June 1983 (fr), *Hamilton & Stockwell 3695* (MO): Pipeline Rd., 9 km NW of Gamboa, 150 m, 11 Feb. 1974 (early fr), *Nee 9598* (F, GH, MO); hills N of Frijoles, 19 Dec. 1923 (fl), *Standley 27444* (GH, US). CHIRIQUÍ: vic. San Felix, 0–120 m, Sep. 1911 (fl), *Pittier 5742* (NY, US). COCLÉ: vic. El Valle, 600–1,000 m, 8 Dec. 1938 (fl, fr), *Allen 1187* (F, GH, MO); 5 hours walk N of Alto Calvario, between La Junta and Limón, 800–1,000 m, 11 Oct. 1977 (fr), *Folsom 5859* (MO). COLÓN: N of Río Guanche, 100–200 m, 16 Nov. 1975 (fl), *Davidse & D'Arcy 10062* (MO, US); 6 mi. SW of Portobelo, 19 July 1970 (fr), *Luteyn 1416* (DUKE, F, MO); 4 km NW of Salamanca, 13 km NE of Buenos Aires, 340–410 m, 30 Dec. 1973 (fl), *Nee 9091* (F, MO); between France Field and Cativa1, 9 Jan. 1924 (fl), *Standley 30189* (US). DARIÉN: Río Chico across from Boca de Tesca, 18 July 1962 (early fr), *Duke 5223* (GH, MO); Santa Fe, ca. 15 m, 18–20 Sep. 1967 (fr), *Duke 14271* (MO, NY); E slope of Cerro Pirre, climbing up from Cana, 7°55′N, 77°40′W, 500–1,000 m, 23 Sep. 1982 (fl, fr), *Hamilton & Stockwell 1504* (MO); Cerro Sapo, 750 m, 1 Feb. 1978 (fl, early fr), *Hammel 1195* (MO); 0.5–1.5 mi. E of Manené, 21 Dec. 1980 (fl), *Hartman 12088* (ENCB); ridges on Punta Guayabo Grande, NW of Enseñada El Guayabo, 7°24′N, 78°07′W, 0–100 m, 22 Jan. 1982 (fl), *Knapp & Mallet 2995* (DUKE, MO); Río Tuquesa, 250 m, 8 July 1975 (early fr), *Mori 7032* (US); trail from Paya to Pucro, 12 June 1959 (early fr), *Stern et al. 416* (GH, MO, US). LOS SANTOS: ca. 10 km SW of El Cortezo, "El Pavo" bridge over Río Los Changuales, 450–600 m, 28 Oct. 1978 (early fr), *Hammel 5413* (MO); Loma Prieta, Cerro Grande, 720–840 m, 8 June 1967 (fr), *Lewis et al. 2201* (MO). PANAMÁ: Río La Maestra, 0–25 m, 4 Dec. 1936 (fl), *Allen 11* (MO); Cerro Campana, 750 m, 17 Aug. 1982 (fr), *D'Arcy & Hamilton 14977* (MO); nr. Jeniné, Río Cañita, 24 Sep. 1961 (fr), *Duke 3886* (GH, MO, US): Piriatí, S of Pan-Am. Hwy., 9°00′N, 78°30′W, 200–400 m, 8 Aug. 1982 (st), *Hamilton 524* (MO); nr. Lago Cerro Azul, 9°10′N, 79°25′W, 500–600 m, 3 Mar. 1983 (early fr), *Hamilton & Krager 3194* (MO); nr. Arenosa, S shore of Gatun Lake N of Chorrera, 9°05′N, 79°55′W, 0–50 m, 27 Feb. 1983 (fl), *Hamilton & Stockwell 3121* (CR, MO); San José Island, 22 Jan. 1946 (fl), *Johnston 1218* (GH, US); 8 km N on El Llano–Cartí Rd., E of Río Terable, 9°15′N, 78°00′W, 450 m, 19 Aug. 1981 (fr), *Knapp 955* (ENCB, MO); 3.0 mi. E of Cañazas checkpoint, 1–2 mi. S of Pan-Am. Hwy., 8°52′N, 78°15′W, 0–50 m, 27 Feb. 1982 (fl, early fr), *Knapp 3877* (MO); Chimán, 12 Dec. 1967 (fl), *Lewis et al. 3248* (MO); nr. Tapia River, Juan Díaz region, 1–3 June 1923 (early fr), *Maxon & Harvey 6694* (GH, US); nr. Arraiján, 15 m, 22 June 1938 (fl), *Woodson et al. 772* (A, F, MO). SAN BLAS: between Río Diablo and Río Acuati, nr. Nargana, 3 Nov. 1967 (fl), *Duke 14869* (MO, US); headwaters of Río Cuadí, Camp Diablo, 18 Dec. 1967 (fl), *Duke et al. 3644* (MO). VERAGUAS: Coiba

Island, Playa Rosario, 26 Aug. 1970 (fl), *Foster 1614* (DUKE).

Psychotria marginata may be recognized by its oblanceolate long-acuminate leaves drying usually red-gray, eucamptodromous secondary venation with axillary domatia, large (usually 10–15 cm long) diffuse panicles of cymes with delicate axes diverging at right angles, and small (3.5–4 mm) spherical fruit drying black. *Psychotria marginata* is remarkably uniform in qualitative and quantitative aspects throughout its broad range.

The exserted pistils in the pin morph are longer than the exserted stamens in the thrum (4–4.5 vs. 3.5 mm).

23. Psychotria orosiana Standley, J. Wash Acad. Sci. 15: 288. 1925. TYPE: Costa Rica. Cartago: vic. Orosí, 30 Mar. 1924 (fl), *Standley 39803* (holotype, US). Figures 2f, 10d, 23.

Shrub or small tree 1.5–4(–5) m tall; young stems glabrous, the bark smooth; stipules lanceolate, 3–5 × 1–2 mm, biaristate, with fringed extensions, caducous, leaving a pale ridge with red-brown fringe (Fig. 2f). *Leaves* sessile to subsessile; petioles to 3 mm long, glabrous; blades membranous, elliptic to oblanceolate, the apex acuminate, the base attenuate to subcordate, (4.5–)5.5–10.5 × 1.7–3.8 cm, glabrous above and below, drying green-black; secondary veins 7–9 pairs, diverging 80°–90°, brochidodromous, constantly arcuate, barely elevated below, glabrous, the axils with domatia below; tertiary veins evident to inconspicuous, orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of cymes; panicle branched to 3–4 degrees; main axis 3.5–10 cm long, the peduncle 2.5–7.5 cm long; secondary axes in (2–)3–4(–5) ranks, the first-rank axes 2(4), 1–2.5 cm long, the shorter pair when present 0.7 cm long, the second-rank axes 2, 0.3–1.5 cm long, the third-rank axes 2, 0.2–1 cm long, the fourth-rank axes 2, 0.2–0.4 cm long, the fifth-rank axes 2, 0.2 cm long; cymes branched to 1 degree; bracts triangular, to 1.5 mm long, fringed; bracteoles lanceolate, 0.5 mm long, glabrous. *Flowers* sessile to pedicellate, the pedicels 0.5–2.5 mm long; calyx cylindrical, the tube 0.5 mm long, the lobes 5, triangular to barely evident, to 0.3 mm long, the lobes puberulent outside; corolla yellow-white, the tube cylindrical, 2.5–5 × 1–1.5 mm, white pubescent in throat, the lobes 5, lanceolate, 1.5 × 1 mm; stamens 5, the filaments 2.5–3.5 mm long in pins, 3.5 mm long in thrums, the anthers 0.7–1 mm long; style (4–)5.5–6.5 mm long in pins, 2 mm long in thrums, the branches short, linear. *Fruit* when dry ellipsoid, 4.5–5(–6) mm long, 3.5–4(–5) mm diam., maturing red, drying black; persistent calyx a minute beak; seed dorsal surface with 4–5 deep longitudinal furrows, the ventral surface with 2 shallow longitudinal furrows (Fig. 10d).

Distribution (Fig. 23). Known from the central cordillera in Costa Rica and western Panama, at 400–1,400 m elevation, usually above 1,000 m, in premontane to low montane wet to rainforest with equatorial-mountainous climate. It has been collected in flower January–June and September and in fruit in March, June, September, and October.

Selected specimens examined. COSTA RICA. ALAJUELA: La Palma de San Ramón, 1,275 m, 30 May 1927 (fl), *Brenes 5534* (CR, F, NY). CARTAGO: Qda. Rojas, 1 km W of Muñeco, 1,240 m, 15 Sep. 1969 (fl), *Lent 1785* (CR, MO, NY); 24 km NE of Turrialba on hwy. to Limón, 9°58′N, 83°34′W, 450–525 m, 10 May 1983 (fl), *Liesner et al. 15377* (CR, MO); vic. Orosí, 30 Mar. 1924 (fl), *Standley 39768* (US). PUNTARENAS: hills NE of Quaker settlement of Monte Verde, 8 May 1971 (fl), *J. Utley 148* (DUKE). PANAMA. CHIRIQUÍ: Proyecto Fortuna, propriedad del IRHE, desde la finca Pittí hasta el filo del Cerro Fortuna, 8°45′N, 82°15′W, 1,000–1,200 m, 25 Sep. 1976 (fl, fr), *M. Correa A. et al. 2726* (MO); Fortuna dam site, 1,400–1,500 m, 14 Sep. 1977 (fl), *Folsom et al. 5454* (MO); La Fortuna project, 1,300–1,400 m, 23 Mar. 1978 (fr), *Hammel 2221* (MO); behind Vivero Forestal de Boquete, 12 km N of Los Planes del Hornito, IRHE Fortuna Hydroelectric Project, 8°43′N, 82°14′W, 17 June 1982 (fl, fr), *Knapp & Vodicka 5522* (MO); lower slopes of Cerro Fortuna, IRHE Fortuna Project, 1,150 m, 18 June 1982 (fl), *Knapp & Vodicka 5595* (MO). VERAGUAS: valley of Río Dos Bocas, 11–13 km beyond Agriculture School at Santa Fe, 350–500 m, 25 July 1974 (early fr), *Croat 25731* (GH, MO).

Psychotria orosiana may be recognized by its resemblance to *P. graciliflora*—leaves drying blackish, secondary veins diverging ca. 80°, inflorescence axes delicate—and by its larger (3.5–10 vs. 3–5 cm long) inflorescences, longer corolla tube (2.5–5 vs. 2–2.5 mm), and seed dorsal surfaces with deeper longitudinal furrows having acute longitudinal ridges between.

The reproductive parts at both levels are longer in pin morphs than in thrums.

24. Psychotria parvifolia Bentham in Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 35. 1853. *Mapouria parvifolia* (Benth.) Oerst., Amér. Centr. p. 17, t. 14, fig. 1. 1863. *Uragoga levyi* Kuntze, Revis. Gen. Pl. 2: 956. 1891. Not *U. parvifolia* (Muell. Arg.) Kuntze (based on *Rud-*

gea parvifolia Muell. Arg.). TYPE of *P. parvifolia* Benth.: Costa Rica. Alajuela: nr. Naranjo, ca. 1,350 m, Apr. 1847 (fl), *Oersted 11637* (holotype, C, n.v., photo, F neg. 22842; isotype, K). Figure 22.

Shrub 1.5–3 m tall; young stems ferrugineous-pubescent, the bark irregularly furrowed; stipules sheathing, lanceolate, (2.5–)4–6 × (1–)1.2–1.7 mm, ferrugineous-pubescent, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 2–10 mm long, ferrugineous-pubescent, flat above; blades membranous, elliptic to slightly obovate, the apex acute, the base cuneate, (1–)1.5–5.2 × (0.6–)0.8–2 cm, glabrous above and below, the midvein often ferrugineous-puberulent, drying dark green-brown to red-brown, paler below; secondary veins 3–5 pairs, diverging 45°–50°, brochidodromous, constantly arcuate, inconspicuous to not evident below, glabrous, the axils lacking domatia or hairs; tertiary veins not evident. *Inflorescences* terminal or pseudoaxillary, panicles of cymes or glomerules; panicle branched to 2–3 degrees; main axis (2–)4–12 mm long, the peduncle lacking; secondary axes in 1–2 ranks, the first-rank axes (1)2, 1–4 mm long, the second-rank axes 2, 1–3 mm long; cymes branched to 1 degree; bracts lanceolate, ca. 2 mm long, glabrous; bracteoles lanceolate, 1 mm long, glabrous. *Flowers* pedicellate, the pedicels 0.5–3 mm long; calyx cup-shaped, the tube 0.3–0.5 mm long, the lobes 4, triangular, to 0.3 mm long, puberulent; corolla white, the tube cylindrical, 2.5–4 × 1–1.5 mm, white pubescent in throat, the lobes 4, lanceolate, 1.5–2 × 0.8 mm; stamens 4, the filaments 2 mm long in pins, 3.5–5 mm long in thrums, the anthers 0.6–0.7 mm long; style 5 mm long in pins, 2–3.5 mm long in thrums, the branches linear. *Fruit* when dry spherical, 4–5 mm long, 4–5 mm diam., maturing red, drying dark red-brown; persistent calyx not evident or a minute beak; seed dorsal surface with 6–8 shallow longitudinal furrows, the ventral surface with 2 deep and sometimes 2–4 shallow longitudinal furrows.

Distribution (Fig. 22). Known from the central cordillera in Costa Rica and western Panama, at 1,300–2,000 m elevation in regions of low montane rainforest with equatorial-mountainous climate. *Psychotria parvifolia* has been collected in flower April–September and December and in fruit December–May.

Selected specimens examined. COSTA RICA. ALAJUELA: La Palma de San Ramón, Socorro, 22 Aug. 1927 (st), *Brenes 5681* (CR, F, NY); 15 km NW of San Ramón by air, Cerro Azahar, Río San Pedro, 10°09′N, 84°34′W, 1,400–1,500 m, 14 May 1983 (fl), *Liesner et al. 15585* (CR, MO); vic. Fraijanes, 1,500–1,700 m, 12–13 Feb. 1926 (fr), *Standley & Torres 47566* (US); *Standley & Torres 47571* (US). CARTAGO: 15 km S of Tapantí, above Río Grande de Orosí, 9°42′N, 83°47′W, 1,500 m, 12–17 Dec. 1969 (fl), *Burger & Liesner 6847* (CR, F, MO, NY); La Congreja, carret. Panamericana al S de Cartago, km 47, 1,950 m, 28 July 1965 (fl), *A. Jiménez M. 3365* (CR, F). HEREDIA: above San José de la Montaña, on W slope of Volcán Barba, 1,950 m, 15 May 1966 (fr), *Fosberg & Hatheway 47806* (K, MO, NY); Río San Rafael, NW slopes of Barba Volcano, 1,780 m, 17 Sep. 1967 (fl), *Lent 1307* (F); Yerba Buena, NE of San Isidro, 2,000 m, 22–28 Feb. 1926 (early fr), *Standley & Valerio 49194* (US); Cerro de Zurquí, NE of San Isidro, 2,000–2,400 m, 3 Mar. 1926 (early fr), *Standley & Valerio 50271* (US); *Standley & Valerio 50396* (US); Cerro de las Caricias, N of San Isidro, 2,000–2,400 m, 11 Mar. 1926 (fr), *Standley & Valerio 51953* (US); *Standley & Valerio 52044* (US); *Standley & Valerio 52223* (A, US). PUNTARENAS: Monteverde, 1,550 m, 1 Aug. 1979 (fl), *Koptur 171* (MO); Monteverde, 10°20′N, 84°48′W, 1,300 m, 18 Aug. 1976 (fl), *Solomon 5375* (CR, MO). SAN JOSÉ: vic. Sta. María de Dota, 1,500—1,800 m, 14–26 Dec. 1925 (fl, fr), *Standley 42857* (A, US); 26 Dec. 1925–8 Jan. 1926 (fl, fr), *Standley & Valerio 44076* (US); La Hondura de San José, 1,300 m, 15 Aug. 1933 (fl), *M. Valerio 708* (F). PANAMA. CHIRIQUÍ: La Popa above Boquete, 1,550 m, 5 Aug. 1972 (fl), *D'Arcy & D'Arcy 6393* (GH, MO, NY); vic. El Boquete, 1,000–1,300 m, 2–8 Mar. 1911 (fr), *W. Maxon 4958* (F).

Psychotria parvifolia may be recognized by its small (usually 1.5–5.2 × 0.8–2 cm) membranous leaves with 3–5 inconspicuous secondary veins, minute (usually 0.4–1.2 cm long) inflorescences, and spherical fruits 4–5 mm in diameter. Collections from Chiriquí, Panama, show more slender inflorescence axes, longer (3 mm) pedicels plus longer corolla tubes and filaments and styles than from Costa Rica.

The exserted pistil in the pin morph is usually longer than the exserted stamens in the thrum (5 vs. 3.8–5.3 mm).

25. Psychotria philacra Dwyer, Ann. Missouri Bot. Gard. 67: 412. 1980. TYPE: Panama. Darién: Cerro Tacarcuna S slope, ridgetop well below summit, 1,250–1,450 m, 26 Jan. 1975 (fr), *Gentry & Mori 13916* (holotype, MO). Figure 22.

Shrub 3 m tall; young stems glabrous or red-brown puberulent, the bark mottled; stipules lanceolate, 4 × 1.2 mm, ferrugineous-pubescent, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 4–10 mm long, glabrous to sparsely puberulent, flat above; blades membranous, elliptic, the apex acuminate, the base attenuate, 5–7 × 1.7–2.7 cm, glabrous above and

below, drying dull red-brown; secondary veins 6–7 pairs, diverging 60°–70°, eucamptodromous, constantly arcuate, prominulous below, glabrous, the axils lacking domatia or hairs; tertiary veins not evident. *Inflorescences* terminal, seen only with few fruits. *Flowers* not seen. *Fruit* when dry obloid, 4.5–5.5 mm long, 5–6 mm diam., maturing red, drying dark red-brown; persistent calyx inconspicuous or a minute beak; seed dorsal surface with 4 deep irregular and several shallow irregular longitudinal furrows, the ventral surface with 2 deep and several irregular longitudinal furrows.

Distribution (Fig. 22). Known only from the type collection from Cerro Tacarcuna, eastern Darién, Panama, at 1,250–1,450 m elevation in low montane rainforest with equatorial-mountainous climate. It was collected in fruit on January 26.

Psychotria philacra may be recognized by its small elliptic (5–7 × 1.7–2.7 cm) leaves drying dull red-brown and with 6–7 secondary veins, obloid fruits, and seeds with shallow irregular furrows on both surfaces.

Group 4. The *remota* Group

The description for the group in Mesoamerica is that of the lone species, *Psychotria remota*. Key recognition characters include leaves drying glossy red-brown and relatively few secondary veins for the large size of the blade. This group is larger in South America, including also *P. anceps* Kunth and *P. cupularis* (Muell. Arg.) Standl.

Psychotria remota appears normally distylous, with no floral-part-length asymmetry between the morphs.

26. Psychotria remota Bentham, J. Bot. (Hooker) 3: 225. 1841. *Mapouria remota* (Benth.) Muell. Arg., Flora 59: 459. 1876. Cf. also Martius, Fl. Bras. 6(5): 407. 1881. *Uragoga remota* (Benth.) Kuntze, Revis. Gen. Pl. 2: 962. 1891. TYPE: Guiana: on the Río Negro, (fl), *Schomburgk 963* (holotype, K, n.v., photo, NY neg. no. 3421; isotypes, F, W, n.v.). Figures 4a, 7j, 10f, 24.

Psychotria alboviridula K. Krause, Notizbl. Koenigl. Bot. Gart. Berlin 6: 208. 1914. TYPE: Brazil: Im Gebiet des Alto Acre, Seringal, San Francisco, Sep. 1911 (fl), *Ule 9846* (holotype, B, destroyed, fragment, F, photo, F neg. no. 468; isotype, US).

Tree 1.5–6 m tall; young stems glabrous to sparsely minute-puberulent, the bark mottled, slightly ridged longitudinally; stipules sheathing, triangular, acuminate or biacuminate, 4–6 × 2.5–4 mm, glabrous, sometimes sparsely fringed, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 0.7–2.5 cm long, glabrous, flat or grooved above; blades membranous to subcoriaceous, elliptic, the apex long-acuminate, the base cuneate, (8–)11–24 × (3–)3.5–8(–9) cm, glabrous above and below, drying glossy red-brown; secondary veins (7–)8–12 pairs, diverging 60°–70°, eucamptodromous to brochidodromous, constantly arcuate, prominent below, glabrous, the axils usually with prominent domatia below (Fig. 4a); tertiary veins evident, orthogonal reticulate to percurrent, the intersecondaries often conspicuous. *Inflorescences* terminal, elongate panicles of cymes (Fig. 7j); panicle branched to 4 degrees, the axes winged; main axis 7–15 cm long, the peduncle 3–5 cm long; secondary axes in (4–)6–7 ranks, the first-rank axes 2(4), 1–5.5 cm long, the shorter pair when present 1.2 cm long, the second-rank axes 2, (0.3–)0.5–1 cm long, the third-rank axes 2, 0.3–0.9 cm long, the fourth-rank axes 2, 0.2–0.6 cm long, the fifth-rank axes 2, 0.1–0.4 cm long, the sixth-rank axes 2, 0.1–0.3 cm long, the seventh-rank axes 2, 0.1–0.3 cm long; cymes branched to 1(–2) degrees; bracts and bracteoles triangular, 0.5–1.5 mm long, ciliate. *Flowers* pedicellate, the pedicels 0.5–1 mm long; calyx cup-shaped, the tube 0.3–0.5 mm long, the lobes 0 or 5, not evident to triangular, to 0.3 mm long, minute puberulent; corolla yellow-green, the tube cylindrical, 1.5 × 1 mm, white pubescent in throat, the lobes 5, lanceolate, 1 × 0.6 mm; stamens 5, the filaments 1.5 mm long in pins, 2.5 mm long in thrums, the anthers 0.3–0.5 mm long; style 2.5 mm long in pins, 2 mm long in thrums, the branches club-shaped. *Fruit* ellipsoidal when dry, (6–)7–9 mm long, (4–)5–6 mm diam., maturing dark red, drying dark red-brown; persistent calyx not evident or rarely a minute beak; seed dorsal surface with 3 deep longitudinal furrows, the ventral surface with 2 longitudinal furrows (Fig. 10f).

Distribution (Fig. 24). Scattered distribution in Caribbean Costa Rica and Panama, at 20–1,000 m elevation in tropical moist to premontane wet forest with equatorial to tropical-equatorial climate. It is more abundant in Colombia, Venezuela, the Guianas, Ecuador, Peru, and Brazil. In Central America, it has been collected in flower in March, April, September, and October and in fruit in March–May and September.

Selected specimens examined. COSTA RICA. HEREDIA: Caño Negro, Río Sarapiquí, 23 km N of Puerto Viejo, 20 m, 19 Apr. 1974 (early fr), *Hartshorn 1444* (CR, MO). LIMÓN: 7 km SW of Bribrí, 100–250 m, 4 May

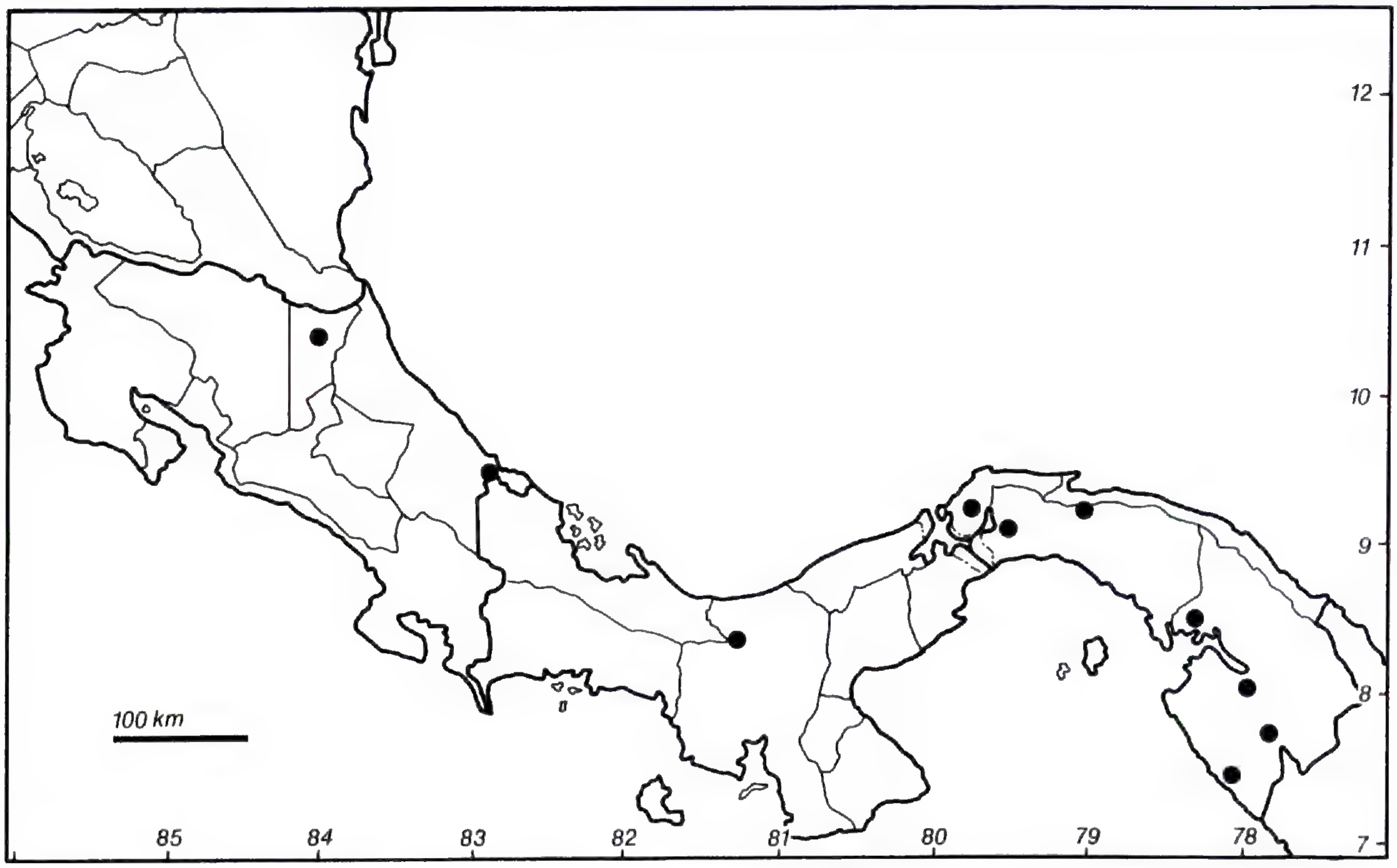

FIGURE 24. Distribution of *Psychotria remota* in Costa Rica and Panama.

1983 (fr), *L. D. Gómez et al. 20381* (MO). PANAMA. COLÓN: Santa Rita lumber rd., ca. 15 km E of Colón, 5 Oct. 1969 (fl), *Dressler & Lewis 3732* (MO, US). DARIÉN: trail from Punta Guayabo Grande to Río Jaqué, 50–200 m, 24 Apr. 1980 (fl), *Antonio & Hahn 4407* (MO); between Río Balsa and Río Aretí at their confluence, 100 m, 13 Sep. 1966 (fl), *Duke 8745* (MO); Puerta St. Dorotea, 21 July 1962 (bud), *Dwyer 2218* (MO—2 sheets); 10 km NE of Jaqué, ridge to headwaters of Río Pavarando, 360–500 m, 1 Feb. 1981 (early fr), *Sytsma & D'Arcy 3443* (MO); Cana-Cuasi Trail, Chipijana, 1,000 m, 9 Mar. 1940 (fr), *Terry & Terry 1436* (F, GH, MO). PANAMÁ: nr. Lago Cerro Azul (Goofy Lake), 9°10′N, 79°25′W, 500–600 m, 3 Mar. 1983 (fl), *Hamilton & Krager 3197* (CR, MO); rd. from El Llano to Cartí-Tupile, 300–500 m, 30 Mar. 1973 (fr), *Liesner 1280* (F, MO, NY); rd. past Cerro Azul, 28 Sep. 1974 (fr), *Mori & Kallunki 2188* (GH, MO): El Llano–Cartí rd., 16–18.5 km N of Pan-Am. Hwy. at El Llano, 400–450 m, 28 Mar. 1974 (fr), *Nee & Tyson 10937* (F, MO). VERAGUAS: 0.6 mi. beyond Escuela Agricola Alto Piedra nr. Santa Fe, 730 m, 4 Apr. 1976 (fr), *Croat & Folsom 34052* (MO, NY).

The inclusion of *P. alboviridula* within *P. remota* is discussed by Steyermark (1972; Mem. New York Bot. Gard. 23: 477).

Psychotria remota may be recognized by its moderately large (usually 11–24 cm long) elliptic leaves drying glossy red-brown, few (usually 8–12) secondary veins generally with prominent domatia in the axils, reduced (except for the first rank) and winged secondary inflorescence axes, and large (usually 7–9 mm long) ellipsoidal fruit.

GROUP 5. THE *NERVOSA* GROUP

Shrub; young stems glabrous or *red-brown to brown tomentose to puberulent*; stipules usually sheathing, linear (Fig. 2c) or ovate, the apex sometimes bilobed or biaristate, uniform in color (except *P. fosteri*, with a darker red-brown midrib), glabrous or fringed or red-brown pubescent, caducous. *Leaf* blades obovate or elliptic or oblanceolate, drying red-brown to green-brown (often chalky yellow-green in *P. fruticetorum*), sometimes pale below; secondary veins (4–)5–17 pairs, diverging 35°–65° (except 70°–80° in *P. fosteri*), eucamptodromous or brochidodromous (with collector vein in *P. chagrensis* and *P. fosteri*), the axils usually with tufts of hairs (lacking in *P. chagrensis*, *P. fosteri*, and usually *P. nervosa*); tertiary veins reticulate or percurrent. *Inflorescences* panicles of cymes (often contracted in *P. nervosa*) or fascicles of flowers (in *P. chagrensis* and *P. fosteri*), *not pedunculate* (except *P. erythrocarpa*, *P. fruticetorum*, and often *P. jinotegensis*); *secondary axes usually in 1 pair* or less commonly 2 size-differentiated pairs per rank (4 equal axes per rank rarely in *P. nervosa*); bracts conspicuously enlarged in *P. chagrensis*, *P. fosteri*, and *P. fruticetorum*. *Corolla* tubes 2–4 mm long (6–7 mm in *P. chagrensis*), the lobes without apical extensions. *Fruit ellipsoid when dry* (narrow in *P. nervosa*); *persistent calyx a tube to 5 mm long* (Fig. 9d)

or a beak or inconspicuous; *seed dorsal surface with 4–5 deep longitudinal furrows* (or 6–8–many irregular furrows in *P. aguilarii* and *P. jinotegensis*), the ventral surface with 2 deep or shallow longitudinal furrows, sometimes incompletely divided in *P. nervosa* or with additional irregular furrows in *P. jinotegensis*.

Of the nine species, three fairly widespread ones do not closely resemble any others: *Psychotria fruticetorum*, with its biaristate stipules, leaves drying chalky yellow-green, pedunculate inflorescences, and bracts as long as 8 mm; *P. erythrocarpa*, with its linear stipules and pedunculate inflorescences often of glomerules; and *P. jinotegensis*, with its often pedunculate inflorescences and many irregular furrows on both seed surfaces. The *P. chagrensis* complex shares a collector vein, an absence of tufts of hairs in the axils of the secondary veins, and inflorescences of fascicles of flowers and with bracts conspicuously enlarged; the complex comprises the widespread *P. chagrensis* and *P. fosteri*, endemic to Coiba Island, Panama (Fig. 26). The *P. nervosa* complex includes that widespread species plus *P. aguilarii* (southern Guatemala), *P. boquetensis* (western Panama), and *P. mirandae* (southern Mexico); none of them deviates morphologically from the predominant character states of the group.

Of the nine species in the group, seven appear distylous. Of those, *Psychotria fruticetorum* has longer exserted parts in the pins than in thrums, and *P. chagrensis* has longer inserted parts in the pins. One species, *P. mirandae*, appears to be thrum-monomorphic. Only *P. fosteri* may not be evaluated for this character due to lack of adequate flowering material.

27. Psychotria aguilarii Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 23. 1943. TYPE: Guatemala. Chimaltenango: rd. between Chimaltenango and San Martín Jilotepeque, 1,500–1,700 m, 22 Dec. 1940 (fr), *Standley 80900* (holotype, F). Figure 25.

Shrub 1–2(–6) m tall; young stems glabrous, the bark pale with shallow fissures; stipules sheathing, ovate, 7–10 × 2–4 mm, lacking fringe, glabrous, caducous, leaving a pale ridge with irregular fringe. *Leaves* petiolate; petioles 2–4(–7) mm long, glabrous, flat above; blades membranous, narrow elliptic to obovate, the apex acuminate, the base attenuate, the margins crenulate, (8–)11–13 × (2.5–)3–4 cm, glabrous above, sparsely puberulent along midvein below, drying red-brown or sometimes greenish; secondary veins 8–11 pairs, diverging (45°–)50°–60°, eucamptodromous, slightly arcuate, prominent below, glabrous, the axils with minute tufts of hair; tertiary veins evident, reticulate to slightly percurrent. *Inflorescences* terminal or pseudoaxillary, sparse panicles of cymes; panicle branched to 2–3 degrees; main axis 3–4 cm long, the peduncle lacking; secondary axes in 2 ranks, the first-rank axes 2, 2–2.2 cm long, the second-rank axes 2, 0.5–1.2 cm long; cymes branched to 1–2 degrees; bracts and bracteoles minute, linear, ca. 0.2 mm long, glabrous. *Flowers* sessile; calyx cup-shaped, the tube 0.5–1 mm long, the lobes 5, acute triangular, 0.2–0.5 × 0.3 mm, glabrous; corolla greenish white, the tube cylindrical, 3–3.5 × 1 mm, white pubescent in throat, the lobes 5, acute triangular, 1–1.5 × 0.7 mm; stamens 5, the filaments 2 mm long in pins, 3.5 mm long in thrums, the anthers 1 mm long; style 3.5 mm long in pins, 2 mm long in thrums, the branches spathulate. *Fruit* when dry ellipsoid, 5–6 mm long, 3–4 mm diam., maturing dark red, drying dark brown; persistent calyx not evident; seed dorsal surface with many irregular shallow longitudinal furrows, the ventral surface with 2 deep longitudinal furrows.

Distribution (Fig. 25). Known only from the Guatemalan states of Chimaltenango, Escuintla, Guatemala, Huehuetenango, and Sacatepéquez, at elevations of 1,000–1,500 m, in tropical-mountainous climate. *Psychotria aguilarii* has been collected in flower in February and May and in fruit in August and December.

Additional specimens examined. GUATEMALA. ESCUINTLA: 6 km W of San Vicente Pacaya, 1,250 m, 31 May 1970 (fl), *Harmon 2431* (MO). GUATEMALA: nr. Finca La Aurora, 1,500 m, 1938–1939 (fr), *I. Aguilar 126* (F); 1939 (early fr), *I. Aguilar 215* (F). HUEHUETENANGO: Paso del Boquerón, along Río Trapichillo, below La Libertad, 1,200–1,300 m, 21 Aug. 1942 (fr), *Steyermark 51133* (F). SACATEPÉQUEZ: nr. Barranco Hondo, SE of Alotenango, 1,000–1,260 m, 9 Feb. 1939 (fl), *Standley 65024* (F).

Psychotria aguilarii may be recognized first by its striking resemblance to *P. nervosa*. The former differs in being generally glabrous (as is *P. nervosa* sometimes) and in having leaves with crenulate leaf margins, inflorescence secondary axes in 2 (vs. 3–4) ranks, longer corolla tubes (3–3.5 vs. 2–3 mm), fruit less narrowly ellipsoidal (length/width = 1.5 vs. ca. 2.2), and seed dorsal surface with many irregular shallow furrows (vs. 4–5 regular furrows).

28. Psychotria boquetensis Dwyer, Ann. Missouri Bot. Gard. 67: 349. 1980. TYPE: Pan-

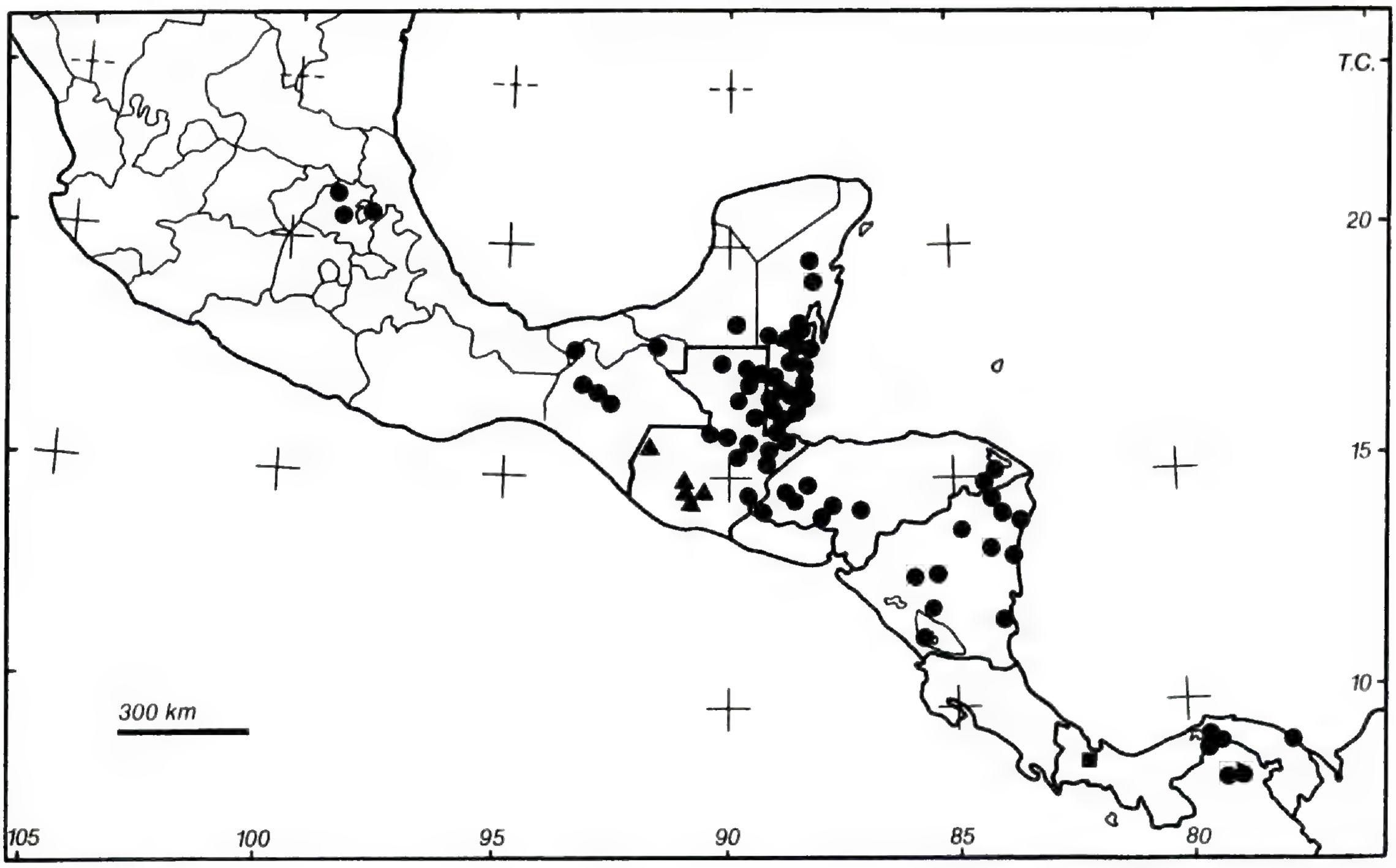

FIGURE 25. Distributions of *Psychotria aguilarii* (triangles), *P. boquetensis* (square), and *P. fruticetorum* (circles) in Mesoamerica.

ama. Chiriquí: Boquete, 1,080 m, 25 May 1938 (fl), *Davidson 709* (holotype, MO; isotypes, F, US). Figure 25.

Shrub 0.5–2 m tall; young stems brown tomentose, the bark gray, longitudinally grooved; stipules sheathing, ovate, bilobed with the lobes 2–6 mm long, (6–)8–11 × 2.5 mm, lacking fringe, glabrous or sometimes sparsely tomentose, caducous, leaving a pale ridge with red-brown fringe. *Leaves* subsessile; petioles 3–6 mm long, brown tomentose, flat or grooved above; blades membranous, elliptic to oblong, the apex long-acuminate, the base attenuate, (6–)9–15 × (1.5–)2–4 cm, glabrous to slightly puberulent along primary and secondary veins above, sparsely tomentose along veins below, the margins ciliate, drying red-brown, paler below; secondary veins (10–)12–15 pairs, diverging 40°–50°, eucamptodromous, slightly arcuate, prominent below, brown tomentose below, the axils with small tufts of hairs below; tertiary veins evident, orthogonal reticulate to slightly percurrent. *Inflorescences* terminal or pseudoaxillary, sparse panicles of cymes; panicle branched to 3 degrees; main axis 1.2–2.0 cm long, the peduncle lacking; secondary axes in (2)3 ranks, the first-rank axes 2, 10–15 mm long, the second-rank axes 2, 4–10 mm long, the third-rank axes 2, 2–3 mm long; cymes branched to (1)2 degrees; bracts appearing to consist of planes of long whitish hairs, 1 mm long, immediately subtending the flowers. *Flowers* sessile to subsessile, the pedicels to 1 mm long; calyx cup-shaped, the tube 0.5–1 mm long, the lobes 5, triangular to linear, (0.5–)1–1.5 × 0.5 mm, glabrous; corolla white, the tube cylindrical, 2–3 × 1 mm, white pubescent in throat, the lobes 5, linear-ovate, 1.5–2 × 0.8 mm; stamens 5, the filaments 2 mm long in pins, 3.5 mm long in thrums, the anthers 0.5–0.7 mm long; style 3.5 mm long in pins, 2 mm long in thrums, the branches club-shaped in pins, linear in thrums, the branches puberulent. *Fruit* not seen.

Distribution (Fig. 25). Known only from the type locality near Boquete, Chiriquí, Panama, in premontane wet forest with equatorial-mountainous climate at about 1,200 m. *Psychotria boquetensis* has been collected in flower in May and June.

Additional specimens examined. PANAMA. CHIRIQUÍ: Boquete, 1,200 m, 30 June 1938 (fl), *M. Davidson 849* (A, F).

Psychotria boquetensis may be recognized first by its striking resemblance to *P. nervosa*. *Psychotria boquetensis* differs in having often linear calyx lobes usually 1–1.5 mm (vs. to 0.2 mm) long; in quantitative characters such as leaf and inflorescence size, *P. boquetensis* falls at the lower end of the *P. nervosa* spectrum.

29. Psychotria chagrensis Standley, J. Wash. Acad. Sci. 15: 105. 1925. TYPE: Panama. Canal Area: Barro Colorado Island, Gatun Lake, 17 Jan. 1924 (fr), *Standley 31373* (holotype, US). Figure 26.

Shrub 1–2.5 m tall; young stems glabrous, the bark smooth; stipules sheathing, the apex aristate and 2–4 mm long, the sheath 4–7 × 3 mm, glabrous, caducous, leaving a pale ridge. *Leaves* petiolate; petioles 2–5(–8) mm long, glabrous, flat or grooved above; blades membranous, elliptic to obovate, the apex acuminate, the base attenuate, (3–)4–7.5(–9.5) × (1–)1.5–2.5(–3.5) cm, glabrous above and below, drying red-brown, often dull green below; secondary veins (6–)8–10 pairs, diverging (45°–)55°–65°, brochidodromous with collector vein distinct, straight to slightly arcuate, scarcely elevated below, glabrous, the axils lacking domatia and hairs; tertiary veins usually inconspicuous, the intersecondaries sometimes faint, the percurrent tertiaries rarely evident. *Inflorescences* terminal or pseudoaxillary, fascicles of several flowers, 5–8 mm long, 5–8 mm across; peduncles lacking; bracts elongate, often irregularly divided, 4–5 × 1.5–2 mm, glabrous, the margins often ciliate. *Flowers* sessile; calyx green, the tube cylindrical, 0.5–2 mm long, the lobes 5, linear, 2–2.5 × 0.5 mm, glabrous to puberulent, the margins ciliate; corolla white, the tube cylindrical, 6–7 × 1 mm, white pubescent in throat, the lobes 5, narrow-elliptic, 2–2.5 × 0.7 mm; stamens 5, the filaments 5–6 mm long in pins, 8 mm long in thrums, the anthers linear, 1 mm long; style 7–9 mm long in pins, 2–5 mm long in thrums, the branches linear, sometimes recurved. *Fruit* when dry ellipsoid, 5–7 mm long, 3–3.5 mm diam., maturing red, drying deep red-brown; calyx persistent, the tube 0.5–2 mm long, the lobes 2–2.5 mm long; seed dorsal surface with 4–5 deep longitudinal furrows, the ventral surface with 2 shallow longitudinal furrows.

Distribution (Fig. 26). Commonly collected on the Caribbean lowlands and slopes in Nicaragua–Panama, with apparently disjunct populations in Veracruz, Mexico, and Izabal, Guatemala. The range extends southward in Colombia and Peru. *Psychotria chagrensis* is found in Central America often near creek beds at elevations of 0 to 1,300 m in tropical moist to premontane moist and wet forest with equatorial to tropical-equatorial climate. It has been collected in flower in December–September, primarily March–July, and in fruit throughout the year, primarily September–December.

Selected specimens examined. MEXICO. VERACRUZ: San Andres Tuxtla, Estación de Biología Tropical Las Tuxtlas, 150 m, 7 Nov. 1968 (fr), *Martínez 1785* (A, ENCB—5 sheets, F, K, MEXU—2 sheets, MO). GUATEMALA. IZABAL: Cerro San Gil, uppermost ridges and summit, 1,200–1,300 m, 26–27 Dec. 1941 (fr), *Steyermark 41949* (F). NICARAGUA. RÍO SAN JUAN: San Juan del Norte, 0 m, 27 Mar. 1971 (fr), *Atwood 5258* (MO); El Castillo Viejo, (fl), *Shimek & Smith 1893* (F). ZELAYA: Comarca del Cabo, swamp nr. Bilwaskarma, 0–100 m, 14 Mar 1971 (fl), *Atwood 4678* (MO); Comarca del Cabo, matorrales del Río Leicus, region de Tronqueras, 60 m, 19 Aug. 1965 (fr), *A. Molina R. 14925* (F, NY, US); "Kurinwacito," 13°08′N, 84°55′W, 90 m, 25 Mar. 1984 (fl), *P. P. Moreno 23901* (MO); El Salto, along Río Pis Pis, 14°04′N, 84°38′W, 100 m, 27 Feb. 1979 (fr), *Pipoly 3572* (MO); 1.8 km N of base camp, 3.6 km SE Cerro San Isidro, Río Kama, Río Escondido, 65 m, 14 Mar. 1966 (fl), *Proctor et al. 27134* (F, NY); trail from Cerro Saslaya to San José de Hormiguero, 13°44′N, 84°57′W, 200–400 m, 13 Mar. 1978 (fl), *W. D. Stevens 7043* (MO); Caño Zamora on Río Rama, 11°57′N, 84°16′W, 10 m, 16 May 1978 (fl), *W. D. Stevens 8867* (MO); about 3.9 km SE of El Empalme on road to Limbaika, 13°39′N, 84°24′W, 65 m, 24 Feb. 1979 (fr), *W. D. Stevens 12910* (MO). COSTA RICA. ALAJUELA: E of Río San Rafael, W of La Marina, 10°23′N, 84°23′W, 500 m, 19 May 1968 (fl), *Burger & Stolze 5032* (CR, DUKE, F, MO); San Carlos, Quesada, 850 m, 12 Mar. 1940 (fr), *A. Smith 2587* (A, F, MO). HEREDIA: Finca La Selva, the OTS field station on Río Puerto Viejo, 100 m, 20 Mar. 1982 (fl), *Folsom 9412* (DUKE); 6 Dec. 1982 (fr), *McDowell 1066* (DUKE); Tirimbina, 210 m, 29 May 1971 (fl), *Proctor 32118* (LL). LIMÓN: Río Toro Amarillo, 5.5 km al SO de Guapiles, 350 m, 10 Aug. 1963 (fr), *Jiménez 1059* (CR, F, MO); drenajes de los ríos Parismina y Reventazon, 0 m, 3 Oct. 1959 (fr), *Shank & Molina 4160* (GH, US). PUNTARENAS: Monte Verde, 10 m, 15 May 1925 (fl), *Stork 2364* (F). PANAMA. BOCAS DEL TORO: Changuinola, nr. Luzón, 20 June 1973 (fl), *Kennedy 3259* (MO). CANAL AREA: Pipeline Road, 14 mi. NW of Gamboa gate, 26 Sep. 1970 (fr), *Croat 12357* (DUKE, F, GH, MO, NY); Barro Colorado Island, 31 May 1969 (fl), *Foster 899* (DUKE—2 sheets); 18 Aug. 1934 (fr), *Shattuck 1152* (F, MO); Fort Sherman and nearby, 9°20′N, 80°00′W, 0–100 m, 16 June 1983 (st), *Hamilton & Stockwell 3682* (MO). COCLÉ: hills N of El Valle de Antón, 1,000 m, 14 July 1940 (fl), *Allen 2186* (F, GH); between Caño Blanco del Norte, Caño Sucio, and Chorro del Río Tife, 8°43′N, 80°37′W, 200–400 m, 3 Feb. 1983 (st), *Davidse & Hamilton 23483* (MO); Alto Calvario, 7 km N of El Copé, ca. 900 m, 14 Jan. 1977 (fr), *Folsom 1304* (MO); divide above El Copé, 8°40′N, 80°35′W, ca. 1,200 m, 25 July 1983 (st), *Hamilton & Krager 4167* (MO). COLÓN: 4 mi. W of Portobelo, ca. 0 m, 9 Sep. 1979 (fr), *Antonio 1771* (MO); Santa Rita Ridge lumber road, 3 Oct. 1968 (fr), *M. Correa A. & Dressler 1072* (DUKE, MO); hillside ca. 7 mi. on way to Nombre de Dios E of junction with road to Isla Grande, 4 Apr. 1980 (fl), *D'Arcy 13615* (MO); trail S of Río Guanche, on ridge to Cerro Pan de Azucar, 200 m, 20 Sep. 1974 (fr), *Mori & Kallunki 2010* (MO). DARIÉN: Camp Summit, between Mortí and Sasardí, ca. 400 m, 14 Feb. 1967 (fr), *Duke 10027* (MO); ridges between Río Jaqué Valley and Pacific Ocean, 7°26′N, 78°05′W, 300–500 m, 24 Jan. 1982 (fl), *Knapp & Mallet 3102* (MO). PANAMÁ: El Llano–Cartí Road, 13.8 km N of Pan-

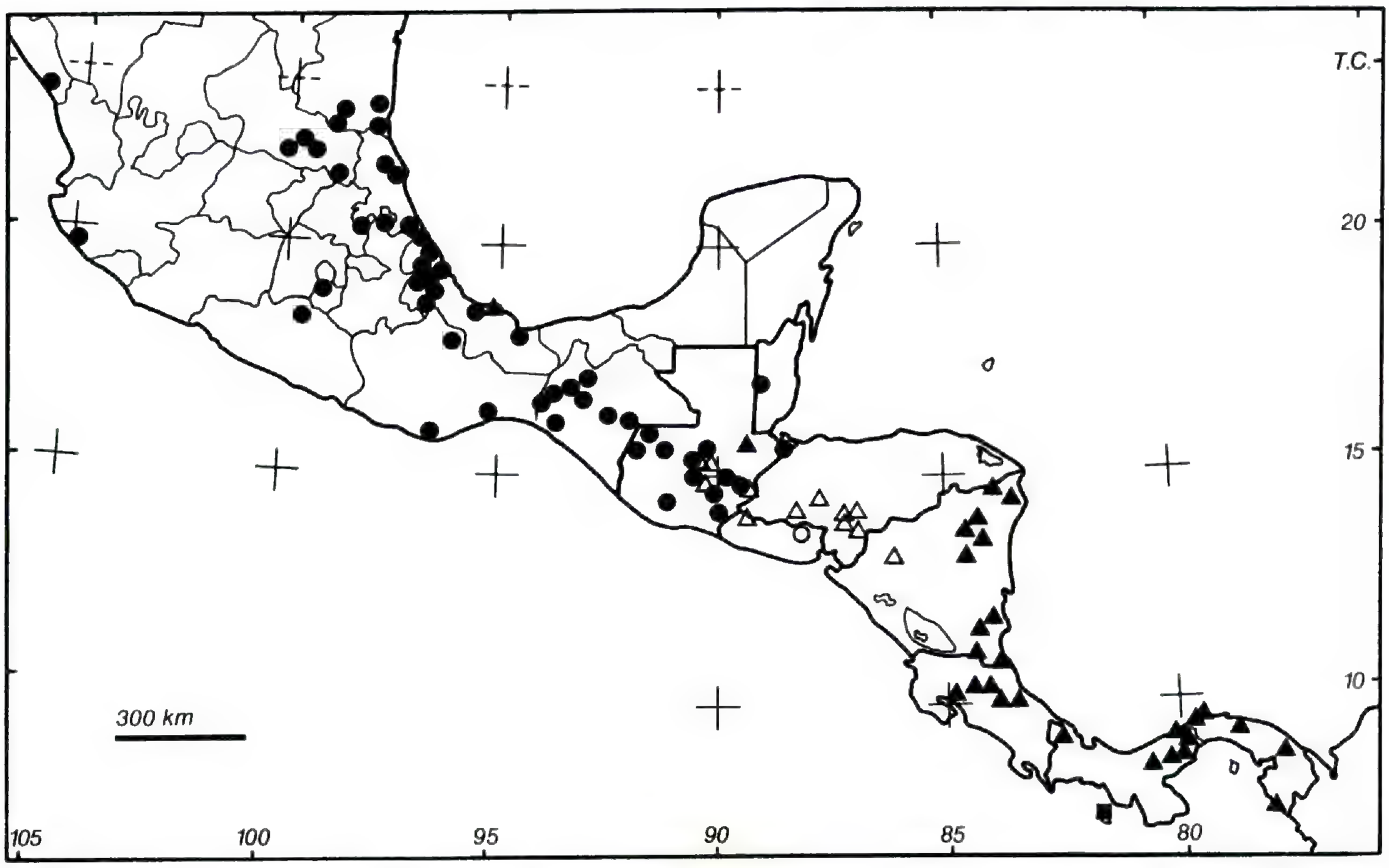

FIGURE 26. Distributions of *Psychotria chagrensis* (solid triangles), *P. erythrocarpa* (solid circles), *P. fosteri* (solid square), *P. jinotegensis* var. *jinotegensis* (open triangles), and *P. jinotegensis* var. *morazanensis* (open circle) in Mesoamerica.

American Hwy., 5 Oct. 1977 (fr), *Folsom et al. 5790* (MO); Cerro Campana, 8°40′N, 79°55′W, 800 m, 17 Aug. 1982 (fr), *Hamilton & D'Arcy 686* (MO); 23 July 1983 (fl), *Hamilton et al. 4043* (MO). SAN BLAS: El Llano–Cartí rd., 19.1 km from Interamerican Hwy., 9°19′N, 78°55′W, 100–350 m, 19 Sep. 1984 (fr), *Nevers et al. 3907* (MO); Cerro Habu, trail from Río Sidro, 9°23′N, 78°49′W, 420–600 m, 20 Dec. 1980 (fr), *Sytsma et al. 2769* (ENCB, MO).

Psychotria chagrensis may be recognized readily by its inflorescences consisting of fascicles of several flowers, its large (5–7 × 3–3.5 mm) fruit with conspicuously persistent calyx usually 3–4 mm long, and small leaves (usually 4–7.5 × 1.5–2.5 cm). Leaves appear at the lower end of the given size range in Costa Rica and at the higher extreme in Mexico and Guatemala.

The inserted stamens of the pin morph are longer than the inserted pistil of the thrum (5.5–6.5 vs. 2–5 mm).

30. Psychotria erythrocarpa Schlechtendahl, Linnaea 9: 385. 1834 [1835]. *Uragoga erythrocarpa* (Schldl.) Kuntze, Revis. Gen. Pl. 2: 960. 1891. TYPE: Mexico. Hda. de La Laguna (fr), *Schiede 385* (holotype, B, destroyed, photo & fragment, F neg. no. 519; isotype, K). Figures 2c, 7c, 26.

Mapouria chamissoana Loesener, Verh. Bot. Vereins Prov. Brandenburg 65: 112. 1923. *Psychotria chamissoana* (Loes.) Standl., J. Wash. Acad. Sci. 17: 341. 1927. TYPE: Mexico. Tecolute, Jan. (fr), *Scheide 1266* (holotype, B, destroyed, photo, F neg. no. 446).

Shrub 1–3 m; young stems pale brown to red-brown tomentose or sometimes glabrous, the bark gray, furrowed longitudinally; stipules linear, 8–12 × 1.5–2 mm, glabrous to sparsely tomentose, caducous, leaving a pale ridge with long red-brown fringe to 1 mm long (Fig. 2c). *Leaves* subsessile to petiolate; petioles to 10 mm long, pale tomentose, flat and grooved above; blades membranous, obovate to sometimes elliptic, the apex acute to obtuse to rounded, the base attenuate, (3.5–)5–8(–10) × (1–)1.5–3.5(–5) cm, sparsely pale tomentose to glabrous above, densely tomentose especially near margins to glabrous below, drying green-brown above, paler green below; secondary veins 6–8(–9) pairs, diverging 35°–50°, eucamptodromous to brochidodromous, straight to arcuate near margin, elevated below, dense pale tomentose to glabrous below, the axils sometimes with tufts of pale hair below; tertiary veins inconspicuous, orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of cymes or glomerules (Fig. 7c); panicle branched to 3–4 degrees; main axis (1.2–)2.5–5.5 cm long, the peduncle (0.5–)1.5–3 cm long; secondary axes in (2–)3

ranks, the first-rank axes 2, (0.4–)0.8–2 cm long, the second-rank axes 2, (0.2–)0.3–1 cm long, the third-rank axes 2, 0.1–0.3 cm long; cymes branched to 1–2 degrees; bracts triangular, 1.5 × 1 mm. *Flowers* sessile to pedicellate, the pedicels to 1 mm long; calyx cup-shaped, the tube 0.5–1 mm long, the lobes 5, barely evident, red-brown tomentose; corolla white, the tube cylindrical to slightly campanulate, 2–2.5 × 1–1.5 mm, white pubescent in throat, the lobes 5, narrow-triangular, 1.5–2 × 1 mm; stamens 5, the filaments 2–2.5 mm long in pins, 3–3.5 mm long in thrums, the anthers 0.5–0.8 mm long; style 3.5–4 mm long in pins, 2–2.5 mm long in thrums, the branches linear in pins and club-shaped in thrums. *Fruit* ellipsoid when dry, 4.5–6 mm long, 3–4.5 mm diam., maturing red, drying brown, glabrous to pale puberulent when dry; calyx persistent as a beak to 0.5 mm long; seed dorsal surface with 4 deep longitudinal furrows, the ventral surface with 2 very deep longitudinal furrows.

Distribution (Fig. 26). Commonly collected in Mexico (primarily Veracruz and Chiapas) and upland Guatemala, and extending to Cayo, Belize, in areas of subevergreen forest with usually tropical-mountainous or sometimes equatorial to subtropical-tropical climate. *Psychotria erythrocarpa* ranges in elevation 0–2,000 m, lower in Veracruz and higher in Chiapas and Guatemala. It has been collected in flower throughout the year, primarily April–July, and in fruit throughout the year, primarily August–January.

Selected specimens examined. MEXICO. CHIAPAS: Mpio. La Trinitaria, Hwy. 190 3 mi. S of La Trinitaria, 1,350 m, 27 June 1965 (fl), *Breedlove 10593* (ENCB, F, NY); 12 mi. E of La Trinitaria along rd. to the Lagos de Monte Bello, 1,440 m, 6 Nov. 1965 (fr), *Breedlove 14126* (ENCB, F, NY); Mpio. Terán, 6.5 km W of Tuxtla Gutiérrez along Hwy. 190, 600 m, 8 Oct. 1971 (fr), *Breedlove 20102* (ENCB, MO, NY); Mpio. Villa Corzo, E base of Cerro Tres Picos nr. Cerro Bola along logging rd. SW of Colonia Agronomos Mexicanos, 1,500 m, 9 Feb. 1972 (bud), *Breedlove 23974* (MEXU, MO); Mpio. Cintalapa de Figueroa, 5–7 km NW of Rizo de Oro along a logging rd. to Cerro Baul and Colonia Figueroa, 100 m, 19 Apr. 1972 (fl), *Breedlove 24698* (DUKE, F, MEXU, MO, NY); Mpio. Ocozocoautla de Espinosa, Río de la Venta at the chorreadero nr. Derna, 800–1,000 m, 24 Aug. 1972 (fr), *Breedlove 27360* (DUKE, MO, NY); Mpio. Suchiapa, steep canyon 15 km SW of Suchiapa along rd. to Villa Flores, 750 m, 3 Oct. 1972 (fr), *Breedlove 28265* (DUKE, MEXU, MO, NY); Mpio. Cintalapa de Figueroa, along Río Cintalapa 5–6 km NW of Las Cruces along logging rd. to La Cienega, 850 m, 5 Oct. 1972 (fr), *Breedlove 28450* (DUKE, ENCB, MO, NY); Mpio. Soyaló, 5 km N of Soyaló along rd. to Bochil, 1,300 m, 26 Oct. 1971 (fr), *Breedlove & Thorne 21313* (DUKE, F, MEXU, MO, NY); Mpio. Amatenango del Valle, creek "Chenek' Ha' " nr. Amatenango, 1,710 m, 28 July 1967 (fr), *Ton 2678* (ENCB, F, MO); Monserrate, 16°33'N, 94°00'W, Apr. 1925 (fl), *Purpus 14334* (A, F); Mpio. Venustiano Carranza, Rancho Carmen along rd. from Acala to Venustiano Carranza, 780 m, 18 July 1966 (fr), *Laughlin 1329* (F, NY). GUERRERO: barr. Cacahuamilpa, 22 Mar. 1941 (st), *Miranda 1935* (MEXU). HIDALGO: San Bartolo Tutotepec, 1,000 m, 3 June 1972 (fl), *Gimate 658* (ENCB, MEXU, SLPM). JALISCO: Estación Biología Chamela, cerca de arroyo Pailles, 8 Dec. 1970 (fr), *Pérez 279* (MEXU). MORELOS: montañas N de Cuernevaca, 2,000 m, 5 Nov. 1972 (fr), *J. Vázquez 3981* (MEXU). OAXACA: 5 km S of Tuxtepec, limestone hill, less than 100 m, 30 Aug. 1974 (fr), *J. Conrad & R. Conrad 3246* (F, GH—3 sheets, MO, NY); Pochutla, Boquerón, camino de Forramoes, 150 m, 7 May 1971 (fl), *Conzatti et al. 3265* (GH); Tehuantepec, Santa Lucía, 1,200 m, 5–6 July 1971 (fl), *T. MacDougall H28* (NY). PUEBLA: Mpio. de Jalpan, Ajenjibre, Nov. 1950 (fr), *Paray 322* (ENCB). SAN LUIS POTOSÍ: Mpio. de Cuidad del Maíz, El Salto, 400 m, 31 July 1960 (fl), *L. González Q. 138* (ENCB); Tamazunchale, 300 m, July 1937 (fr), *Lundell & Lundell 7144* (F, MEXU, NY); El Abra, 10 km E of Ciudad Valles, 1,500 m, 17 June 1956 (fl), *Rzedowski 7772* (ENCB, MEXU, SLPM); Mpio. de Tamasopo, San Nicolás de los Montes, 800 m, 28 May 1959 (fl), *Rzedowski 10664* (ENCB). SINALOA: Mazatlán, Mpio. Rosario, Chametla, Cuacoyolitos, 20 m, (fr), *J. González Ortega 5875* (GH, MEXU, US). TAMAULIPAS: 8 mi. N of Aldama, rd. to San Rafael, oak scrub, 330 m, 10 Dec. 1959 (fr), *M. Johnston 4945* (MEXU); vic. Tampico, 15 m, 1–22 May 1910 (fl), *Palmer 478* (GH, K, MO, NY, US); Mpio. de Ocampo, 3 km NE of Flores Magón, 400 m, 7 Aug. 1969 (early fr), *Puig 5135* (ENCB); Mpio. de Gómez Farías, 2 km E of Gómez Farías, 500 m, 11 June 1982 (fl), *Valiente & Viveros 161* (ENCB, MEXU—2 sheets, MO). VERACRUZ: Mpio. Vega de Altorre, Canada de Mesillas, entrada por Santa Ana, 360 m, 24 July 1981 (fr), *Calzada 7740* (MEXU); Mpio. Coatepec, Cerro de la Palmas entre Jalcomulco y Tuzamapan, 19°23'N, 96°48'W, 800 m, 1 Apr. 1979 (fl), *Castillo & Tapia 501* (MEXU); Isla Lobos, 0 m, 1 June 1966 (fl), *E. Chávez s.n.* (ENCB, MEXU); Mpio. de Naolinco, corriente de lava al S de La Concepción, 1,000 m, Aug. 1973 (fr), *Chazaro & Dorantes 255* (ENCB, MEXU); Mpio. Ozuluama, 5 km adelante de Ozuluama, hacia Tampico, 6 Dec. 1970 (fr), *Chiang 224* (GH, MEXU); carret. Nautla a Veracruz, 1 km al S del Raudel, 20 m, 15 July 1977 (fl), *Fay & Calzada 927* (ENCB, F, NY, US); carret. San Andrés Tuxtla a Alvarado 6 km, 100 m, 6 July 1977 (fl), *Fay & C. Hernández 832* (F, US); Mpio. Apazapan, 2 km NE of Emiliano Zapata (= Carrizal), 19°23'N, 96°38'W, 400 m, 27 June 1980 (fl), *Hansen & Nee 7522* (F, MO); Atoyac, 14 May 1937 (fl), *Matuda 1484* (MEXU), *Matuda S-4* (A, F, MO); Casitas-Gutiérrez Zamora, cerca ejido villa Cuauhtemoc, 30 m, 21 June 1970 (fl), *Nevling & Gómez-Pompa 1163* (GH, MEXU); Coatzacoalcos, 21 Mar. 1910 (fl), *Orcutt 3106* (F); Cerro Monte de Oro, 300 m, 20 June 1972 (fl), *C. Vázquez Y. 614* (MEXU); Mpio. Coetzala, limites con Omealca, 600 m, 16 July 1976 (fr), *V. Vázquez T. 458* (ENCB, MEXU—2 sheets); Mpio. Puente Nacional, 50 m, 16 Oct. 1970 (fr), *Ventura 2635* (ENCB, MEXU); Mpio. de Totutla, Mata Oscura, 750 m, 25 Nov. 1971 (fr), *Ventura 4575* (ENCB); Mpio. de Dos Ríos, Cerro Gordo, 450 m, 15 Jan. 1975 (fr), *Ventura 10809* (ENCB, MO). GUATEMALA. BAJA VERAPAZ: 13 km S of turnoff to

Salamá on hwy. to Cobán, 1,000 m, 14 July 1977 (early fr), *Croat 41119* (MO); 5 km SE of Granados, 15 July 1970 (early fr), *Harmon & Dwyer 3105* (ENCB, F, GH, MO, US); 6 km from Rabinal, rd. to Guatemala City, thickets of Pachirax River, Sierra Chuacús, 1,140 m, 2 Oct. 1972 (fr), *A. Molina R. & A. Molina 27784* (F). CHIQUIMULA: between Chiquimula and La Laguna, 500–1,000 m, 27 Oct. 1939 (fr), *Steyermark 30684* (F). ESCUINTLA: sin. loc., 1942 (fr), *J. I. Aguilar 1729* (F). GUATEMALA: Estancia Grande, 600 m, 8 Dec. 1938 (st), *Standley 59208* (F). HUEHUETENANGO: between Nentón and Las Palmas, via Yalisjao, Rincón Chiquite, Chiaquial, Guaxacaná, in Sierra de los Cuchumatanes, 800–1,200 m, 30 Aug. 1942 (fr), *Steyermark 51630* (F); mountains nr. El Reposo, 8 km from Mexican frontier, 900–1,000 m, 14–18 Dec. 1972 (fl), *L. O. Williams et al. 41394* (F, US). IZABAL: St. Thomas, 29 May 1909 (fl), *Deam 6047a* (GH, US). JALAPA: hills NE of Jalapa, rocky scrub-oak forest, 1,400–1,600 m, 10 Nov. 1940 (fl), *Standley 76783* (F); mountains along rd. between Jalapa and San Pedro Pinula, 1,400–1,800 m, 12 Nov. 1940 (fr), *Standley 77070* (F). JUTIAPA: vic. Jutiapa, 850 m, 24 Oct.–5 Nov. 1940 (fr), *Standley 76317* (F, NY, US); quebrada above Ovejero, on rd. between Monjas (Dept. Jalapa) and El Progreso, 1,400 m, 19 Nov. 1940 (st), *Standley 77633* (F). QUICHÉ: sin. loc., 1942 (fl), *J. I. Aguilar 1143* (F); 1942 (fr), *J. I. Aguilar 1371* (F). ZACAPA: Loma El Picacho, above Santa Rosalía, dry SW-facing rocky slopes and bluffs of metamorphosed dolomitic rock, 1,200–1,600 m, 15 Jan. 1942 (st), *Steyermark 42705* (F, NY). BELIZE. CAYO: Cuevas de Río Frío, a 1 km al O de Augustine, 400 m, 2 Sep. 1973 (fr), *Sousa 4183* (MEXU).

A minority of glabrous individuals appear in many populations of *Psychotria erythrocarpa* (D. Lorence, pers. comm.), so *P. chamissoana*, defined by its glabrous aspect, is included within *P. erythrocarpa*.

Psychotria erythrocarpa may be recognized by its usually pale brown to red-brown tomentose aspect, obovate leaves with few (usually 6–8) secondary veins diverging acutely (35°–50°), and small (usually 2.5–5.5 cm long) inflorescences with secondary axes two per rank in three ranks. The fruits occupy the small end of the spectrum in Veracruz and the large end in Chiapas and southward.

31. Psychotria fosteri C. Hamilton, Phytologia 64: 224. 1988. TYPE: Panama. Veraguas: Playa Rosario, northern tip of Coiba Island, 26 Aug. 1970 (fl, fr), *Foster 1605* (holotype, DUKE; isotypes, F, GH, MO). Figure 26.

Shrub ca. 1 m high; young stems glabrous, the bark slightly furrowed longitudinally; stipules sheathing, narrow, with 2 triangular lobes, the sheath 8–12 × 1–3 mm, the lobes 2–3 mm long, fringed, with darker red-brown midrib leading to apex of each lobe, caducous, leaving a red-brown ridge with irregular fringe. *Leaves* petiolate; petioles 5–10 mm, glabrous, flat above; blades membranous, elliptic-obovate, the apex acuminate to mucronate, the base attenuate, (6–)8–12 × (2–)3–5 cm, glabrous above and below, drying green-brown above, deep red-brown below; secondary veins 11–14 pairs, diverging 70°–80°, brochidodromous often with collector vein distinct, slightly arcuate, prominulous below, glabrous, drying deeper red-brown than blade, the axils lacking domatia or hairs; tertiary veins inconspicuous, reticulate. *Inflorescences* terminal, fascicles of several flowers, ca. 8 mm long, 10 mm across; peduncles lacking; bracts broadly triangular, irregularly cleft, ca. 5 × ca. 5 mm, fringed. *Flowers* sessile; calyx cup-shaped, the tube 1.5 mm long, the lobes 5, triangular, 0.5–1 × 0.5 mm, slightly fringed; corolla white, the tube cylindrical, 3.5 × 0.8 mm, white pubescent in throat, the lobes 5, triangular, 2 × 0.7 mm; stamens 5, the filaments 3 mm long in pins, not seen in thrums, the anthers 0.5 mm long; style 4–4.5 mm long in pins, not seen in thrums, the branches linear. *Fruit* when dry ellipsoid, 5–6 mm long, 2.5–3 mm diam., maturing orange (probably to red), drying dark red-brown; calyx persistent, the tube 1–1.5 mm long, the lobes ca. 1 mm long; seed dorsal surface with 5 longitudinal furrows, the ventral surface with 2 longitudinal furrows.

Distribution (Fig. 26). Known only from the type collection from Coiba Island, Panama, in tropical moist forest with tropical-equatorial climate. It was collected in flower and fruit on August 26.

Psychotria fosteri may be recognized as a magnified version of *P. chagrensis*, having an inflorescence consisting of a fascicle of flowers and fruit ellipsoid with a conspicuous persistent calyx. *Psychotria fosteri* differs in having larger (sheath 8–12 vs. 4–7 mm long) biaristate (vs. aristate) stipules, larger mature leaves (usually 8–12 × 3–5 vs. 4–7.5 × 1.5–2.5 cm), shorter calyx lobes (0.5–1 vs. 2–2.5 mm), and much shorter corolla tubes (3.5 vs. 6–7 mm).

The lone flowering collection is a pin morph.

32. Psychotria fruticetorum Standley, J. Arnold Arbor. 11: 42. 1930. TYPE: Honduras. Comayagua: vic. Siguatepéque, 1,080–1,400 m, 14–27 Feb. 1928 (fr), *Standley 56197* (holotype, F; isotype, A). Figure 25.

Shrub, 0.5–3 m tall; young stems glabrous, the bark red-brown or pale, smooth; stipules sheathing, biaristate with extensions arising from apical corners of sheath, 1.5–2 × 1.5–2 mm, glabrous,

caducous, leaving a pale or red-brown ridge with or without fringe. *Leaves* petiolate; petioles 2–5 mm long, glabrous, flat above; blades membranous to subcoriaceous, elliptic to slightly obovate, the apex acute to acuminate, the base narrowly cuneate to attenuate, the margin often inrolled, (3–)5–7(–9) × (1–)2–4(–4.5) cm, glabrous above and below, drying chalky yellow-green to red-brown; secondary veins (4–)5–7(–8) pairs, diverging 55°–65°, eucamptodromous, straight then constantly arcuate toward margin, barely elevated below, glabrous, the axils often with minute tufts of white hairs below; tertiary veins inconspicuous, orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of cymes; panicle branched to 3 degrees; main axis 1.5–4.5 cm long, the peduncle 0.3–2.5 cm long or rarely lacking; secondary axes in (2–)3–4(–5) ranks, the first-rank axes 2 or 4, the longer pair 0.5–1.8 cm long, the shorter pair when present 0.5 cm long, the second-rank axes 2, 0.1–1.1 cm long, the third-rank axes 2(4), the longer pair 0.2–0.7 cm long, the shorter pair when present 0.2 cm long, the fourth-rank axes 2, 0.4–0.5 cm long, the fifth-rank axes 2, 0.3 cm long; cymes branched to 2 degrees; bracts broad, irregular, to 1 mm long, glabrous to puberulent, often minutely fringed. *Flowers* on pedicels 0.5–1 mm long; calyx cup-shaped, the tube 0.5 mm long, the lobes 5, triangular to barely evident, to 0.5 × 0.5 mm, often minutely fringed; corolla white, the tube cylindrical, 2 × 1.5 mm, white pubescent in throat, the lobes 5, linear, 1.5–2 × 1 mm; stamens 5, the filaments 1.5–2 mm long in pins, 3–3.5 mm long in thrums, the anthers 0.8 mm long; style 3.5–5 mm long in pins, 2.5 mm long in thrums, the branches short, linear, often recurved. *Fruit* when dry ellipsoid, 4–5 mm long, 3–3.5 mm diam., maturing red, drying red-brown; persistent calyx to 0.5 mm long; seed dorsal surface with 4 deep longitudinal furrows, the ventral surface with 2 deep longitudinal furrows.

Distribution (Fig. 25). Widespread from Mexico through Panama, mostly on the Caribbean side, with greatest concentration in Belize and eastern Petén, Guatemala, in tropical to premontane moist forest with equatorial to tropical climate. *Psychotria fruticetorum* ranges in elevation 0–2,000 m, reaching over 1,300 m only in Mexico and parts of Guatemala. It has been collected in flower throughout the year, primarily March–July, and in fruit throughout the year.

Selected specimens examined. MEXICO. CAMPECHE: Tuxpeña, 13 Dec. 1931 (fr), *Lundell 1062* (F). CHIAPAS: Mpio. Tenejapa, Ala Shashib River below Habenal, paraje of Mahben Chauk, 990 m, 15 July 1964 (fl), *Breedlove 6489* (F, NY); Mpio. Ocozocoautla de Espinosa, selva del Ocote 32 km NW of Ocozocoautla, 600 m, 27 Aug. 1972 (fr), *Breedlove 27427* (MEXU, MO); Mpio. Ocosingo, nr. Laguna Ocotal Grande, 800 m, 27 Nov. 1972 (fr), *Breedlove & Dressler 29846* (MEXU). HIDALGO: Mpio. de Juárez-Hidalgo, barrancas al N de Juárez-Hidalgo, 1,800 m, 10 May 1981 (fl), *R. Hernández M. et al. 6114* (MEXU, MO); Mpio. de Molango, 3 km SW of Molango, 1,600 m, 2 May 1980 (fl), *G. Pérez S. 574* (ENCB, MEXU—2 sheets). QUINTANA ROO: carret. Chetumal–Felipe Carrillo Puerto, 15 Nov. 1980 (fr), *Cabrera & Cortés 343* (MEXU); 110 km SW of Chetumal, 8 km N of Unión, 100 m, 7 May 1982 (fl), *Davidse et al. 20183* (MO); Mpio. Felipe Carrillo Puerto, 21 Aug. 1971 (fr), *G. Pérez S. 411* (ENCB, MEXU). TABASCO: Mpio. Huimanguillo, km 15 de Huimanguillo a Francisco Rueda, 12 June 1979 (fl), *Cowan 2284* (ENCB, MEXU); Balancán, La Palma, 1–6 June 1939 (fr), *Matuda 3266* (A, F, MEXU, NY); Mpio. Huimanguillo, 1 km al N de Chontalpa, 12 Nov. 1971 (fr), *Puig 322* (ENCB, MEXU). VERACRUZ: Mpio. de Huayacocotla, camino a Rancho Nuevo, 1,600 m, 8 Mar. 1972 (fl, fr), *R. Hernández M. & B. Rosales A. 1559* (MEXU). GUATEMALA. ALTA VERAPAZ: Chahal, El Mago, ca. 90 m E of Sebol Road, 15 Oct. 1968 (fr), *Contreras 7938* (F, NY); Rubelsanto, Balastrera, 23 July 1975 (fl), *Lundell & Contreras 19548* (MO); SW of Lanquín, vic. caves, 600–1,000 m, 21 Feb. 1942 (st), *Steyermark 44128* (F, US); savanna N of Concepción, 3–5 mi. SE of Finca Yalpemech, nr. Alta Verapaz–Petén boundary, 100–110 m, 23 Mar. 1942 (fl), *Steyermark 45272* (F, NY). CHIQUIMULA: 3 mi. SE of Quezaltepeque, Montaña Castilla, vic. Montaña, Cebollas, along Río Lucía Saso, 1,200–1,500 m, 6 Nov. 1939 (fr), *Steyermark 31237* (F); *Steyermark 31321* (F). IZABAL: Cadenas/Puerto Méndez, 8 Sep. 1969 (fr), *Contreras 9099* (MO); vic. Quiriguá, 75–225 m, 15–31 May 1922 (fl), *Standley 23922* (GH, US); *Standley 24248* (GH, US); seashore around Punta Palma, across bay from Puerto Barrios, 22 Apr. 1940 (st), *Steyermark 39830* (F). PETÉN: San Clemente to Dos Arroyos, 1 May 1931 (fl), *Bartlett 12819* (F, US); Tikal, on top of Temple IV, 28 June 1960 (fl), *Contreras 1192* (DUKE, F, NY); La Cumbre, W of km 139 on Cadenas Road, 23 Sep. 1966 (fr), *Contreras 6198* (F, NY); Carmelita, in thicket bordering aviation field, 2 July 1942 (fr), *Egler 42-302* (F); Tikal National Park, Bajo del Hormiguero, 6 July 1959 (fl, fr), *Lundell 16214* (DUKE, MEXU, NY); km 62 of Flores–Poptún Rd., 16 Sep. 1976 (fr), *Lundell & Contreras 20369* (MO); +35 km E de Sta. Elena, brecha El Remate-Tikal, 200 m, 9 Nov. 1965 (fr), *A. Molina R. 15443* (F, NY, US); sitio arqueológico en el camino que conduce a cienaga "Bajo la Juventud," km 10 lado E de la aldea Uaxactún, 26 May 1973 (fl), *Ortíz 2655* (ENCB, F, MO, NY). BELIZE. BELIZE: Gracie Rock, 8 June 1974 (fl), *Dwyer 12787* (MO, US); Maskall, Nov. 1933 (fr), *Gentle 946* (A, F, MO, NY); 9 Apr. 1934 (fl), *Gentle 1188* (A, F, GH, K—2 sheets, MO, NY, US); Isabella Pine Ridge, June 1933 (fl), *Lundell 4243* (F); nr. Manatee Lagoon, pine ridge, 9 June 1905 (fl), *Peck 23* (GH, K). CAYO: Duck Run, 11 May 1931 (fl), *Bartlett 13122* (F, K); vic. Cuevas S of Millionario, 600 m, 29–30 May 1973 (fl), *Croat 23589* (F, MO); Mountain Pine Ridge, San Agustín, banks of Río Frío, July–Aug. 1936 (fr), *Lundell 6702* (F, GH, NY, US). COROZAL: 1.5 km N of Buena Vista, 1.5 km W of Northern Highway on secondary rd., 23 June 1973 (early fr), *Dwyer 11373A*

(F, MO, NY); Corozal–Consejo rd., Aug. 1933 (fr), *Gentle 4913* (NY). ORANGE WALK: Mile 50 Northern Highway to New River Toll Bridge, 7 June 1974 (fl), *Dwyer 12746* (GH, MO—2 sheets); Honey Camp, 19 Oct. 1929 (fl, fr), *Lundell 617* (F, GH, K, MO—2 sheets, NY, US). STANN CREEK: Silk Grass Creek Reserve, 20 Sep. 1939 (fr), *Gentle 3002* (A, F, K, MEXU, NY); Stann Creek Valley, Big Eddy Ridge, 6 Apr. 1941 (fl), *Gentle 3546* (A, MO, NY); Mullins River Rd., swampy places, 30 m, 1 June 1929 (fl), *Schipp 204* (A, F, GH, K, MO, NY, US). TOLEDO: San José, 6.7 mi. N of Columbia Forest Station, 13 June 1973 (fl), *Dwyer 11150* (MO); Río Temash, between 3 km upriver and mouth, 26 July 1979 (fr), *Dwyer 14779* (MO); Monkey River, 25 Aug. 1941 (fr), *Gentle 3600* (A, K, MO, NY, US); mi. 13 on rd. W from Punta Gorda, nr. junction of Southern Hwy. and rd. to San Antonio, 30 m, 14 June 1973 (fl), *Gentry 8212* (DUKE, MO). HONDURAS. COMAYAGUA: 3 km S of Siguatepéque, 1,300 m, 9 Jan. 1969 (fr), *A. Molina R. 23303* (F, NY). COPÁN: Qda. La Honduras, 2 km NO de Santa Rosa de Copán, 1,000 m, 15 Feb. 1982 (fr), *Mejía 124* (TEFH). FRANCISCO MORAZÁN: 1 km from Agalteca, 800 m, 22 Nov. 1966 (fr), *A. Molina R. 18705* (F, NY). GRACIAS A DIOS: Puerto Lempira, orilla laguna de Caratusca, 5–8 Sep. 1978 (fr), *C. Nelson 4828* (TEFH); camino entre Dursuna y Mocorón, 70 m, 14–21 Feb. 1979 (fr), *C. Nelson & Vargas 4906* (TEFH). LA PAZ: Agua Blanca River between Chinacla and Planes de Mulle, 1,300 m, 22 Mar. 1969 (fr), *A. Molina R. & A. Molina 24350* (F—2 sheets, NY). LEMPIRA: aguas termales, 4 km de Gracias, 1,000 m, 7–9 Dec. 1971 (fr), *C. Nelson et al. 91* (MO). OCOTEPEQUE: between El Agua Caliente and Machuca, hwy. to Guatemala–Honduras border, 1,000 m, 4 Sep. 1975 (fr), *A. Molina R. & A. Molina 31091* (ENCB, F, MO). SANTA BARBARA: al N de Sta. Barbara, región La Cuesta, 500 m, 13 Dec. 1950 (fr), *A. Molina R. 3784* (F, GH). NICARAGUA. CHONTALES: Hda. Corpus, W of Juigalpa, 12°07′N, 85°28′W, 100 m, 5 Sep. 1982 (early fr), *W. D. Stevens 21782* (MO). MATAGALPA: 7 km al SO de Buenavista, carret. a Matagalpa, 13°15′N, 85°24′W, 300–440 m, 1 Mar. 1983 (fr), *P. P. Moreno & Robleto 21016* (MO); Hda. Sta. María de Ostuma, 1,300–1,600 m, 17 Jan. 1977 (st), *Tomlin 145* (MO). RIVAS: Isla de Ometepe, al lado N del Volcán Concepción, 11°34′N, 85°37′W, 250–350 m, 12 Mar. 1981 (fr), *Sandino 545* (MO). ZELAYA: Prinzapolka, 23 June 1978 (fr), *Neill 4551* (MO); Caño El Hormiguerro, on E slope of El Hormiguerro, 13°46′N, 84°59′W, 750–800 m, 17 Mar. 1980 (fr), *Pipoly 6104* (MO); nr. Tala Has and Puente Mango, over Río Kisalaya, 14°41′N, 84°03′W, 40–60 m, 18 Apr. 1978 (fl), *W. D. Stevens 7597* (MO); rd. to Panua, entrance ca. 7.6 km NW of Sta. Marta, 4.2–5.0 km from main rd., 14°18′N, 83°41′W, 30–40 m, 20 Apr. 1978 (fl), *W. D. Stevens 7761* (MO); SW of Bluefields, 11°59′N, 83°46′W, 10–40 m, 2–3 Apr. 1981 (fl), *W. D. Stevens 19836* (MO); vic. jct. of rd. to Alamikamba with rd. between El Empalme and Limbaika, 13°32′N, 84°30′W, 25 m, 4 July 1982 (fl, fr), *W. D. Stevens 21675* (MO); 4 km N of Puerto Cabezas, 10–20 m, 11 June 1978 (fr), *Vincelli 533* (MO). PANAMA. CANAL AREA: Ancón Hill, 25 Feb. 1923 (fr), *Piper 5554* (US). PANAMÁ: nr. Calzada Larga, swampy area over exposed limestone, 27 Sep. 1970 (fl, fr), *Croat 12389* (F, GH, MO, NY); San José Island, Perlas archipelago, 13 June 1945 (fl), *Erlanson 279* (GH, NY, US); 8 Jan. 1946 (fl, early fr), *I. Johnston 1071* (GH, MO, US); along Río Tocumen, N of Chepo rd., 0–30 m, 27 Jan. 1935 (fl), *Hunter & Allen 240* (MO); southern tip of Isla de Rey, Punta de Cocos, 8°17′N, 78°55′W, 0–20 m, 19 Jan. 1982 (fl, fr), *Knapp & Mallet 2948* (MO). SAN BLAS: mainland opposite Isla Mosquito (Kwitupu), 19 Oct. 1966 (fr), *Duke 8989* (MO—2 sheets).

Psychotria fruticetorum may be recognized by its small leaves (usually 5–7 × 2–4 cm) drying chalky yellow-green to red-brown with barely elevated secondary veins and inconspicuous tertiaries, its small inflorescences (1.5–4.5 cm long) with secondary axes usually 2 per rank in 3–4 ranks, and small (4–5 × 3–3.5 mm) ellipsoid fruit. Mexican collections differ from those from the rest of the range in having generally smaller leaves, 5 vs. 6–7(8) secondary veins, and a higher fruit length-to-diameter ratio.

The exserted pistil of the pin morph is often longer than the exserted stamens of the thrum (3.5–5 vs. 3.5–4 mm).

33. Psychotria jinotegensis Nelson, Molina & Standley, Phytologia 50: 1. 1981. TYPE: Nicaragua. Jinotega: region of La Montañita and Las Mesitas, in sierra W of Jinotega, ca. 1,100–1,400 m, 29 June 1947 (fl), *Standley 10314* (holotype, EAP, n.v.; isotype, F, n.v.). Figures 9d, 26.

Shrub (0.5–)1–4(–6) m tall; young stems ferrugineous-pubescent or very sparsely tomentose, the bark smooth; stipules sheathing, ovate to linear, 15–23 × 4–6 mm, usually ferrugineous-pubescent, caducous, leaving a pale ridge with dark red-brown fringe. *Leaves* petiolate; petioles 0.5–1.5 cm long, pubescent or glabrous, flat above; blades membranous, elliptic to oblanceolate, the apex acute or sometimes acuminate, the base attenuate, (7–)9–14(–15.5) × (2–)2.5–4.5(–5.5) cm, pale tomentose or glabrous above, densely pubescent or glabrous below, drying gray-green to red-brown; secondary veins 9–14 pairs, diverging 40°–50°, eucamptodromous to brochidodromous, straight then arcuate near margin, elevated below, pubescent or glabrous below, the axils with tufts of hairs below; tertiary veins evident, orthogonal reticulate to slightly percurrent. *Inflorescences* terminal or pseudoaxillary, few-branched panicles of condensed cymes; panicle branched to 3–4 degrees; main axis (2.5–)4–6.5 cm long, the peduncle lacking or to 1(–3) cm long; secondary axes in (2–)3 ranks, the first-rank axes 1–2, (1–)1.5–5 cm long, the second-rank axes 2, 0.5–2.5 cm long, the third-rank axes 2(4), the longer pair 0.2–0.8 cm long, the shorter pair when present 0.1 cm long; cymes branched to (1)2 degrees; bracts and bracteoles

linear, 1.5–3 mm long; usually ferrugineous-pubescent. *Flowers* sessile or on pedicels to 1.5 mm long; calyx cup-shaped, the tube cylindrical, 0.5–1 mm long, the lobes 5–6, triangular, 0.5–1 × 0.7 mm, puberulent; corolla white, the tube cylindrical to campanulate, 3.5–4 × 1.5–2 mm, white pubescent in throat, the lobes 5–6, 1.5–2.5 × 1.2 mm; stamens 5–6, the filaments 3 mm long in pins, 5–5.5 mm long in thrums, the anthers 1 mm long; style 5 mm long in pins, 3–4 mm long in thrums, the branches linear. *Fruit* when dry ellipsoid, (5–) 5.5–6.5 mm long, 4–5 mm diam., maturing red, drying red-brown, ferrugineous-pubescent or glabrous; persistent calyx conspicuous, 1–3 mm long (Fig. 9d); seed dorsal surface with 6–8 irregular longitudinal furrows, the ventral surface with 2 deep regular plus several irregular longitudinal furrows.

Distribution (Fig. 26). Known from southeastern Guatemala through northwestern Nicaragua in tropical moist forest with tropical to tropical-mountainous climate.

Psychotria jinotegensis may be recognized by its usually ferrugineous aspect, elliptic to oblanceolate leaves with secondary veins diverging 40°–50°, and ellipsoid fruit with conspicuous (1–3 mm long) persistent calyx tube.

KEY TO THE VARIETIES OF *PSYCHOTRIA JINOTEGENSIS*

1a. Ferrugineous-pubescent and/or tomentose on young stems, both leaf surfaces, and on dry fruit; secondary vein axils with tufts of reddish hairs ..... 30a. var. *jinotegensis*
1b. Generally glabrous or only sparsely tomentose; secondary vein axils with tufts of white hairs ..... 30b. var. *morazanensis*

33a. Psychotria jinotegensis Nelson, Molina & Standley var. **jinotegensis.** Figure 26.

Shrub; young stems ferrugineous-pubescent. *Leaves:* petioles ferrugineous-pubescent; blades pale tomentose above, densely ferrugineous-pubescent below, drying green-brown to deep red-brown; secondary veins (9–)10–14 pairs, ferrugineous-pubescent, the axils with tufts of reddish hairs below. *Fruit* when dry ferrugineous-pubescent.

Distribution (Fig. 26). Known from southeastern Guatemala eastward across southern Honduras and northern El Salvador to northwestern Nicaragua at elevations of 1,000–2,000 m. It has been collected in flower June–July and December–February and in fruit August–February.

Selected specimens examined. GUATEMALA. BAJA VERAPAZ: Unión Barrios, 27 Feb. 1972 (fr), *Contrereas 11062* (MO); along hwy. to Cobán, ca. 1.5 km S of turnoff to Salamá, pine forest, 1,300 m, 16 July 1977 (early fr), *Croat 41138* (MO); nr. La Unión (Barrios), Sierra de las Minas, 1,800 m, 18 Jan. 1974 (fl, fr), *L. O. Williams et al. 43559* (F). CHIQUIMULA: Montaña Nonojá, 5–8 km E of Camotán, 600–1,800 m, 11 Nov. 1939 (fr), *Steyermark 31675* (F). EL PARAISO: between Calera and middle slopes of quebradas of Volcán Siglo, 2,000–2,200 m, 20 Jan. 1942 (fr), *Steyermark 42992* (F, US). HONDURAS. COMAYAGUA: ravine nr. El Achote, hills above plains of Siguatepeque, 1,350 m, 30 July 1936 (early fr), *Yuncker et al. 6229* (F, GH, K, MO). DISTRITO CENTRAL: 2.5 km N of Zambrano along rd. to San Francisco de Soroguara, 1,370 m, 1 July 1970 (fl), *Davidse & Pohl 2245* (F, MO, NY); nr. Zambrano, 26 Sep. 1969 (fr), *Lauvert & Barkley 39552* (MO, TEFH); San Matías NO de Tegucigalpa, 1,400 m, 25 Sep. 1983 (fr), *Paredes 97* (TEFH). EL PARAISO: drainage of Río Yeguare, márgenes del Río Lizapa entre Guinope y Las Casitas, 1,300 m, 1 Nov. 1950 (fr), *A. Molina R. 3357* (MO); Francisco Morazán, Cerro Canta Gallo, 14 km NE de Tegucigalpa, 1,046 m, 2 Oct. 1983 (fr), *M. Castro M. 83* (TEFH); along Río Rancho Quemado, S of Tegucigalpa, km 20–25 on rd. to Sabana Grande, 1,300 m, 9 Nov. 1966 (fr), *A. Molina R. 18648* (GH, NY). INTIBUCÁ: 2 km de La Esperanza, orillas de La Pozona, 28 June 1974 (fl), *J. Martínez & Bejarano 236* (TEFH). EL SALVADOR. CHALATENANGO: S del Río Nomiapa, La Palma, 1,100 m, 6 July 1976 (early fr), *Montalvo 4695* (MO). NICARAGUA. JINOTEGA: sierra W of Jinotega, trail to Cerro de la Cruz, 1,050–1,350 m, 27 June 1947 (fl), *Standley 10214* (F).

33b. Psychotria jinotegensis Nelson, Molina & Standley var. **morazanensis** C. Hamilton, Phytologia 64: 226. 1988. TYPE: El Salvador. Morazán: easternmost peak, Montes de Cacaguatique, nr. summit on N side, 13°46′N, 88°13′W, 1,500 m, 25 Dec. 1941 (fr), *Tucker 610* (holotype, US: isotypes, F, K, NY). Figure 26.

Shrub; young stems very sparsely tomentose. *Leaves:* petioles glabrous; blades glabrous above and below, drying gray-green to pale red-brown; secondary veins 9–11 pairs, glabrous, the axils with tufts of whitish hairs below. *Fruit* glabrous when dry.

Distribution (Fig. 26). Known only from the type collection from eastern El Salvador, at ca. 1,500 m. This variety was collected in fruit December 25.

34. Psychotria mirandae C. Hamilton, Phytologia 64: 229. 1988. TYPE: Mexico. Chiapas: Berriozábal a Las Vistas, 17 July 1949 (fl), *Miranda 5395* (holotype, US; isotype, MEXU). Figure 27.

Shrub ca. 1 m tall; young stems red-brown tomentose, the bark pale, smooth; stipules sheath-

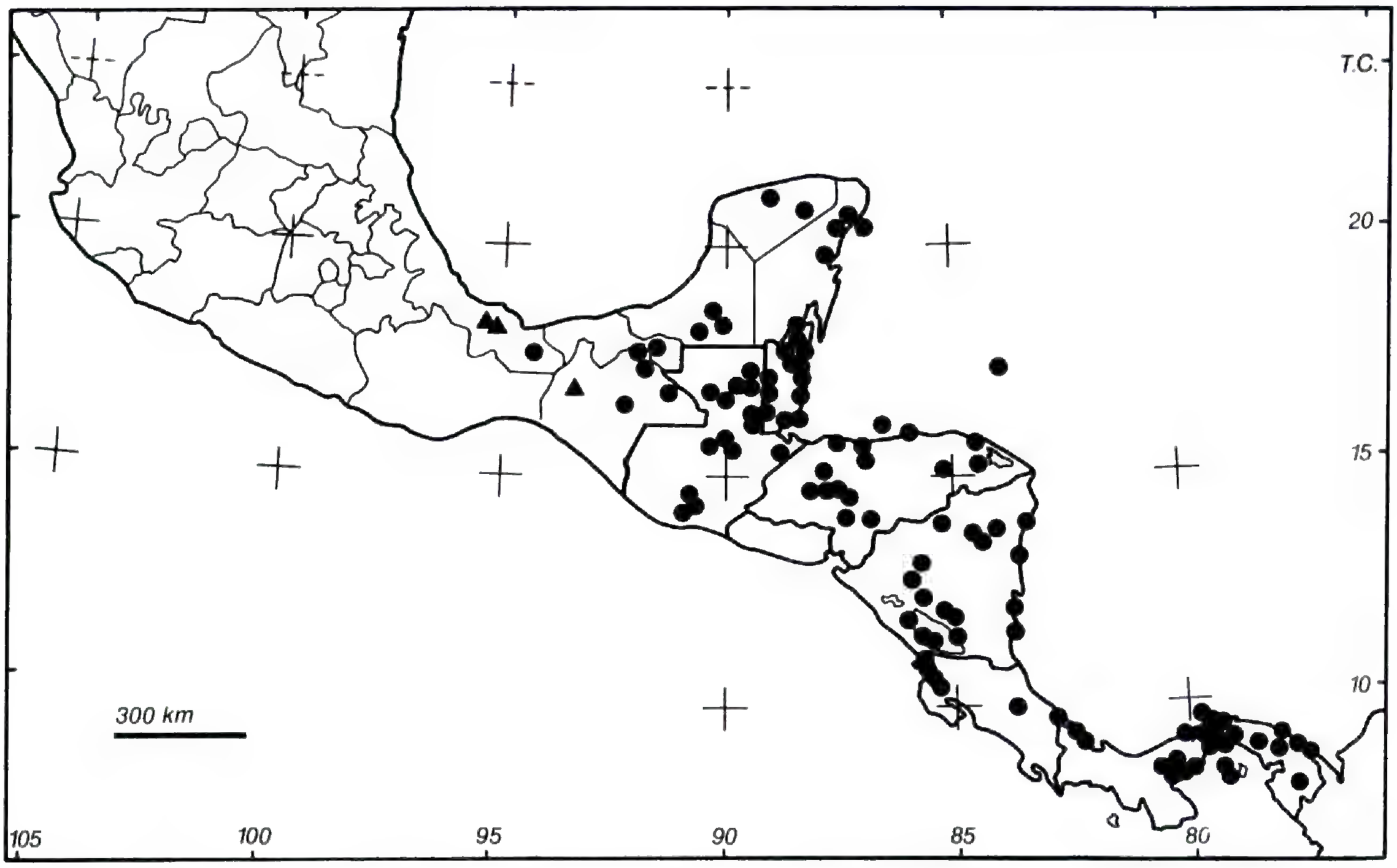

FIGURE 27. Distributions of *Psychotria mirandae* (triangles) and *P. nervosa* (circles) in Mesoamerica.

ing, rounded at apex, 4–8 × 3–4 mm, red-brown tomentose outside, caducous, leaving a pale ridge. *Leaves* subsessile to petiolate; petioles 1–4 mm long, red-brown tomentose, furrowed above; blades membranous, narrowly obovate, the apex caudate, the base attenuate, 6–12 × 2–4 cm, glabrous above and below, drying dull red-brown; secondary veins 7–10 pairs, diverging 48°–55°, eucamptodromous, slightly arcuate, prominent below, red-brown sparsely tomentose below, the axils with small tufts of hair below; tertiary veins evident, reticulate to slightly percurrent. *Inflorescences* terminal, fascicles of flowers or with several short axes, 1–1.5 cm long, 1–2.5 cm across; peduncle lacking; bracts triangular, 0.5 × 0.5 mm, glabrous to sparsely tomentose. *Flowers* subsessile, the pedicels 1–2 mm long; calyx cylindrical, the tube 2–2.5 mm long, the lobes 5, linear, 2–3 × 1.2 mm, sparsely ciliate on margin; corolla white(?), the tube cylindrical, 3 × 1 mm, white pubescent in throat, the lobes 5, linear, 1.5–2 × 0.5 mm; stamens 5, the filaments not seen in pins, 4 mm long in thrums, the anthers 0.8 mm long; style not seen in pins, 2.5–3 mm long in thrums, the branches club-shaped. *Fruit* ellipsoid when dry, 5–7 mm long, 4–5 mm diam., maturing red, drying red-brown, red-brown tomentose; calyx persistent, the tube 2–2.5 mm long, the lobes ca. 2 mm long; seed dorsal surface with 5 longitudinal furrows, the ventral surface with 2 longitudinal furrows.

Distribution (Fig. 27). Limited to eastern Veracruz and northwestern Chiapas, Mexico, at 700–1,000 m elevation in evergreen forest with equatorial-tropical to tropical climate. It has been collected in flower in March and May–July and in fruit in August and December.

Additional specimens examined. MEXICO. CHIAPAS: Mpio. Berriozábal, 13 km N of Berriozábal nr. Pozo Turipache and Finca El Suspiro, 900 m, 15 May 1973 (fl), *Breedlove 35316* (MEXU); Cerro de San Martín, Mar. 1845 (fl), *Galeotti 2684* (F—3 sheets, US); Berriozábal a Las Vistas, 4 Dec. 1949 (fr), *Miranda 5834* (MEXU, US); San Fernando, Predio del Rosario, 21 June 1951 (fl), *Miranda 7216* (MEXU). VERACRUZ: Mpio. Catemaco, cerro entre Zapoapan y San Juan Seco al SW de Lago Catemaco, 700 m, 7 June 1972 (fl), *Beaman 6094* (F, MEXU—2 sheets); region of San Andrés Tuxtla, nr. Zapoapan, SE of Catemaco, 17 Aug. 1953 (fr), *Dressler & Jones 93* (GH, NY, US); Catemaco, 25 Mar. 1956 (fl), *Paray 1946* (ENCB); km 156.5 of Veracruz–Coatzacoalcos rd., 13 July 1974 (fl), *Sohmer 9409* (MEXU).

Psychotria mirandae may be recognized first by its marked resemblance to *P. nervosa* and second by its contracted (sometimes contracted to fascicles of flowers) inflorescences and wider (4–5 mm vs. 2.5–3 mm diam. in *P. nervosa*) fruit with persistent calyx having a conspicuous tube and lobes ca. 4 mm long.

The seven flowering collections examined are all of the thrum morph, which suggests strongly that the species is thrum-monomorphic.

35. Psychotria nervosa Swartz, Prodr., 43. 1788. TYPE: Jamaica. (fl), *Swartz s.n.* (holotype, S, n.v., photo, A). Cf. also Swartz, Fl. Ind. Occid., 403. 1797. Figure 27.

Psychotria undata Jacquin, Pl. Hort. Schoenbr. 3: 5, pl. 260. 1798. *Uragoga undata* (Jacq.) Baill., Hist. Pl. 7: 371. 1880. *Uragoga undata* (Jacq.) Kuntze, Revis. Gen. Pl. 2: 958. 1891. *Myrstiphyllum undatum* (Jacq.) Hitchc., Annual Rep. Missouri Bot. Gard. 4: 95. 1893. TYPE: Bahamas. July–Aug. (fl), Coll. ign. (n.v.).

Psychotria rufescens Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 3: 364. 1819. *Uragoga rufescens* (Kunth) Kuntze, Revis. Gen. Pl. 2: 962. 1891. *Psychotria nervosa* subsp. *rufescens* (Kunth) Steyerm., Mem. New York Bot. Gard. 23: 480. 1972. Non *Psychotria rufescens* Roem. & Schultes (which is a synonym of *Psychotria micrantha* Kunth), Syst. Veg. 5: 192. 1819. TYPE of *P. rufescens* Kunth: Peru? (holotype, P, n.v.).

Psychotria hirta Roemer & Schultes, Syst. Veg. 5: 191. 1819. *Psychotria nervosa* subsp. *rufescens* var. *hirta* (Roem. & Schultes) Steyerm., Mem. New York Bot. Gard. 23: 481. 1972. TYPE: Colombia. Quindiu, *Humboldt & Bonpland s.n.* (holotype, B—Willdenow 4092, photo F neg. 550).

Psychotria oligotricha A. P. de Candolle, Prodr. 4: 514. 1830. *Uragoga oligotricha* (DC.) Kuntze, Revis. Gen. Pl. 2: 961. 1891. TYPE: Insular Caribbean. 1822 (fl), *Balbis s.n.* (holotype, G, n.v., photo, F neg. 33534).

Psychotria chimarrhoides A. P. de Candolle, Prodr. 4: 514. 1830. TYPE: Cuba. 1829 (fl), *Sagra 289* (holotype, G, n.v., photo, F neg. 33535).

Psychotria portoricensis A. P. de Candolle, Prodr. 4: 515. 1830. TYPE: Puerto Rico. 1820 (fl), *Bertero s.n.* (holotype, G, n.v., photo, F neg. 33537).

Psychotria elongata Bentham in Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 32. 1853. TYPE: Nicaragua. Granada: Volcán Mombacho, June 1846 (early fr), *Oersted 11594* (holotype, C, n.v., photo, F neg. 22829, photo & fragment, US).

Psychotria quiinifolia Dwyer, Ann. Missouri Bot. Gard. 53: 108. 1966. TYPE: Panama. Bocas del Toro: Almirante, Changuinola Canal, (fl), *Blum 1402* (holotype, MO).

Shrub 0.5–2(–3) m tall; young stems ferrugineous-tomentose to sometimes glabrous, the bark smooth; stipules sheathing, rounded-ovate, sometimes short-acuminate, 6–11 × 3–6 mm, ferrugineous-pubescent to glabrous, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 0.3–1.2(–2.5) cm long, ferrugineous-pubescent to glabrous, grooved above; blades membranous, oblanceolate to rarely elliptic, the apex long-acuminate, the base attenuate, (6–)11–17(–18) × (2–)4–6.5(–7.5) cm, sparsely tomentose to sometimes glabrous above and below, usually denser below, the midvein usually ferrugineous-pubescent, the margin often red-brown ciliate, drying pale red-brown to green-brown, the veins usually drying reddish; secondary veins (10–)12–17 pairs, diverging 55°–65°, eucamptodromous to brochidodromous, increasingly arcuate toward margin, elevated below, sparsely ferrugineous-pubescent, the axils lacking domatia or hairs or rarely with fascicles of several red-brown hairs; tertiary veins inconspicuous to evident, orthogonal reticulate to percurrent. *Inflorescences* terminal or pseudoaxillary, panicles of cymes, the cymes often contracted; panicle branched to 3 degrees; main axis 1–4(–5) cm long, the peduncle lacking; secondary axes in 3(4) ranks, the first-rank axes 2(4), equal, 0.8–2.5(–4) cm long, the second-rank axes (1)2(3), equal, 0.6–1.5 cm long, the third-rank axes 2, equal, 0.2–0.7 cm long, the fourth-rank axes 2, equal, 0.2 cm long; cymes branched to 2–3 degrees; bracts and bracteoles triangular, inconspicuous, to 0.5 mm long, ferrugineous-pubescent. *Flowers* sessile to subpedicellate, the pedicels to 0.5 mm long; calyx cup-shaped, the tube 0.3–0.5 mm long, the lobes 5, triangular to not evident, to 0.2 mm long, puberulent; corolla white, the tube cylindrical, 2–3 × 1 mm, white pubescent in throat, often puberulent without, the lobes 5, lanceolate, 1.5 × 0.8 mm; stamens 5, the filaments 1.5–2.5 mm long in pins, 3.5–5 mm long in thrums, the anthers 0.7–1 mm long; style 4–5 mm long in pins, 2–2.5 mm long in thrums, the branches short, clublike. *Fruit* narrow ellipsoid, 5.5–7 mm long, 2.5–3 mm diam., maturing red, drying red-brown, usually red-brown puberulent; persistent calyx inconspicuous or a minute beak; seed dorsal surface with 4–5 longitudinal furrows, the ventral surface with 2 sometimes incompletely divided longitudinal furrows.

Distribution (Fig. 27). Ubiquitous, from southern Mexico and the Yucatán peninsula through Panama, most common on the Caribbean coast, at 0–1,200 m elevation in tropical moist to premontane moist to sometimes tropical dry forest with equatorial to tropical (usually equatorial-tropical) climate. It occurs also in Florida, the Bahamas, throughout the Greater and Lesser Antilles, Colombia, and Venezuela. It has been collected in flower throughout the year, primarily February–June in Mexico–Costa Rica and throughout the year in Panama, and in fruit throughout the year.

Selected specimens examined. MEXICO. CAMPECHE: 28 km al N de Escárcega, rumbo a Champotón, 7 Mar. 1982 (fl), *Cabrera et al. 2037* (MEXU); Campo Experimental Forestal Tropical "El Tormento," km 5 carr. Escárcega a Candelaria, 4 Jan. 1966 (st), *Chavelas et al. ES-1247* (MEXU); Tuxpeña, 23 Feb. 1932 (fl), *Lundell 1373* (F, US). CHIAPAS: a lo largo de las cascadas

de Agua Azul, a 60 km al N de Palenque, 3 Mar. 1982 (fr), *Cabrera et al. 1875* (ENCB, MEXU); along Hwy. 199 at Chital, 9 mi. SW of Ocosingo, 1,190 m, 7 July 1977 (fl), *Croat 40371* (MO); 17 km SE of Palenque on road to Bonampak, ejido León Brindis, 300 m, 12 May 1982 (fl), *Davidse et al. 20385* (MO); Mpio. de Ocosingo, Centro Arqueológico Bonampak, 350 m, 24 Dec. 1981 (fr), *Meave et al. B-128* (MEXU). QUINTANA ROO: 1 km NW of Puerto Morelos, Campo Agropecuario del Centro de Investigaciones de Quintana Roo, 5 m, 4 May 1982 (fl), *Davidse et al. 20033* (MO); 5 km al W de Vigia Chico, 13 June 1983 (fl), *Durán & Olmsted 126* (MEXU); Isla de Cozumel, 24 May 1977 (fr), *L. A. Pérez J. & Ramos 1620* (ENCB, MEXU); 1 km al N de Playa del Carmen, 9 Mar. 1980 (fl), *Tellez & Cabrera 1807* (MEXU). TABASCO: Balancán, San Isidro, 7–11 June 1939 (fl), *Matuda 3366* (F, GH, K, MEXU, MO, NY). VERACRUZ: Mpio. Minatitlán, 6.9 km al N de la terraceria La Laguna–Río Grande, una depresión kárstica, 120 m, 12 July 1980 (fl), *Wendt et al. 2534* (ENCB, MEXU). YUCATÁN: Chichen Itza, 28 June 1929 (fl), *Bequaert 101* (F, GH); Izamal, (fl), *Gaumer 974* (A, F—2 sheets, GH, US). GUATEMALA. ALTA VERAPAZ: Semococh, 17 km from Sebol, on Cobán Road, 17 May 1964 (fr), *Contreras 4708a* (F); SW of Languín, vic. caves, 600–1,000 m, 21 Feb. 1942 (st), *Steyermark 44127* (F, GH); 1.5–2 mi. S of Cubilgüitz, 300–350 m, 1 Mar. 1942 (fr), *Steyermark 44433* (F). ESCUINTLA: 8 km S of Palín, 8 July 1970 (early fr), *Harmon & Dwyer 2960* (MO); between Río Jute and Río Pantaleón, on rd. between Esquintla and Santa Lucía Cotz, 540–720 m, 24 Jan. 1939 (fr), *Standley 63602* (F, NY). IZABAL: between Bananera and "La Presa" in Montaña del Mico, 40–300 m, 28 Mar. 1940 (fl), *Steyermark 38056* (F). PETÉN: La Libertad and vicinity, 15 May 1934 (fl), *M. Aguilar H. 292* (F, GH, MO); Tikal, on top of Temple V, 11 June 1960 (fl), *Contreras 1077* (DUKE, F, NY); 8 July 1959 (fr), *Lundell 16253* (F, LL, NY); Dolores, bordering Arroyo Ixcol, 14 Apr. 1961 (fl), *Contreras 2070* (DUKE, LL, NY); La Cumbre, km 139–140 of Cadenas Rd., in swamp, 20 Sep. 1966 (fr), *Contreras 6159* (DUKE); nr. archaeological camp on N shore of Lake Yaxja, 150 m, 18 June 1973 (fl), *Croat 24668* (GH, MO, NY); bordeando Lago Petén Itzá, en San Miguel, 21 Jan. 1969 (fl), *Ortíz 124* (ENCB, F, MO, NY); San Luis, en orillando el camino para Poptún, a km 116, 6 Dec. 1970 (fr), *Ortíz 1482* (DUKE, F, MO); Santa Elena, en la orilla del camino para San Francisco, a km 14, 28 June 1971 (early fr), *Ortíz 1859* (ENCB, F, MO, NY); sitio arqueológico en el camino que conduce a cienaga "La Juventud," km 8.5 E de la aldea Uaxactún, 26 May 1973 (early fr), *Ortíz 2657* (F, MO, NY, US). SACATEPÉQUEZ: nr. Las Lajas, ca. 1,200 m, 28 Nov. 1938 (fl), *Standley 58081* (F). BELIZE. BELIZE: along Northern Hwy., vic. Maskall River, 6 June 1973 (early fr), *Croat 23930* (MO); Sibun River 1.5 km in from mi. 34.5 on Western Highway, 5 July 1973 (early fr), *Dwyer 11491* (DUKE, MO); Big Fall, 21 Mar. 1933 (fl), *Lundell 4159* (F, MEXU); forest nr. Manatee Lagoon, 25 Mar. 1906 (fl), *Peck 385* (GH, K). CAYO: El Cayo, river bluffs, 13 Feb. 1931 (fl), *Bartlett 11435* (F, K, US); bordering Río Mopan, Sucotz, 14 Oct. 1967 (fr), *Contreras 7128* (MEXU, NY). COROZAL:Corozal–Consejo road, Aug. 1933 (fr), *Gentle 4862* (A, GH, MO, NY). ORANGE WALK: Indian Church, Sawmill Rd., 12 May 1977 (fl), *Arnason & Lambert 17293* (MO); nr. Honey Camp, 1930 (fr), *Meyer 98* (F). STANN CREEK: Sittee River, secondary forest, 5 m, 11 Sep. 1930 (fr), *Schipp 644* (A, F, GH, K, MO, NY). TOLEDO: Columbia Forest Station, 24 June 1972 (fr), *Dwyer 9843* (MO, US); Punta Gorda, 1 Aug. 1980 (fr), *Dwyer 15166* (MO); Nicolas Cay, 5 July 1972 (early fr), *Spellman & Stoddart 2341* (MO). HONDURAS. ATLANTIDA: nr. La Ceiba, 0 m, 11 Mar. 1928 (fl), *Standley 56733* (A, F, US); nr. Tela, sandy soil nr. beach, 20 July 1934 (fl, early fr), *Yuncker 4664* (A, F). COLÓN: N bank of Río Guaimoreto between old bridge and opening of Laguna Guaimoreto, 7.5 km NE of Trujillo, 15°57′N, 85°54′W, 20 Feb. 1981 (fl), *Saunders 1039* (MO). COMAYAGUA: Esquias, 75 km NE of Comayagua, 550 m, 28 Dec. 1981 (fr), *A. Hernández O. 132* (TEFH); colinas rocosas de los alrededores de La Libertad, 400 m, 21 May 1956 (fl), *A. Molina R. 7068* (F, GH, US); villa de Taulabé, qda. La Caliche, 600 m, 21 Apr. 1978 (fl), *Trochez 41* (MEXU, MO). DISTRITO CENTRAL: Tegucigalpa, Mont. de la Flor, 950 m, Dec. 1937 (st), *Hagen & Hagen 1194* (F, NY). EL PARAISO: matorrales de la Qda. El Coyol entre El Junquillo y El Robledal, 1,300 m, 12 June 1964 (fl), *A. Molina R. 14185* (F, NY). FRANCISCO MORAZÁN: 5 km O de Cedros, pinares, orillas de riachuelo Chimbo, 900–1,000 m, 28–30 May 1976 (fl), *C. Nelson & Vargas 3456* (TEFH). GRACIAS A DIOS: nr. Wampusilpi, nr. Río Patuca, 30 Aug.–2 Sep. 1973 (fr), *Clewell 4554* (MO, TEFH); Cocobila, coastal thicket, 0 m, 9 Feb. 1981 (fl), *Proctor 38954* (TEFH). ISLAS DE LA BAHIA: Isla de Roatan, Aug. 1886 (fl), *Gaumer 127* (US). ISLAS DEL CISNE: larger island, 14 Apr. 1913 (st), *G. Nelson 12* (GH, US—2 sheets). OLANCHO: vaguada del río de la población de Culmí, 500 m, 17–22 July 1978 (fr), *C. Nelson & Romero 4640* (MO). YORO: Santa Rita, orillas del Río Humuya, 23 Apr. 1971 (fl), *Mancías & J. Hernández 1138* (MO, TEFH); Aguan River valley, vic. Coyoles, 300 m, June–Aug. 1938 (early fr), *Yuncker et al. 8173* (F, GH, K, MO, NY, US). NICARAGUA. BOACO: NE de Mombachito, 11 May 1982 (fl), *Sandino 2837* (MO). CHONTALES: 2 km al N de Santo Tomas, carret. a Santo Domingo, 12°04′N, 85°06′W, 340–380 m, 30 Apr. 1982 (fl), *P. P. Moreno 16224* (MO); E of El Narajal, between Juigalpa and La Libertad, ca. 12°11′N, 85°15′W, 500 m, 6 Aug. 1983 (fl, early fr), *W. D. Stevens 22435* (MO). JINOTEGA: Salto Kayaska, Río Bocay, 13°51′N, 85°22′W, 190–340 m, 7 Mar. 1980 (fl), *W. D. Stevens et al. 16569* (MO). MATAGALPA: entre las fincas La Castilla y Sta. Basilia, bordeando las márgenes del Río Yasica, 13°01′N, 85°46′W, 400 m, 19 Jan. 1982 (fr), *D. Castro 2264* (MO); Mt. Yasica, 26 km S of Matagalpa, rd. to El Tuma, 400 m, 10 Mar. 1967 (fl), *A. Molina R. 20466* (F, NY, US). RÍO SAN JUAN: San Miguelito, drenaje del Lago Granada, 30 m, 13 Nov. 1951 (fr), *Shank & Molina 4564* (F, GH). RIVAS: Isla Ometepe, faldas del Volcán Maderas al S de la Hda. Magdalena, 11°27′N, 85°30′W, 300–900 m, 28 Nov. 1982 (fl), *P. P. Moreno 18846* (MO); Isla de Ometepe, N de Volcán Concepción, entrada a Los Angeles, 11°33′N, 85°37′W, 480 m, 10 Mar. 1981 (fl), *Sandino 483* (MO). ZELAYA: Puerto Isabel, nr. seabeach, 4 Jan. 1970 (fl), *Atwood & Seymour 2990* (MO—3 sheets); 1.5 km al NW de Monkey Point, 11°36′N, 83°38′W, 1–5 m, 21 Oct. 1981 (fl), *P. P. Moreno & Sandino 12008* (MO); Cerro Kana Coperna, 30 km E of Siuna, 250 m, 17 June 1978 (fl), *Neill 4520* (MO); Cerro Waylawás, summit of northern range, 13°39′N, 84°49′W, 260–268 m, 12 Mar. 1979 (fr), *Pipoly 4507* (MO); El Falso Bluff a E de El Bluff, 11°59′N, 83°41′W, 30 m, 2 Feb. 1982 (fl), *Sandino 2180* (MO); costa N de Puerto Cabezas, 14°02′N, 83°22′W, 12 m, 5 Feb.

1983 (early fr), *Sandino 3959* (MO); vic. Waní, including Río Ulí, 13°42′N, 84°51′W, 90–110 m, 22 Apr. 1978 (fl), *W. D. Stevens 7978* (MO). COSTA RICA. CARTAGO: Río Reventazón, entre Florencia y Turrialba, 500–600 m, 10 July 1965 (fl), *A. Jiménez M. 3269* (CR—2 sheets, F—2 sheets). GUANACASTE: between Liberia and Bagaces, nr. Río Potrero along Interamerican Hwy., 10°33′N, 85°23′W, 80 m, 29 Dec. 1966 (fl), *Burger & Ramírez 4124* (CR, DUKE, F, MO); Sta. Rosa National Park, 10°51′N, 85°37′W, 200–300 m, 22 Jan. 1978 (fl, fr), *Liesner 4342* (CR, MO); 23 June 1977 (fl, fr), *Liesner & Lockwood 2409* (CR, MO); 13–16 km N of Liberia along Camino Sta. María, 600–700 m, 9 July 1976 (fl), *J. Utley & K. Utley 5394* (CR, DUKE); ca. 5 km S of La Cruz, 260 m, 10 June 1967 (fl), *Weston 5017* (CR, DUKE, MO, NY). LIMÓN: between Hone Creek and Cahuita, 5 May 1983 (early fr), *L. D. Gómez et al. 20521* (MO—2 sheets). PANAMA. BOCAS DEL TORO: vic. Almirante, Jan.–Mar. 1928 (fl, fr), *Cooper 557* (F, NY, US); Bar Mouth, Changuinola Valley, 9 Mar. 1924 (fl, fr), *Dunlap 538* (US). CANAL AREA: nr. beach at Fort Kobbe, 12 Oct. 1961 (fr), *Duke 4728* (GH, MO); Madden Dam, Boy Scout Rd., 23 July 1968 (fl, fr), *Dwyer & Lallathin 8813* (F, GH, MO, NY); forest nr. Curundu, 8°58′N, 79°33′W, 0 m, 10 Mar. 1983 (early fr), *Hamilton & Gentry 3272* (MO); Fort Sherman and nearby, 9°20′N, 80°00′W, 0–100 m, 16 June 1983 (fl), *Hamilton & Stockwell 3696* (MO); 6 km E of Gamboa, 160–190 m, 24 Dec. 1973 (fl), *Nee 8993* (F, MO). COCLÉ: Penonomé, 14 July 1962 (fl), *Dwyer 2007* (MO); W of Río Guias, 10 Sep. 1972 (fr), *Gentry 5847* (F, MO); El Espino de Antón–Río Arenales, 7 Oct. 1973 (fr), *E. Jaén 17* (DUKE); between Las Margaritas and El Valle, 15 July–8 Aug. 1938 (fl, fr), *Woodson et al. 1745* (F, GH, MO, NY). COLÓN: Isla Grande, 11 Apr. 1970 (fr), *D'Arcy 4036b* (MO); coastline between Garrote and La Guaira, 4 Nov. 1975 (fr), *D'Arcy 9364* (MO, NY); beach between Fató and Playa de Damas, 8–10 July 1911 (fr), *Pittier 3936* (NY, US); vic. Sta. Isabel, 12–14 Aug. 1911 (fl, fr), *Pittier 4181* (NY, US). DARIÉN: vic. Yaviza, along Río Chucunaque, above El Punteadero, 7 June 1959 (fl), *Stern et al. 145* (GH, MO, US). PANAMÁ: San Carlos (Corona), 21 Oct. 1972 (fr), *Buitrago 1* (DUKE, MO); rd. between Panama and Chepo, 29 Nov. 1934 (fr), *Dodge et al. 16637* (GH, MO, NY); Isla de Pedro Gonzales, Perlas, 21 Aug. 1961 (fl), *Dwyer 1725* (MO); vic. Goofy Lake, 26 Nov. 1966 (fl, fr), *Dwyer 7128* (GH, MO, US); San José Island, Pearl archipelago, 15 July 1945 (fl), *Erlanson 475* (GH, NY, US); 12 Oct. 1944 (fr), *I. Johnston 142* (GH, MO, US); Majé, along bank of Río Majé, 18 Nov. 1970 (fl, fr), *Foster & Kennedy 2017* (DUKE, F, MO); 3.4 mi. E of Cañasas, 8°52′N, 78°15′W, ca. 100 m, 12 Sep. 1981 (early fr), *Knapp 1185* (ENCB, MO); Río Tocumen, 3 Jan. 1924 (fl), *Standley 29433* (US). SAN BLAS: mainland in front of Ustupo, 9 Nov. 1975 (fl, fr), *D'Arcy 9524* (MO, NY); Soskatupu, island 1.5 × 0.5–0.7 mi., 0–45 m, 15 Aug. 1967 (fl, early fr), *Elias 1691* (GH, MEXU, MO, US); nr. Puerto Obaldía, 8°40′N, 77°25′W, 0 m, 16 Apr. 1982 (fl, fr), *Knapp & Mallet 4649* (MO).

All the species in synonymy have been properly synonymized before, with the exception of *P. quiinifolia*, the morphology of which does not differ from that of *P. nervosa*. Degree of pubescence varies within populations, and infraspecific taxonomy based on this character (e.g., subsp. *rufescens*) is not recognized.

Psychotria nervosa may be recognized by its usually reddish pubescent aspect, leaves with usually eucamptodromous secondary veins diverging 55°–65°, small (1–4(–5) cm long) inflorescences lacking peduncles and with secondary axes usually 2 per rank in usually 3 ranks, and narrow-ellipsoidal fruit (5.5–7 × 2.5–3 mm). There appears to be no geographic component to the variation between glabrous and densely tomentose aspect. Collections from Florida are noteworthy for small leaves and relatively large inflorescences.

GROUP 6. THE *PANAMENSIS* GROUP

Shrub or tree; *young stems glabrous or* (*often red-brown*) *puberulent*; stipules usually sheathing, lanceolate (Fig. 2d) or ovate, or less commonly linear or triangular with the apex sometimes bilobed or biacuminate, uniform in color, glabrous or fringed or puberulent, caducous. *Leaf* blades usually elliptic, or sometimes obovate, ovate, or lanceolate, drying green-brown to red-brown to brown, sometimes paler below; secondary veins (4–)6–19(–22) pairs, diverging (30°–)45°–75°(–80°), *eucamptodromous to brochidodromous*, the axils sometimes with domatia (sometimes *P. cocosensis* and *P. lundellii*) or with tufts of hair (sometimes *P. chiriquina*, *P. lundellii*, and *P. mexiae*) or usually lacking; tertiary veins orthogonal reticulate to percurrent. *Inflorescences* panicles of cymes (or of glomerules sometimes in *P. panamensis* or of individual flowers in *P. hornitensis*), *nonpeduncu-late* (Fig. 7e) except in *P. olgae*, *P. stockwellii*, and sometimes in *P. cascajalensis*, *P. chiriquina*, *P. dwyeri*, *P. lundellii*, *P. panamensis*, *P. sarapiquensis*, and *P. trichotoma*; *secondary axes usually in 1 pair per rank* or less commonly 2 equal pairs or 2 size-differentiated pairs per rank, *diverging acutely except in P. stockwellii*; bracts not conspicuously enlarged, to 3 mm long only in *P. chiriquina*. *Corolla* tubes (1.5–)2–5 mm long, the lobes without apical extensions. *Fruit* ellipsoid, obovoid, or spherical when dry; *persistent calyx a beak* or less commonly a conspicuous tube (*P. cocosensis* [Fig. 9c] and *P. olgae* and sometimes *P. panamensis*) *or often not evident*; *seed dorsal surface with (3–) 4–10 often irregular longitudinal furrows*, the ventral surface with 2 deep plus often several irregular longitudinal furrows (Figs. 10g, 10h).

Half of the 12 species of the group are assigned to the *Psychotria panamensis* complex; *P. pana-*

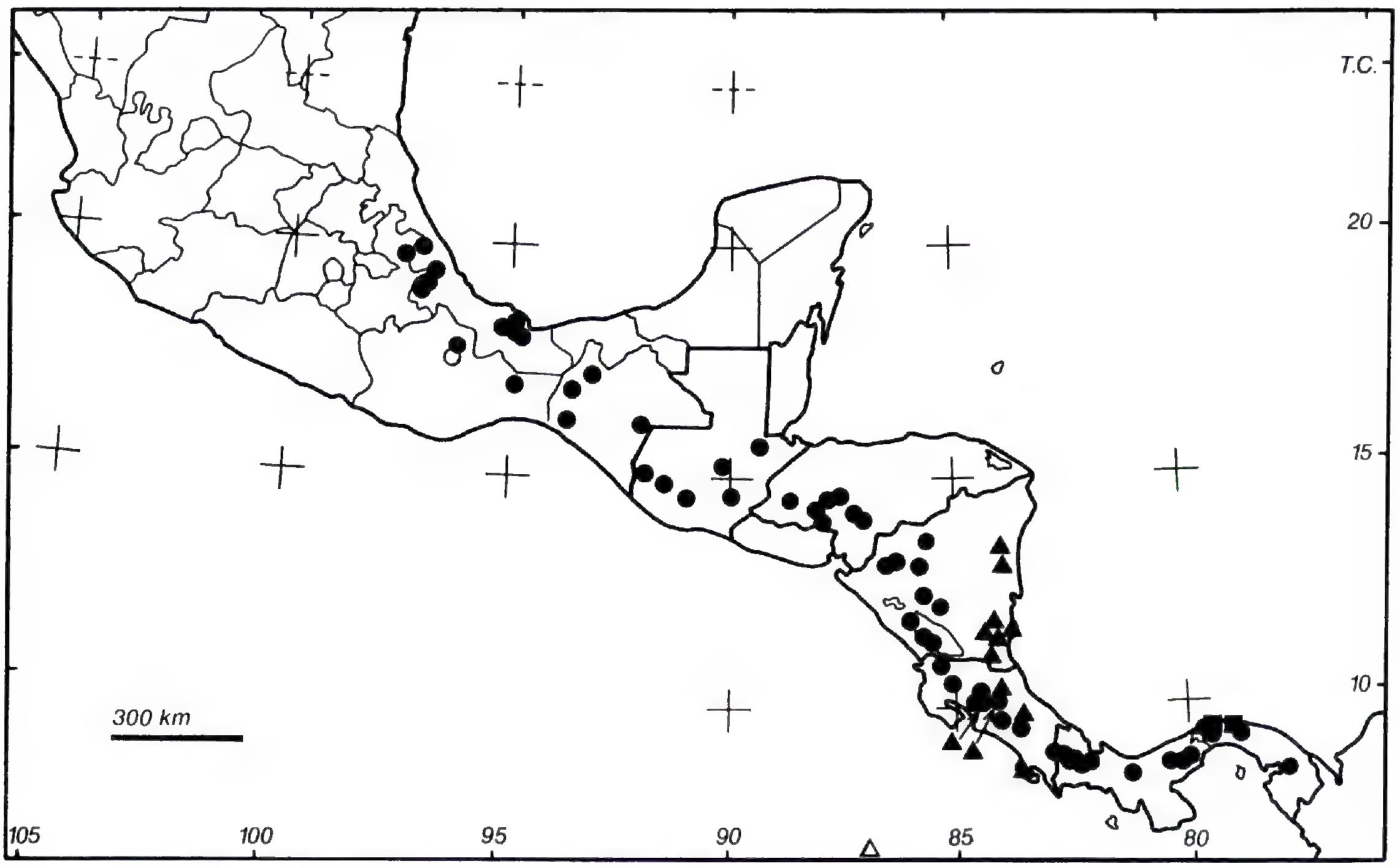

FIGURE 28. Distributions of *Psychotria cocosensis* (open triangle), *P. panamensis* var. *compressicaulis* (solid triangles), *P. panamensis* var. *ixtlanensis* (open circle), *P. panamensis* var. *magna* (solid squares), and *P. panamensis* var. *panamensis* (solid circles) in Mesoamerica.

mensis is widespread (Fig. 28), the other five much less so: *P. cascajalensis* (Coclé, Panama; Fig. 29), *P. cocosensis* (Cocos Island, Costa Rica; Fig. 28), *P. dwyeri* (southern Mexico; Fig. 29), *P. olgae* (eastern Panamá Province; Fig. 29), and *P. stockwellii* (Costa Rica and Panama; Fig. 30). Three other widespread species have character states that distinguish them from typical members of the group and are of uncertain affinities, although analysis might reveal they belong in the *panamensis* complex: *P. trichotoma* has obovoid fruits and conspicuously brochidodromous venation; *P. sarapiquensis* has usually narrowly oblanceolate leaves; and *P. mexiae* has 5–8 deep irregular furrows on the seed dorsal surface. The most cohesive complex is that of *P. chiriquina*, which includes that species (Nicaragua through Panama; Fig. 29), *P. lundellii* (Chiapas through El Salvador; Fig. 29), and *P. hornitensis* (western Panama; Fig. 30); they share ovate stipules and shallow furrows on the seed ventral surface.

Of the 15 taxa in the group, eight appear distylous; of those, *Psychotria dwyeri*, *P. mexiae*, *P. olgae*, *P. stockwellii*, and *P. trichotoma* show some between-morph asymmetry in floral part lengths. *Psychotria lundellii* appears to be pin-monomorphic in Belize, but recently I examined a thrum collection from Guatemala. *Psychotria panamensis* var. *compressicaulis*, on the other hand, is thrum-monomorphic. *Psychotria cocosensis* and *P. hornitensis* are long-homostylous. *Psychotria cascajalensis*, *P. panamensis* var. *ixtlanensis*, and *P. panamensis* var. *magna* do not have sufficient flowering material for analysis.

36. Psychotria cascajalensis C. Hamilton, Phytologia 64: 220. 1988. TYPE: Panama. Coclé: N of Penonomé, between Llano Grande and Cascajal, rd. to Coclesito, 480 m, 2 May 1979 (fl), *Hammel 7227* (holotype, MO-2901097; isotypes, ENCB, MO). Figure 29.

Tree 10 m tall; young stems glabrous to sparsely puberulent, the bark smooth; stipules oval, rounded, 6–7 × 3–3.5 mm, fringed, glabrous, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 2–4 mm long, glabrous, flat above; blades coriaceous, elliptic, the apex acute, the base attenuate, 3.5–6(–7) × (1.5–)2–2.7 cm, glabrous above and below, drying dull red-brown to green-brown; secondary veins 4–6 pairs, diverging 55°–65°, brochidodromous with secondary loops inconspicuous, straight then arcuate near margin, not elevated below, glabrous, the axils lacking domatia or hairs; tertiary veins inconspicuous. *Inflorescences* terminal, panicles of cymes or glomerules;

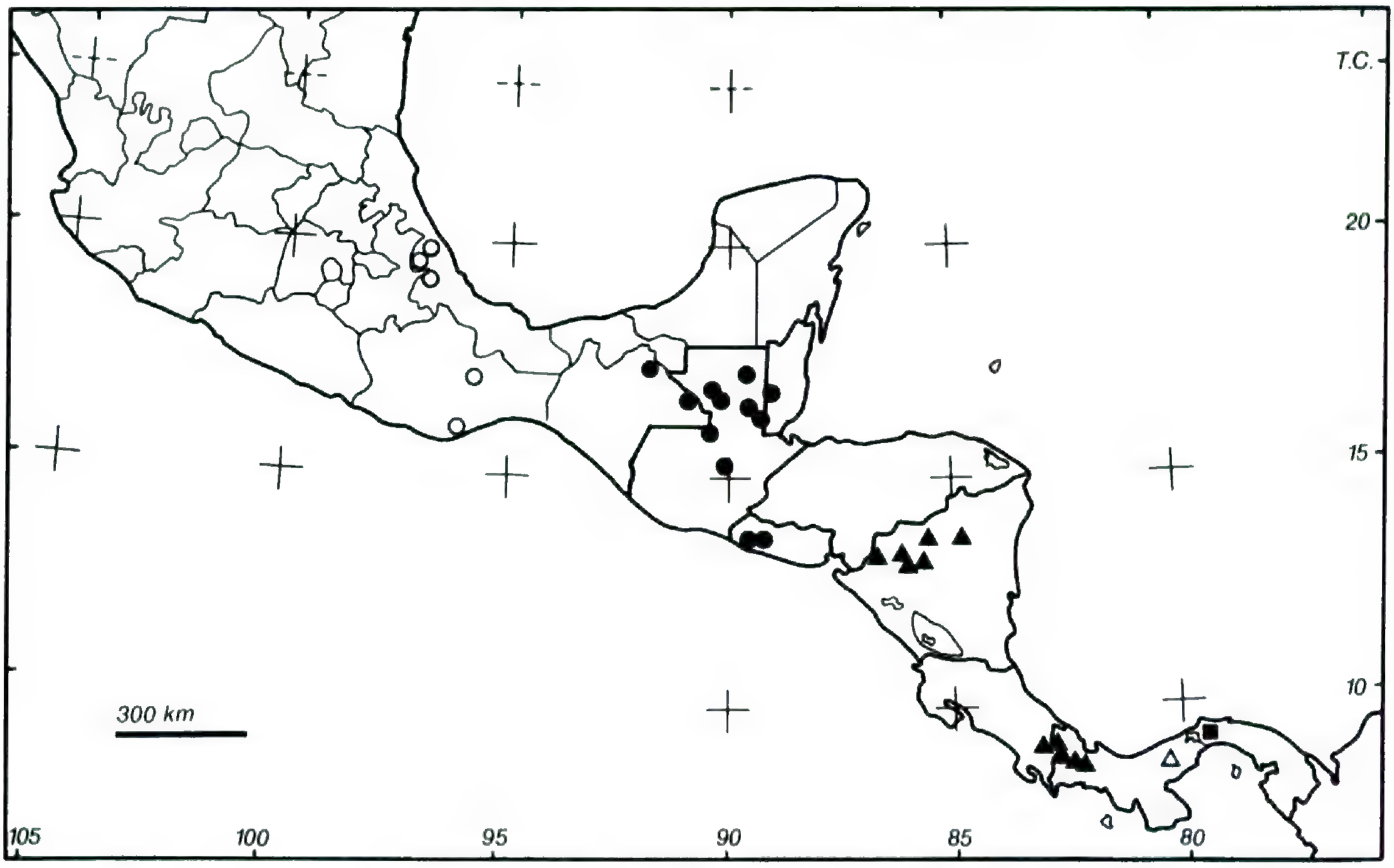

FIGURE 29. Distributions of *Psychotria cascajalensis* (open triangle), *P. chiriquina* (solid triangles), *P. dwyeri* (open circles), *P. lundellii* (solid circles), and *P. olgae* (solid square).

panicle branched to 3 degrees; main axis 6 cm long, the peduncle 2–3.5 cm long; secondary axes in 3 ranks, the first-rank axes 2 or 4, the longer pair 1–2 cm long, the shorter pair 0.4–1.2 cm long when present, the second-rank axes 2, 0.5–0.8 cm long, the third-rank axes 2, 0.1–0.3 cm long; cymes branched to 1–2 degrees; bracts and bracteoles broadly triangular, 1–2 mm long, red-brown pubescent. *Flowers* subsessile, the pedicels 0.5 mm long; calyx cup-shaped, the tube 0.8 mm long, the lobes 5, triangular to barely evident, to 0.3 × 0.8 mm, puberulent, fringed; corolla green-white, the tube cylindrical, 1.5 × 1.5 mm, thickly white pubescent in throat, the lobes 5, triangular, 1.5 × 1 mm; stamens 5, the filaments not seen in pins, 1.5 mm long in thrums, the anthers 1 mm long; style not seen in pins, 1 mm long in thrums, the branches linear. *Fruit* not seen.

Distribution (Fig. 29). Known only from the type collection from the foothills south of the divide in Coclé, Panama, at 480 m in a region of tropical moist to premontane wet forest with equatorial-mountainous climate. It was collected in flower on May 2.

Psychotria cascajalensis may be recognized by its small (usually 3.5–6 × 2–2.7 cm), coriaceous, elliptic leaves and robust pedunculate inflorescences with secondary axes 2(4) per rank in three ranks.

The only flowering collection appears to be a thrum morph.

37. Psychotria chiriquina Standley, Contr. U.S. Natl. Herb. 18: 129. 1916. TYPE: Panama. Chiriquí: Alto de la Cuesta, E slope of Chiriquí Volcano, 2,100–2,200 m, 10–13 Mar. 1911 (fl), *Pittier 3118* (holotype, US). Figure 29.

Shrub or small tree, 1–6 m tall; young stems glabrous, the bark gray, deeply fissured longitudinally; stipules sheathing, ovate, sometimes bilobed, 8–10 × 3–5 mm, glabrous to red-brown puberulent, fringed, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 0.6–1.5 cm long, glabrous to red-brown puberulent, flat above; blades membranous, elliptic, the apex long-acuminate, the base attenuate, (4–)6.5–9(–12) × (1–)1.5–2.5(–3) cm, glabrous above and below, drying deep red-brown; secondary veins 5–11(–12) pairs, diverging 30°–65°, eucamptodromous, constantly arcuate, prominulous to not elevated below, glabrous, the axils with or without minute tufts of hair; tertiary veins evident to inconspicuous, orthogonal reticulate to percurrent. *Inflorescences* terminal, panicles of cymes; panicle branched to 2–4 degrees; main axis (1–)2–7 cm long, the peduncle lacking or 1–4.5 cm long; secondary axes in 3(4) ranks, the first-rank axes

2, (0.4–)1–3.2 cm long, the second-rank axes 2, (0.3–)0.5–1.4 cm long, the third-rank axes 2, (0.1–)0.3–0.5 cm long, the fourth-rank axes 2, 0.2 cm long; cymes branched to 1–2 degrees; bracts linear, 2–3 mm long, glabrous to ciliate; bracteoles irregular, to 0.8 mm long, sparsely ciliate. *Flowers* sessile to pedicellate, the pedicels to 3 mm long; calyx cup-shaped, the tube 1 mm long, the lobes 5, triangular to barely evident, 0–0.6 × 0.8 mm, glabrous to minute-puberulent; corolla white, the tube cylindrical, 4–6 × 1.5–2 mm, white pubescent in throat, the lobes 5, linear, 1.5–2 × 1 mm; stamens 5, the filaments 4–4.5 mm long in pins, 5.5–6 mm long in thrums, the anthers 1 mm long; style 6 mm long in pins, 4–5 mm long in thrums, the branches minute, clublike. *Fruit* when dry ellipsoid, 5–6 mm long, 4–4.5 mm diam., maturing red, drying deep red-brown; persistent calyx a minute beak to 1 mm long; seed dorsal surface with 4 shallow longitudinal furrows, the ventral surface with 2 shallow longitudinal furrows.

Distribution (Fig. 29). Known from northern Nicaragua and from both sides of the Costa Rica–Panama border at elevations of 900 to 2,500 m in premontane to lower montane moist forest to rainforest with equatorial-mountainous to tropical-mountainous climate. *Psychotria chiriquina* has been collected in flower July–August in Nicaragua and primarily February–May in Costa Rica and Panama, and in fruit November–May in Nicaragua and August–April in Costa Rica and Panama.

Selected specimens examined. NICARAGUA. JINOTEGA: carret. Matagalpa–Jinotega, km 133–134, a 10 km al SE de Jinotega, 13°01′N, 85°55′W, 1,400–1,480 m, 24 Feb. 1979 (fr), *Grijalva & Araquistain 175* (MO); Montaña Cuspire, 13°17′N, 86°09′W, 1,500–1,539 m, 10 Apr. 1981 (fr), *P. P. Moreno 8036* (MO); NE del Cerro Kilambé, "Filas el Portal," 13°37′N, 85°40′W, 600–900 m, 26 Mar. 1981 (fr), *P. P. Moreno & Sandino 7583* (MO). MADRIZ: Cerro Pataste, 1,600 m, 8 May 1975 (fr), *Neill 129* (MO). MATAGALPA: Cerro El Picacho, N del hotel Selva Negra, 13°00′N, 85°55′W, 1,500 m, 7 July 1983 (fl), *P. P. Moreno 21678* (MO); Hda. Santa María de Ostuma, 10 km N of Matagalpa, 1,500 m, 12 Aug. 1977 (fl), *Neill 2304* (MO); Macizos de Peñas Blancas, SE side, drainage of Qda. El Quebradon, slopes N and W of Hda. San Martín, 13°15′N, 85°38′W, 1,000–1,400 m, 18–20 Jan. 1982 (fr), *W. D. Stevens et al. 21145b* (MO); Sta. María de Ostuma, Cordillera Central between Matagalpa and Jinotega, 1,300–1,500 m, 8–15 Jan. 1963 (fr), *L. O. Williams et al. 23342* (F, GH, NY, US). RIVAS: Isla Ometepe, faldas del Volcán Maderas al S de la Hda. Magdalena, 11°27′N, 85°30′W, 300–900 m, 28 Nov. 1982 (fr), *P. P. Moreno 18854* (MO). ZELAYA: Cerro La Pimienta, N slope facing La Garrapata, 13°45′N, 84°59′W, 900–1,180 m, 16 Mar. 1980 (fr), *Pipoly 6050* (MO). COSTA RICA. PUNTARENAS: valley of Río Cotón between Sitio Cotón (Cotonsito) and Sitio Tablas, 8°57′N, 82°46′W, 1,500–1,600 m, 2 Sep. 1983 (early fr), *Davidse 24415* (CR, MO); trail between Tres Colinas and Cerro Bekom, 9°08′N, 83°04′W, 2,300 m, 28 Mar. 1984 (fr), *Davidse & Herrera 26175* (CR, MO); vic. Helechales, along Río Guineal, 9°04′N, 83°05′W, 1,100–1,200 m, 29 Mar. 1984 (fl), *Davidse & Herrera 26219* (MO); Cerro Burú, 9°00′N, 82°49′W, 2,000–2,300 m, 20 Aug. 1983 (fr), *Davidse et al. 23825* (MO); upper Río Burú, 2,010 m, 19 Aug. 1983 (fr), *Gómez et al. 21509* (MO). PANAMA. BOCAS DEL TORO: Valle de Silencio, 9°05′N, 82°56′W, 8–10 Aug. 1979 (fr), *Antonio 1586* (MO). CHIRIQUÍ: slopes of Las Cumbres nr. Cerro Punta, 20 Feb. 1971 (fl, fr), *Croat 13737* (F, MO—2 sheets, NY); E slope of Volcán Barú, 10 mi. from Boquete, 2,500 m, 18 May 1976 (fl), *Croat 34982* (MO, NY); Caldera–Chiriquicito trail, 21 Apr. 1968 (fr), *Kirkbride & Duke 1007* (MO); Cerro Hornito, above Los Planes de Hornito, 8°42′N, 82°06′W, 2,100 m, 14 Mar. 1982 (fl), *Knapp et al. 4196* (MO); slopes approachng Cerro Horqueta, 1,500–1,800 m, 5 Jan. 1975 (fl), *Wilbur & Luteyn 19316* (DUKE); E of Guadaloupe along Río Chiriquí Viejo ca. 2 mi. NE of Cerro Punta, Cerro Respinga ridge, 13 Jan. 1971 (fl, fr), *Wilbur et al. 13106* (DUKE, MO).

Psychotria chiriquina may be recognized by its small (usually 6.5–9 × 1.5–2.5 cm) narrow-elliptic leaves drying deep red-brown, deeply longitudinally fissured bark, long (4–6 mm) corolla tube, and robust (5–6 × 4–4.5 mm) ellipsoid fruits drying deep red-brown. There are several differences noted in collections from Nicaragua as opposed to those from Panama. Nicaraguan material shows fewer (5–7 vs. usually 8–11[–12]) secondary veins and more acute (30°–50° versus 55°–65°) angles of divergence of secondaries. Panamanian material shows often pedicellate inflorescences and fruits with a more prominent persistent calyx.

38. Psychotria cocosensis C. Hamilton, Phytologia 64: 222. 1988. TYPE: Costa Rica: Cocos Island, 18 June 1898 (fr), *Pittier 12375* (holotype, US). Figures 9c, 28.

Shrub; young stems glabrous, the bark furrowed longitudinally; stipules lanceolate, 12–35 × 2–5 mm, glabrous, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 7–14 mm long, glabrous, grooved or flat above; blades subcoriaceous to coriaceous, elliptic, the apex acuminate to subcaudate, the base attenuate, (12–)14–17 × 5.5–7 cm, glabrous above and below, drying red-brown to green-brown; secondary veins (9–)10–12 pairs, diverging 45°–50°, eucamptodromous to brochidodromous, straight then arcuate near margin, elevated below in less coriaceous leaves, the axils with small domatia below; tertiary veins inconspicuous to evident, percurrent to reticulate. *Inflorescences* terminal, panicles of cymes; panicle branched to 2–3 degrees; main axis 1 cm long, the peduncle lacking; secondary axes in 2 ranks, the first-rank axes 2, 0.6 cm long, the second-rank axes 2, reduced; cymes branched to

1 degree; bracts triangular, 0.7–1.5 mm long, glabrous. *Flowers* pedicellate, the pedicels 2–3 mm long; calyx cup-shaped, the tube 1 mm long, the lobes 5, broadly triangular to barely evident, glabrous; corolla color unknown, the tube cylindrical, 3 × 3 mm, white pubescent in throat, the lobes 5, linear, 4 × 2 mm; stamens 5, the filaments 7 mm long, the anthers 2 mm long; style 9–10 mm long, the branches minute, linear. *Fruit* when dry spherical to ellipsoid, 6 mm long, 5.5–6 mm diam., drying dark red-brown; persistent calyx cuplike, coriaceous, 1.5 mm long (Fig. 9c); seed dorsal surface with 4 shallow, irregular, longitudinal furrows, the ventral surface with 2 deep, irregular, longitudinal furrows.

Distribution (Fig. 28). Known only from the type locality, Cocos Island, at 50 m elevation in premontane rainforest. *Psychotria cocosensis* has been collected in fruit in January and June.

Additional specimens examined. COSTA RICA. COCOS ISLAND: La vallée de Chatham, 50 m, Jan. 1902 (fl, fr), *Pittier 16279* (GH, US).

Psychotria cocosensis may be recognized by its close resemblance to *P. panamensis* and by its coriaceous leaves and large (6 × 5.5–6 mm) spherical to ellipsoid fruits with calyx persisting as a coriaceous cup ca. 1.5 mm long.

Style and stamens are both exserted in the one flowering collection seen, suggesting strongly that the species is long-homostylous.

39. Psychotria dwyeri C. Hamilton, Phytologia 64: 223. 1988. TYPE: Mexico. Oaxaca: Dto. Choapan (Santiago Choapan), Sta. María, Montaña Sta. María, 1,500 m, 7 Apr. 1938 (fr), *Mexia 9265* (holotype, NY; isotypes, B, F, GH, K, MO, US). Figure 29.

Shrub or small tree, 3–6 m tall; young stems glabrous, the bark smooth; stipules sheathing, triangular, 8–13 × 3–5 mm, glabrous, caducous, leaving a pale ridge often with red-brown fringe. *Leaves* petiolate; petioles (5–)15–40(–45) mm long, glabrous, furrowed above; blades membranous, elliptic, the apex cuspidate, the base cuneate to attenuate, (12 –)15–23 × 5–10 cm, glabrous above, glabrous to minutely white puberulent below, drying green-brown, paler below; secondary veins (12–)15–18 pairs, diverging 55°–70°(–80°), eucamptodromous, straight to slightly arcuate, elevated below, often white puberulent below, the axils lacking domatia or hairs; tertiary veins evident, orthogonal reticulate, the loops near margin evident. *Inflorescences* terminal, panicles of cymes; panicle branched to 4 degrees; main axis 5.5–10.5 cm long, the peduncle lacking or to 2 cm long; secondary axes in 4–5(–6) ranks, the first-rank axes 2, (2.5–)7–9 cm long, the second-rank axes 2(4), (2–)3–5.5 cm long, the third-rank axes 2, (0.5–)1.5–4 cm long, the fourth-rank axes 2(4), (0.5–)1–2 cm long, the fifth-rank axes 2, 0.6–0.8 cm long, the sixth-rank axes 2, 0.3 cm long; cymes branched 1–2 degrees; bracts inconspicuous. *Flowers* pedicellate, the pedicels 0.5–1.5 mm long; calyx cup-shaped, the tube 0.5 mm long, the lobes 5, broadly triangular, minute, glabrous to minutely fringed; corolla white, the tube cylindrical, 2–2.5 × 2 mm, white pubescent in throat, the lobes 5, triangular, 1.5–2 × 1 mm; stamens 5, the filaments 2–2.5 mm long in pins, 2.5–3 mm long in thrums, the anthers 1 mm long; style 4–4.5 mm long in pins, 1.5–2 mm long in thrums, the branches linear in pins, clublike in thrums. *Fruit* when dry spherical, 4.5–5 mm long, 4.5–5 mm diam., maturing red, drying deep red-brown; calyx persistent as a beak, to 0.8 mm long; seed dorsal surface with 4 irregular longitudinal furrows, the ventral surface with 2 deep longitudinal furrows.

Distribution (Fig. 29). Known from Veracruz and Oaxaca, Mexico, at elevations of 50–1,500 m in a region of subevergreen forest with tropical to tropical-mountainous climate. This species has been collected in flower in April and May and in fruit April, June, and December.

Specimens examined. MEXICO. OAXACA: Ubero, 30–90 m, June 1937 (fr), *Ll. Williams 9475* (F). VERACRUZ: San Lorenzo Tenochtitlán, 9 Dec. 1967 (st), *Chavelas et al. ES-2832* (MEXU); El Mirador, 1853 (fl), *F. Muller 424* (NY); Apr. 1932 (fl), *Purpus 14124* (A, F); Zacuapan, 1915 (fl), *Purpus 7525* (MO, US); May 1926 (fl), *Purpus 10705* (US); Jalapa, 1,200–1,350 m, 1894 (fl), *C. Smith 1844* (F, US).

Psychotria dwyeri resembles *P. panamensis* in inflorescence and vegetative characters and is distinguished most easily in fruit. *Psychotria dwyeri* has spherical (vs. ellipsoid to obovoid) fruit 4.5–5 mm (vs. 4.5–8 mm) long.

Reproductive organs at both levels appear to be longer in the pin morph than in the thrum.

40. Psychotria hornitensis Dwyer & C. Hamilton in C. Hamilton, Phytologia 64: 225. 1988. TYPE: Panama. Chiriquí: ridge and summit of Cerro Hornito, above Los Planes de Hornito, 8°42′N, 82°06′W, 2,100 m, 14 Mar. 1982 (fl, early fr), *Knapp et al. 4198* (holotype, MO). Figure 30.

Shrub 2 m tall; young stems glabrous, the bark deeply furrowed longitudinally; stipules sheathing,

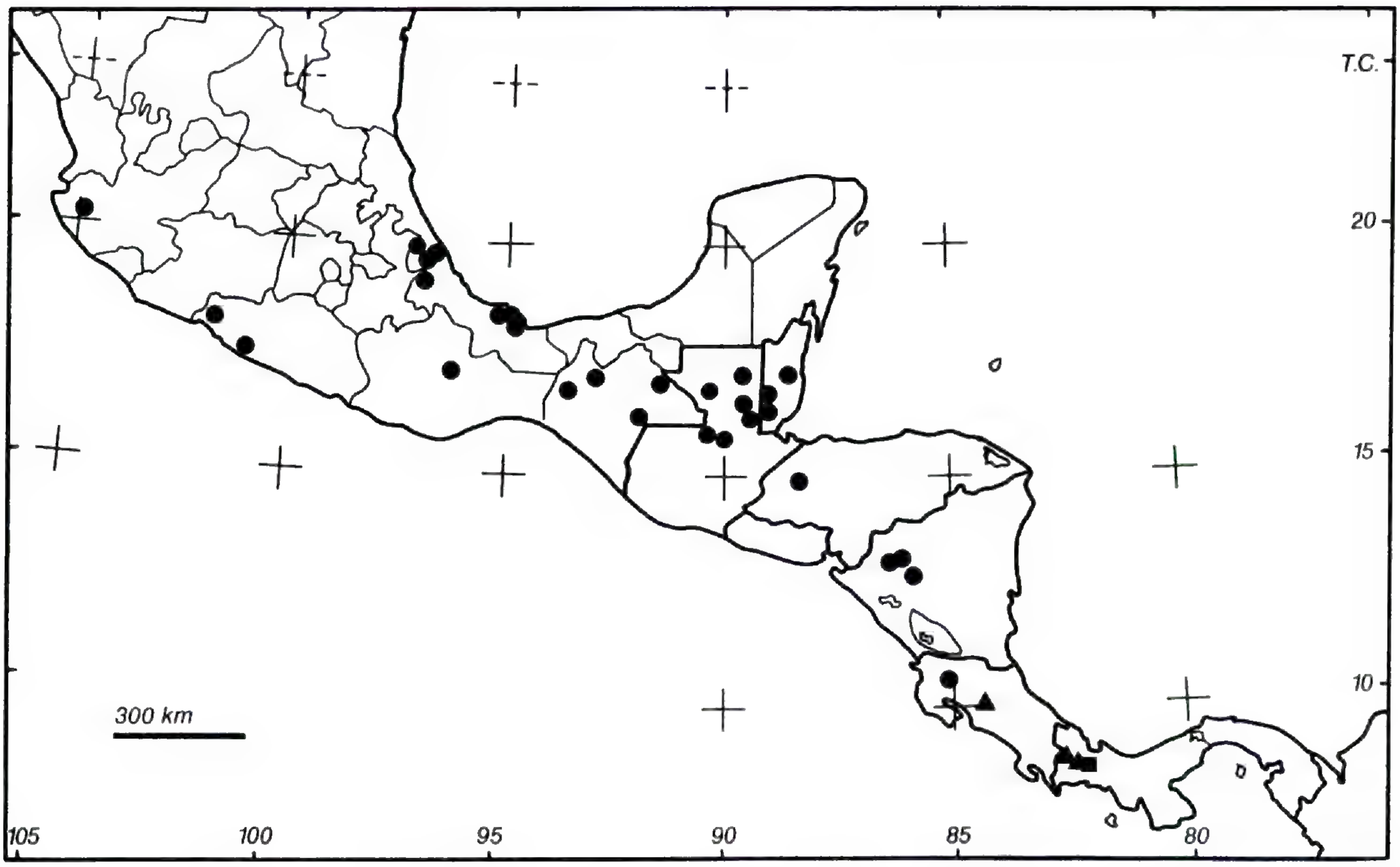

FIGURE 30. Distributions of *Psychotria hornitensis* (square), *P. mexiae* (circles), and *P. stockwellii* (triangles) in Mesoamerica.

ovate to lanceolate, 3–4 × 1–1.5 mm, glabrous, caducous, leaving a pale ridge with red-brown fringe. *Leaves* subsessile; petioles to 2 mm long, glabrous, flat above; blades membranous, narrowly elliptic, the apex long acuminate, the base attenuate, 2.5–3.5 × 0.5–0.7 cm, glabrous above and below, drying dull green-brown above, dull green below; secondary veins 5–6 pairs, diverging ca. 50°, eucamptodromous, constantly arcuate, not evident above, barely evident below, glabrous, the axils lacking domatia or hairs; tertiary veins inconspicuous. *Inflorescences* terminal, panicles of 3–5 individual flowers or cymes; panicle branched to 2 degrees; main axis 2.5–3 cm long, the peduncle 1.5–2 cm long; secondary axes in 1–2 ranks, the first-rank axes 1–2, 0.3–0.4 cm long, the second-rank axes 1–2, 0.1 cm long; cymes branched to 1 degree; bracts and bracteoles linear, 1.5–2 × 0.7 mm, glabrous to puberulent within near base. *Flowers* sessile to pedicellate, the pedicels to 1 mm long; calyx cup-shaped, the tube ca. 1 mm long; the lobes 5, triangular, 0.8–1 × 0.8 mm, glabrous; corolla white, the tube cylindrical, 3.5–4 × 1.5 mm, white pubescent in throat, the lobes 5, ovate, 1–1.5 × 0.8 mm; stamens 5, 3–4 mm long, the anthers 1 mm long; style 4–6 mm long, the branches short, linear. Mature *fruit* not seen.

Distribution (Fig. 30). Known only from the type locality, Cerro Hornito, Chiriquí, Panama, at ca. 2,000 m elevation in low montane rainforest with equatorial-mountainous climate. *Psychotria hornitensis* has been collected in flower in February and March and with immature fruit in March.

Additional specimen examined. PANAMA. CHIRIQUÍ: ridge nr. top of Cerro Hornito, 1,950 m, 15 Feb. 1979 (fl), *Hammel 6189* (MO).

Psychotria hornitensis may be recognized readily by its small, narrow (2.5–3.5 × 0.5–0.7 cm) leaves and small (2.5–3 cm long) few-flowered inflorescences.

The one flower morph found does not show significant differentiation in length between the exserted style and stamens, so the species is presumed to be long-homostylous.

41. Psychotria lundellii Standley in Lundell, Contr. Univ. Michigan Herb. 4: 29. TYPE: Belize. Cayo: Valentin, 26 June 1936 (fl), *Lundell 6260* (holotype, F; isotypes, GH, MICH, n.v., NY, US). Figure 29.

Tree or shrub, (1–)2–15 m tall; young stems glabrous or red-brown puberulent, the bark pale, cracked and furrowed longitudinally; stipules ovate, rounded, 5–6 × 2–4 mm, glabrous, often ciliate, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 0.8–2 cm long, glabrous, grooved above; blades subcoriaceous, elliptic, the

apex acuminate, the base attenuate, (5–)7.5–15 × (1.8–)2.5–5 cm, glabrous above and below, drying pale to glossy red-brown; secondary veins (5–)6–8(–12) pairs, diverging (30°–)60°–65°, brochidodromous, constantly arcuate, prominulous below, glabrous, the axils usually with minute tufts of red-brown hair and/or domatia below; tertiary veins not evident. *Inflorescences* terminal or pseudoaxillary, panicles of cymes; panicle branched to (3)4 degrees; main axis 4–7.5 cm long, the peduncle (0–)1–3 cm long; secondary axes in 4(5) ranks, the first-rank axes 2(4), the longer pair 1.5–3.5 cm long, the shorter pair when present 1.6 cm long, the second-rank axes 2, 0.8–1.7 cm long, the third-rank axes 2, 0.5–0.7 cm long, the fourth-rank axes 2, 0.2–0.3 cm long, the fifth-rank axes 2, 0.2 cm long; cymes branched to 1–2 degrees; bracts sheathing, irregular, to 1.5 mm long, ciliate; bracteoles triangular, 0.3–0.5 mm long, ciliate. *Flowers* pedicellate, the pedicels 0.7–1 mm long; calyx cup-shaped, the tube 0.5 mm long, the lobes 5, triangular, 0.3 × 0.6 mm, minutely ciliate; corolla green-white, the tube campanulate, 2–2.5 × 1.5 mm, white pubescent in throat, the lobes 5, ovate-acuminate, 1.5–2 × 1 mm; stamens 5, the filaments 1.5–2 mm long in pins, 4 mm long in thrums, the anthers 0.7 mm long; style 3–4 mm long in pins, 2 mm long in thrums, the branches linear. *Fruit* spherical when dry, (4–)4.5–5(–5.5) mm long, (4–)4.5–5(–5.5) mm diam., maturing red, drying red-brown; persistent calyx not conspicuous or rarely to 0.3 mm long; seed dorsal surface with 3–6 shallow irregular longitudinal furrows, the ventral surface with 2 deep and often 2–4 additional irregular longitudinal furrows.

Distribution (Fig. 29). Eastern Chiapas, Guatemala, western Belize, and El Salvador, at elevations below 500 m except in El Salvador, where this species occurs at 1,800–2,000 m. It is found in evergreen forest with equatorial-tropical or sometimes tropical to tropical-mountainous climate. *Psychotria lundellii* has been collected in flower April–July and in fruit July–April, primarily January–March.

Selected specimens examined. MEXICO. CHIAPAS: 23 mi. SE of Palenque, rd. to Chancala, 160 m, 6 July 1977 (fl), *Croat 40294* (MO); Mpio. Ocosingo, 3 km al S del Centro Arqueológico Bonampak, orillas del Río Lacanja, 300 m, 2 Apr. 1982 (fr), *Meave et al. B-407* (MEXU, MO). GUATEMALA. ALTA VERAPAZ: Rubelsanto, between Pozo #4 and Laguneta Los Lagartos, 29 July 1975 (fr), *Lundell & Contreras 19575* (MO). BAJA VERAPAZ: Unión Barrios, 12 Mar. 1972 (fr), *Contreras 11268* (MO); Niño Perdido, Qda. Seca, 31 May 1977 (fl), *Lundell & Contreras 21037* (MO). PETÉN: Uaxactún, 7 Apr. 1931 (fr), *Bartlett 12533* (F, GH, K, NY, US); Tikal National Park, in ramonal on Temple 27, 16 Mar. 1966 (fr), *Contreras 5609* (ENCB, F, MO, NY); Chinchila, 8 km from San Luis, on Sebol Rd., 10 Oct. 1966 (fr), *Contreras 6357* (MO); 5 km from La Cumbre, bordering Pusila River, 22 Aug. 1969 (fr), *Contreras 9004* (MO); Dolores, lado SE, ca. 100 m del camino, a km 86, 14 Feb. 1971 (fr), *Ortíz 1578* (F, US); en el camino que conduce a citio arqueológico "Ceibal," a 9 km SE de Sayaxché, 13 June 1973 (fl), *Ortíz 2681* (F). BELIZE. CAYO: Valentin, in advanced forest, limestone valley, June–July 1936 (fl), *Lundell 6194* (F, GH, NY, US); *Lundell 6234* (A, F—2 sheets, MO, NY, US); *Lundell 6249* (A, F—2 sheets, MEXU, MO, NY). EL SALVADOR. SAN SALVADOR: Volcán San Salvador, forest El Picacho NE of El Boquerón, 1,950 m, 1 Mar. 1968 (fr), *A. Molina R. & Montalva 21831* (F, NY). SONSONATE: Sierra Apaneca, cut-over forest, Cerro El Pilón, 1,800 m, 23 Feb. 1968 (fr), *A. Molina R. & Montalvo 21607* (F, NY).

Psychotria lundellii may be recognized by its narrow (length/width = 3) leaves drying glossy red-brown with few (usually 6–8) secondary veins and tertiary veins not evident, and its spherical fruit drying often glossy red-brown and appearing smooth outside due to the seed dorsal surface having 3–6 shallow irregular longitudinal furrows. *Psychotria lundellii* differs from the similar *P. chiriquina* in having smaller (5–6 vs. 8–10 mm long) stipules, brochidodromous (vs. eucamptodromous) secondary venation, shorter (2–2.5 vs. 4–6 mm) corolla tubes, and spherical (vs. ellipsoid) fruits. Material from El Salvador shows generally more secondary veins in the leaves than material gathered elsewhere.

Eight flowering specimens from Belize have been examined, and only the long-style morph has been found, suggesting that the short-style morph has been lost in populations in that country. One thrum has been found in Baja Verapaz, Guatemala (*Lundell & Contreras 21037*).

42. Psychotria mexiae Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 296. 1929. TYPE: Mexico. Jalisco: Santa Cruz de Vallarta, wooded ravine on mountain side, 300 m, 9 Dec. 1926 (fr), *Mexia 1262* (holotype, F; isotypes, A, GH, MO, US–2 sheets). Figures 10h, 30.

Palicourea nigrescens M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11(50): 136. 1844. TYPE: Mexico. Veracruz: Cordillera, June–Oct. 1840 (fl), *Galeotti 2653* (holotype, C). Not *Psychotria nigrescens* De Wild., Pl. Bequaert. 2: 393. 1924.

Psychotria schippii Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 24. 1943. TYPE: Belize. Cayo: Valentin, limestone valley, June–July 1936 (fr), *Lundell 6193* (holotype, F; isotypes, GH, NY, US).

Tree or shrub, 2–5(–10) m tall; young stems sparsely puberulent, the bark pale, mottled, with

irregular ridges and raised lenticels; stipules sheathing, linear, 12–20(–40) × 1.5–3(–5) mm, glabrous, caducous, leaving a pale ridge with or without red-brown fringe. *Leaves* petiolate; petioles 3–20 mm long, glabrous or sometimes sparsely tomentose below, flat above; blades membranous to subcoriaceous, elliptic, the apex long-acuminate, the base cuneate, (8–)10–20 × (2.5–)3–8.5 cm, glabrous above and below, sometimes sparsely tomentose along midvein below, drying green-brown to sometimes red-brown, the veins often reddish below; secondary veins 12–16(–18) pairs, diverging (55°–)60°–70°(–75°), brochidodromous to eucamptodromous, constantly arcuate, prominent below, glabrous, the axils sometimes with minute tufts of hairs below; tertiary veins inconspicuous to evident, orthogonal reticulate to rarely random reticulate. *Inflorescences* terminal or pseudoaxillary, globose panicles of cymes; panicle branched to 4 degrees; main axis (1–)2–4.5 cm long, the peduncle lacking; secondary axes in (3)4(5) ranks, the first-rank axes 2 or 4, equal, 1–3 cm long, the second-rank axes 2 or 4, equal, 0.5–1.5 cm long, the third-rank axes 2, 0.2–1 cm long, the fourth-rank axes 2, 0.2–0.7 cm long, the fifth-rank axes 2, 0.1 cm long; cymes branched to (1)2 degrees; bracts and bracteoles not evident. *Flowers* on pedicels 0.5–1 mm long; calyx cup-shaped, the tube 0.3 mm long, sometimes minutely puberulent; corolla white, often drying pink, the tube cylindrical, 2.5–4.5 × 1.5 mm, white pubescent in throat, the lobes 5, lanceolate, 1.5–2 × 1 mm; stamens 5, the filaments 2–3.5 mm long in pins, 3–5 mm long in thrums, the anthers 0.8–1 mm long; style 4–7 mm long in pins, 2–3 mm long in thrums, the branches spathulate. *Fruit* when dry ellipsoid to spherical, 4.5–5(–6) mm long, 3.5–4.5(–5) mm diam., maturing red, drying often shiny red-brown; persistent calyx a tubular beak to 0.5 mm long; seed dorsal surface with 5–8 deep irregular longitudinal furrows, the ventral surface with 2 deep regular plus usually 2–4 additional irregular longitudinal furrows (Fig. 10h).

Distribution (Fig. 30). Scattered from Mexico through northern Costa Rica, most common in a band from Veracruz and Chiapas, Mexico, through Petén, Guatemala, into Belize, at elevations of 400–1,800 m in regions of premontane moist forest with equatorial to tropical climate. *Psychotria mexiae* has been collected in flower February–July and in fruit September–April.

Selected specimens examained. MEXICO. CHIAPAS: Mpio. Jitotol, adjacent to large double waterfall, 6–8 km W of Jitotol, 1,450 m, 16 Dec. 1971 (fr), *Breedlove 23269* (ENCB, F, MO, NY); Mpio. Ocosingo, nr. La Canja, 350 m, 2 Apr. 1973 (fl), *Breedlove 34538* (ENCB, MO, NY); Mpio. Ocozocoautla de Espinosa, 18–20 km N of Ocozocoautla along rd. to Mal Paso, 800 m, 20 Oct. 1971 (fr), *Breedlove & Thorne 20960* (DUKE, ENCB, F, MO, NY); Mpio. La Trinitaria, along Comitan River at its sumidero, Lago de Montebello, 42 km NE of La Trinitaria, 1,300 m, 23 Oct. 1971 (fr), *Breedlove & Thorne 21203* (DUKE, ENCB, F, MO, NY). GUERRERO: Montes de Oca, San Antonio–Buenos Aires, 10 June 1937 (fl), *Hinton et al. 10295* (B, K, US); Dto. Mina, Puerto Rico, 1,750 m, 15 Apr. 1939 (fl), *Hinton et al. 14166* (NY, US). OAXACA: Dto. Ixtlán, Sierra de Juárez, ruta 175 Tuxtepec a Oaxaca, 0.5 km al SW de La Esperanza, 1,700 m, 28 May 1983 (fl), *Cedillo & Lorence 2345* (MEXU); *Lorence & Cedillo 4180* (MEXU). VERACRUZ: Mpio. Soteapan, Sierra de Sta. Marta al N de Ocotal Grande, 1,365 m, 7 Jan. 1972 (fr), *Beaman 5410* (MEXU—2 sheets); Mpio. San Andres Tuxtla, Cerro Vigia, 18°27′N, 95°21′W, 950 m, 24 Jan. 1972 (fr), *Beaman 5513* (F, MEXU—2 sheets, NY); Mpio. San Andres Tuxtla, Cerro Mantagaga, 13 km al NE de San Andres Tuxtla, 1,400 m, 1 Feb. 1972 (fr), *Beaman 5594* (MEXU—2 sheets); Mpio. San Andres Tuxtla, Cerro Vigia, 23 Feb. 1972 (fl), *Beaman & Alvarez 5772* (F, MEXU—3 sheets, NY); vertiente E de Pico de Orizaba, camino de Coscomatepec a Calcahualco, 1,800 m, 10 Mar. 1982 (st), *Lorence et al. 3891* (MEXU); Mpio. de Yecuatla, Loma Santa Rita, 1,480 m, 12 Jan. 1972 (fr), *Ventura 4763* (ENCB, MEXU); Mpio. Banderilla, Banderilla, 1,500 m, 29 Nov. 1976 (fr), *Ventura 13658* (ENCB); Mpio. Atzalán, Alseseca, 1,100 m, 6 June 1980 (fl), *Ventura 17258* (MO). GUATEMALA. ALTA VERAPAZ: Sebol, ca. 4 km on Coban rd., 120 m, 16 Apr. 1964 (fl), *Contreras 4345* (MO); Rubelsanto, Balastrera, 16 July 1975 (early fr), *Lundell & Contreras 19523* (MO). PETÉN: Dolores, km 86–87 E of Machaquila Rd., 25 Sep. 1961 (fr), *Contreras 2968* (MO); Tikal National Park, in ramonal between Temple 4 and "H" group, 13 Mar. 1966 (fr), *Contreras 5580* (ENCB, F, MO, NY); La Cumbre, E of km 138 bordering village, 29 Sep. 1966 (fr), *Contreras 6282* (MO); entre Cristo Rey y Poptún, Yaltutú, 433 m, 11 Nov. 1965 (fr), *A. Molina R. 15578* (F). BELIZE. BELIZE: Western Hwy., mi. 35–36, 23 June 1973 (fl), *Dwyer 10905* (GH, MO); cuevas at Little John's Camp, 10 July 1973 (early fr), *Dwyer 11577* (GH, MO—2 sheets). CAYO: vic. Cuevas S of Millionario, 570 m, 29–30 May 1973 (fl), *Croat 23581* (DUKE, MO—2 sheets, US); Macal River, bridge between Augustine & Cuevas, 10 July 1972 (fl), *Dwyer & Pippin 10193* (ENCB, MO, NY). TOLEDO: 2.3 km S of Mayan village of San José, ca. 8 km W of Columbia Forest Station, river banks on limestone, 12 June 1973 (fl), *Croat 24302* (F, MO, NY). HONDURAS. SANTA BARBARA: Montaña Sta. Barbara, above Sauce nr. Lake Yojoa, 1,000 m, 7 Aug. 1948 (early fr), *L. O. Williams & Molina 14515* (F, GH, MO). NICARAGUA. ESTELÍ: Laguna de Miraflor, 13°15′N, 86°15′W, ca. 1,300 m, 21 Feb. 1982 (fr), *P. P. Moreno 15476, 15487* (MO). JINOTEGA: Laguna Miraflores, 13°15′N, 86°15′W, 1,250–1,300 m, 10–11 June 1981 (fl), *Henrich & Stevens 325* (MO). MATAGALPA: 6–10 km NE of Matagalpa, rd. to El Tuma, 1,000 m, 14–16 Jan. 1963 (fr), *L. O. Williams et al. 23844* (NY, US). COSTA RICA. GUANACASTE: La Tejona, N of Tilarán, 600–700 m, 25 Jan. 1926 (fr), *Standley & Valerio 45770* (US); Naranjos Agrios, 600–700 m, 29 Jan. 1926 (fr), *Standley & Valerio 46375* (US).

Palicourea nigrescens and *Psychotria schippii* are morphologically identical to *P. mexiae* and are therefore included. The existing name *Psychotria nigrescens* De Wild. (dating to 1924) leaves "*mexiae*" as the oldest available epithet.

Psychotria mexiae may be recognized by its elliptic long-acuminate leaves drying green-brown to red-brown with veins drying reddish below; globose panicles without peduncle and with 4 equal secondary axes in each of the first 2 ranks; long (2.5–4.5 mm) corolla tube often drying pink; and ellipsoid to spherical fruit drying often shiny red-brown and appearing smooth outside due to the irregularity of the furrows on the dorsal surface of the seed. Corolla tubes are shorter in specimens from Belize (2.5 mm) than in those from Mexico (4–4.5 mm), and the stamens and styles are scaled down accordingly. Fruits are larger (5–6 mm long) in specimens from Veracruz and Guatemala than from elsewhere (4.5–5 mm long).

The exserted pistil of the pin morph is usually longer than the exserted stamens of the thrum (4–7 vs. 3.5–5.5 mm).

43. Psychotria olgae Dwyer & Hayden, Ann. Missouri Bot. Gard. 55: 42, fig. 3. 1968. TYPE: Panama. Panamá: between Cerro Jefe and Eneida, 630–870 m, 17 Jan. 1968 (fr), *Dwyer et al. 8193* (holotype, MO; isotypes, DUKE, F, NY). Figures 10g, 29.

Tree 2–8(–10) m tall; young stems puberulent, the bark pale, slightly ridged longitudinally; stipules lanceolate, sometimes biacuminate, 3–5 × 1.5 mm, ciliate at apex, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 2–3 mm long, glabrous, flat above, robust; blades coriaceous, elliptic to obovate, the apex obtuse to rounded, the base subcordate, the margins inrolled, (5–)6–10 × (1.5–)2.5–4.5 cm, glabrous above and below, drying green-brown to red-brown; secondary veins 5–7 pairs, diverging 60°–65°, eucamptodromous to brochidodromous, constantly arcuate, prominulous below, glabrous, the axils lacking domatia or hairs; tertiary veins not evident. *Inflorescences* terminal or pseudoaxillary, panicles of glomerules; panicle branched to 3 degrees; main axis 2.5–9 cm long, the peduncle 1.5–5.5 cm long; secondary axes in 2 ranks, the first-rank axes 2, 1–3 cm long, the second-rank axes 2, 0.4–1 cm long; bracts and bracteoles irregular, 1 mm long, ciliate. *Flowers* pedicellate, the pedicels 2–3 mm long; calyx cup-shaped, the tube 1 mm long, the lobes 5, broad triangular to not evident, to 0.5 mm long, minutely ciliate; corolla green, leathery, the tube cylindrical, 2.5–3.5 × 2 mm, white pubescent in throat, the lobes 5, ovate, 2.5–3 × 1.5 mm; stamens 5, the filaments 3–3.5 mm long in pins, 4 mm long in thrums, the anthers 1–1.5 mm long; style 6 mm long in pins, 2.5–3 mm long in thrums, the branches linear. *Fruit* when dry ellipsoid to slightly obovoid, 9–10 mm long, 5.5–7 mm diam., maturing red, drying red-brown; persistent calyx a tubular beak to 1 mm long; seed dorsal surface with 4 deep regular and numerous irregular longitudinal furrows, the ventral surface with 2 deep regular and several irregular longitudinal furrows (Fig. 10g).

Distribution (Fig. 29). Known only from the region of Cerro Jefe, eastern Panamá Province, Panama, at 800–1,200 m elevation in premontane wet forest with equatorial-mountainous climate. This species has been collected in flower in March, June, and July and in fruit in October and January.

Additional specimens examined. PANAMA. PANAMÁ: Cerro Jefe, to 930 m, 12 Mar. 1968 (fl), *Dwyer et al. 7288* (F, MO); rd. from Pan-American Hwy. to Cerro Jefe, 21.7 km from Pan-Am. Hwy., 22 June 1977 (fl), *Folsom 3817* (CR, MO); Cerro Jefe, on top nr. antenna, ca. 1,200 m, 19 Jan. 1977 (fr), *Folsom & Harp 1368* (CR, MO); Cerro Jefe region, 1,000 m, 8 Jan. 1975 (fr), *Luteyn & Wilbur 4655* (DUKE); Cerro Jefe, ca. 1,000 m, 14 July 1975 (fl), *Mori 7122* (MO, US); 14 July 1975 (fl), *Mori 7133* (MO); 5 June 1975 (fl), *Mori & Kallunki 6507* (MO—2 sheets, US); Cerro Jefe, 1.5 km before weather station, 850–900 m, 8 Oct. 1980 (fr), *Sytsma 1504* (MO); Cerro Jefe, 850–900 m, 29 Oct. 1980 (fr), *Sytsma 1990* (MO).

Psychotria olgae may be recognized by its coriaceous leaves with subcordate base and inrolled margins and by its large (9–10 × 5.5–7 mm) ellipsoid to slightly obovoid fruit.

The reproductive organs are longer at both levels in the pin morph that in the thrum.

44. Psychotria panamensis Standley, Contr. U.S. Natl. Herb. 18: 132. 1916. TYPE: Panama. Chiriquí: S slope of Cerro Horqueta, Los Siguas Camp, ca. 1,700 m, 17–19 Mar. 1911 (fl, fr), *Pittier 3194* (holotype, US). Figures 2d, 7e, 28.

Shrub or tree, (1–)2–13 m tall; young stems minutely puberulent to short-ferrugineous pubescent, the bark usually furrowed longitudinally; stipules usually sheathing, lanceolate, (10–)20–80 × (2.5–)3.5–7 mm, glabrous, minutely puberulent or red-brown ciliate, caducous, leaving a pale ridge with red-brown fringe (Fig. 2d). *Leaves* petiolate; petioles (0.5–)2–4.5(–5) cm long, glabrous or puberulent, flat or grooved above; blades membranous

to subcoriaceous, elliptic to obovate, the apex acuminate, the base subcordate to cuneate, (7–)9–28 × (2.5–)4–11(–13) cm, glabrous above and below, the midvein sometimes puberulent below, drying red-brown to green-brown; secondary veins (6–)8–19(–22) pairs, diverging 45°–70°, eucamptodromous to sometimes brochidodromous, constantly arcuate or straight then arcuate near margin, elevated below, glabrous or minute-puberulent, the axils lacking domatia or hairs, or having segments of red-brown hairs along midvein and secondary vein; tertiary veins inconspicuous, orthogonal reticulate to percurrent. *Inflorescences* terminal or pseudoaxillary, panicles of cymes or glomerules (Fig. 7e); panicle branched to 3–5 degrees; main axis 1.5–12 cm long, the peduncle usually lacking or 1.5–3 cm long; secondary axes in 3–7(–8) ranks, the first-rank axes 2 or 4, equal or subequal, 0.8–7 cm long, the second-rank axes 2, 0.4–4 cm long, the third-rank axes 2, 0.2–3 cm long, the fourth-rank axes 2, 0.2–2 cm long, the fifth-rank axes 2, 0.1–1 cm long, the sixth-rank axes 2, 0.2–0.6 cm long, the seventh-rank axes 2, 0.1–0.2 cm long, the eighth-rank axes 2, 0.1 cm long; cymes branched to 1–3 degrees; bracts and bracteoles irregular or not evident, to 1 mm long, ciliate. *Flowers* pedicellate, the pedicels 0.5–1 mm long, sometimes (var. *ixtlanensis*) with minute spheroidal glands; calyx cup-shaped, the tube 0.3–0.5 mm long, the lobes 0 or 5, triangular to not evident, to 0.3 mm long, minutely ciliate; corolla white or cream, the tube cylindrical, 2–3 × 1.5–2 mm, white pubescent in throat, the lobes 5, lanceolate or triangular, 1.5–2.5 × 0.8–1 mm; stamens 5, the filaments 2–3 mm long in pins, 3.5–5 mm long in thrums, the anthers 0.7–1 mm long; style 4–6 mm long in pins, 2.5–3 mm long in thrums, the branches clublike, spathulate, or linear. *Fruit* when dry ellipsoid to obovoid, 4.5–8 mm long, 3.5–6.5(–7) mm diam., maturing red, drying red-brown to sometimes (var. *ixtlanensis*) red-black; persistent calyx inconspicuous or a beak to 1 mm long; seed dorsal surface with 4 deep irregular or 7–10 irregular longitudinal furrows, the ventral surface with 2 central furrows often plus 2 deep or several irregular lateral longitudinal furrows.

Distribution (Fig. 28). Southern Mexico through Panama, at elevations of 0–2,100 m. Varieties *compressicaulis* and *magna* occur at lower elevations, while varieties *ixtlanensis* and *panamensis* occur mostly above 1,000 m.

Psychotria panamensis may be recognized by its large (usually 20–80 mm long) lanceolate sheathing stipules, leaves drying usually dark red-brown, inflorescences with robust secondary axes usually 2 per rank in 3–7(–8) ranks and usually with no peduncle, and large (usually 4.5–8 × 3.5–6.5 mm) ellipsoid fruit drying almost always red-brown and without a conspicuous persistent calyx.

KEY TO VARIETIES OF *PSYCHOTRIA PANAMENSIS*

1a. Inflorescence main axis 1.5–3 cm long, the secondary axes in 3(4) ranks; fruit obovoid; endemic to Oaxaca ..... 44b. var. *ixtlanensis*
1b. Inflorescence main axis 5–12 cm long, the secondary axes in 5–7 ranks; fruit usually ellipsoid.
  2a. Fruit 4.5–5 × 3.5–4 mm; Caribbean eastern Panama ..... 44c. var. *magna*
  2b. Fruit 5.5 × 4.5 mm and larger.
    3a. Leaf blades 15–28 × 5.5–13 cm, the secondary veins 16–19; fruit 5.5–7 × 4.5–6 mm; lowland Caribbean Nicaragua and Costa Rica ..... 44a. var. *compressicaulis*
    3b. Leaf blades generally 9–15 × 4–6 cm, the secondary veins 8–16; fruit generally 7–8 × 5.5–6.5 mm; Mexico through Panama, mostly above 500 m ..... 44d. var. *panamensis*

44a. Psychotria panamensis Standley var. **compressicaulis** (K. Krause) C. Hamilton, Phytologia 64: 233. 1988. *Psychotria compressicaulis* K. Krause, Bot. Jahrb. Syst. 54: Beibl. 119: 44. 1916. TYPE: Costa Rica. Cartago: Tuis, 600 m, July 1898 (fl), *Pittier 12412* (holotype, B, destroyed, photo, GH; isotype, US). Figure 28.

Shrub or *tree* (1–)2–10 m tall; stipules sheathing, lanceolate, (10–)20–35 × (3–)3.5–5 mm, glabrous. *Leaves:* blades membranous, the base cuneate to rarely subcordate, (8–)15–28 × (3–)5.5–13 cm, drying dark red-brown; secondary veins (13–)16–19(–20) pairs, the axils lacking domatia or hairs; tertiary veins inconspicuous, orthogonal reticulate to percurrent. *Inflorescences:* panicle branched to 4–5 degrees; main axis 7–9 cm long, the peduncle usually lacking or ca. 1.5 cm long; secondary axes in 6–7 ranks, the first-rank axes 2, 4.5–7 cm long, the second-rank axes 2, 2.2–4 cm long, the third-rank axes 2, 1–2 cm long, the fourth-rank axes 2, 0.8–1.5 cm long, the fifth-rank axes 2, 0.4–0.9 cm long, the sixth-rank axes 2, 0.2–0.6 cm long, the seventh-rank axes 2, 0.1–0.2 cm long; cymes branched to 2 degrees. *Flowers:* corolla white, the tube 2–2.5 × 1.5–2 mm, the lobes lanceolate, 1.5–2 × 1 mm; stamens 5, the filaments not seen in pins, 3.5–4 mm long in thrums; style not seen in pins, 2.5–3 mm long in thrums, the branches linear. *Fruit* when dry ellipsoid, 5.5–7 mm long, 4.5–6 mm diam., drying

red-brown; persistent calyx not evident; seed dorsal surface with 4 deep irregular longitudinal furrows, the ventral surface with 2 deep incompletely divided plus several irregular longitudinal furrows.

Distribution (Fig. 28). Caribbean lowlands of Nicaragua and Costa Rica, at 0–200 m elevation in tropical moist to wet (to premontane wet) forest with equatorial climate. This variety has been collected in flower July–August and in fruit November–July.

Selected specimens examined. NICARAGUA. RÍO SAN JUAN: nr. Caño Chontaleño, 20 km NE of El Castillo, Río Indio watershed, 200 m, 7–9 Mar. 1978 (fr), *Neill 3402* (MO). ZELAYA: Mpio. de Nueva Guinea, Bocas de Piedra, 2 Nov. 1982 (st), *Laguna 131* (MO); logging camp nr. Qda. La Talolinga, 11°51′N, 84°26′W, 170 m, 19 Aug. 1983 (fl), *J. Miller & Sandino 1165* (MO); Monkey Point, 3 km al S, 11°37′N, 83°40′W, 10 m, 24 Oct. 1981 (early fr), *P. P. Moreno & Sandino 12259* (MO); Río Punta Gorda, Atlanta, "La Richard," 200 m al SE, 11°32′N, 84°05′W, 20 m, 13 Nov. 1981 (fr), *P. P. Moreno & Sandino 13027a* (MO); new rd. to Mina Nueva America, leading more or less W from 14.3 km N of El Empalme on main rd. to Rosita, 7.7 km from main rd., 23 Feb. 1979 (fr), *W. D. Stevens 12708* (MO); vic. junction of rd. to Alamikamba with rd. between El Empalme and Limbaika, 13°32′N, 84°30′W, 25 m, 24 Feb. 1979 (fr), *W. D. Stevens 12740* (MO). COSTA RICA. ALAJUELA: 2–3 km NW of Bajo, Rodríguez, ca. 30 km N of La Balsa de San Ramón, 300 m, 8 June 1976 (fr), *J. Utley & K. Utley 5137* (DUKE). HEREDIA: Finca La Selva, the OTS field station on the Río Puerto Viejo, 100 m, 5 Apr. 1979 (fr), *Beach 1418* (CR, DUKE, MO); 4 Aug. 1980 (fl), *MacDougal 1092* (DUKE); Sarapiquí, Tirimbina, Istarú Farm, 220 m, 26 Nov. 1971 (fr), *Lent 2246* (CR, DUKE, MO, NY, US). PUNTARENAS: Corcovado National Park, slopes above Llorona, 8°36′N, 83°42′W, 13 July 1977 (fl), *Liesner 3263* (CR, MO).

All eleven flowering collections are thrum morphs, suggesting that the variety is thrum-monomorphic.

44b. Psychotria panamensis Standley var. **ixtlanensis** C. Hamilton, Phytologia 64: 233. 1988. TYPE: Mexico. Oaxaca: Dto. de Ixtlán, 21.4 km al S de Valle Nacional, 17°41′N, 96°18′W, 1,140 m, 28 Nov. 1979 (fr), *Wendt et al. 2258* (holotype, MEXU—317322; isotype, ENCB). Figure 28.

Shrub 2–4 m tall; stipules lanceolate-acuminate, (10–)30–60 × (2.5–)5–7 mm, minutely puberulent. *Leaves:* blades membranous, the base cuneate to attenuate, (9–)16–21 × (3–)5–7.5 cm, drying green-brown; secondary veins 12–17 pairs, the axils lacking domatia or hairs; tertiary veins inconspicuous, orthogonal reticulate. *Inflorescences:* panicle branched to 3–4 degrees; main axis 1.5–3 cm long, the peduncle lacking; secondary axes in 3(4) ranks, the first-rank axes (2)4, subequal, 0.8–2.2 cm long, the second-rank axes 2, 0.4–1.0 cm long, the third-rank axes 2, 0.2–0.6 cm long, the fourth-rank axes 2, 0.2 cm long; cymes branched to 1–2 degrees. *Flowers:* corolla cream, the tube 3 × 1.5 mm, the lobes triangular, 1.5 × 1 mm; stamens 5, the filaments 2–2.5 mm long in pins, not seen in thrums; style 4 mm long in pins, not seen in thrums, the branches short, club-like. *Fruit* when dry obovoid, 5–6 mm long, 4–4.5 mm diam., drying dark red-brown to red-black; persistent calyx inconspicuous or a minute beak to 0.5 mm long; seed dorsal surface with 4 deep irregular longitudinal furrows, the ventral surface with 2 incompletely divided central plus 2 deep lateral longitudinal furrows.

Distribution (Fig. 28). Known only from type region of Ixtlán, Oaxaca, Mexico, at ca. 900–1,140 m elevation in a region of evergreen to subevergreen forest with tropical-mountainous climate. This variety has been collected in flower April–June and in fruit September, November, and April.

Selected specimens examined. MEXICO. OAXACA: Dto. de Ixtlán, Sierra de Juárez, a 2.5 km al NE de Puerto Eligio, 900 m, 2 June 1983 (fl), *Cedillo & Lorence 2397* (MEXU); entre Vista Hermosa y Comaltepec, a 1.5 km al S de Vista Hermosa, Sierra Juárez, 16 Sep. 1965 (fr), *G. Martínez C. 296* (ENCB, MO); Dto. de Ixtlán, 5.3 km al N de Vista Hermosa, carr. a Oaxaca–Tuxtepec, 27 Sep. 1982 (fr), *Torres & Cedillo 1461* (ENCB, MEXU).

This variety, with its leaves drying greenish and fruit obovoid, may be the result of local introgression involving *Psychotria trichotoma* in the Ixtlán region of Oaxaca.

Four flowering collections are all of the pin morph, suggesting (albeit weakly; $p = 0.125$) that the variety may be pin-monomorphic.

44c. Psychotria panamensis Standley var. **magna** (Standley) C. Hamilton, Phytologia 64: 234. 1988. *Psychotria magna* Standl., Contr. U.S. Natl. Herb. 18: 131. 1916. TYPE: Panama. Colón: Loma de la Gloria, nr. Fató (Nombre de Dios), 10–104 m, Aug. 1911 (fl), *Pittier 4092* (holotype, US-679188; isotype, US-693188). Figure 28.

Shrub; stipules not seen. *Leaves:* blades membranous, the base cuneate, 17–24 × 7–11 cm, drying red-brown; secondary veins 14–22 pairs, the axils lacking domatia or hairs; tertiary veins inconspicuous, percurrent. *Inflorescences:* panicle branched to 5 degrees; main axis 10–12 cm long, the peduncle lacking; secondary axes in 6 ranks,

the first-rank axes 2, 6 cm long, the second-rank axes 2, 4 cm long, the third-rank axes 2, 3 cm long, the fourth-rank axes 2, 2 cm long, the fifth-rank axes 2, 1 cm long, the sixth-rank axes 2, 0.6 cm long; cymes branched to 1–3 degrees. *Flowers:* corolla color unknown, the tube 2–2.5 × 1.5 mm, the lobes lanceolate, 1.5–2 × 0.8 mm; stamens 5, the filaments not seen in pins, 3.5 mm long in thrums; style not seen in pins, 2.5 mm long in thrums, the branches clublike or linear. *Fruit* when dry ellipsoid to slightly obovoid, 4.5–5 mm long, 3.5–4 mm diam., drying dark red-brown; persistent calyx a minute beak; seed dorsal surface with 4 deep irregular longitudinal furrows, the ventral surface with 2 incompletely divided central plus 2 deep lateral longitudinal furrows.

Distribution (Fig. 28). Known only from the Caribbean coast of Panama just east of the Panama Canal in tropical moist forest with equatorial-tropical climate. This variety has been collected in flower in August and in fruit in October.

Additional specimens examined. PANAMA. SAN BLAS: trail E of Cangandí–Mandinga airport rd., 2–5 mi. S of Mandinga airport, 27 Oct. 1967 (fr), *Duke 14782* (MO, US).

The only flowering collection is of a thrum flower morph.

44d. **Psychotria panamensis** Standley var. **panamensis**. Figure 28.

Psychotria grandistipula Standley, J. Wash. Acad. Sci. 18: 276. 1928, not *Psychotria grandistipula* Merr., J. Asiat. Soc. Mal. 1: 42. 1923. TYPE of *P. grandistipula* Standl.: Costa Rica. San José: vic. Sta. María de Dota, ca. 1,600 m, 26 Dec. 1925 (fr), *Standley & Valerio 43268* (holotype, US).

Psychotria yunckeri Standley in Yuncker, Publ. Field Mus. Nat. Hist., Bot. Ser. 17: 397. 1938. TYPE: Honduras. Comayagua: nr. summit of range above El Achote, above plains of Siguatepeque, 1,850 m, 21 July 1936 (fl), *Yuncker et al. 6013* (holotype, F; isotypes, GH, K, MO).

Psychotria molinae Standley, Ceiba 1: 46. 1950. TYPE: Honduras. Francisco Morazán: drainage of Río Yeguare, 14°N, 87°W, 2,000 m, 20 Aug. 1946 (fl), *L. O. Williams & Molina 10390* (holotype, F—1264188; isotypes, F, GH).

Psychotria durilancifolia Dwyer, Ann. Missouri Bot. Gard. 67: 372. 1980. TYPE: Panama. Panamá: El Llano–Cartí Rd., vic. Gorgas Lab Mosquito Control Project site at km 12, 1 Aug. 1974 (fl), *Croat 26028* (holotype, MO—2240525).

Tree (2–)4–13 m tall; stipules sheathing, lanceolate, (10–)30–80 × (3.5–)5–7 mm, red-brown ciliate. *Leaves:* blades membranous to subcoriaceous, the base cuneate to subcordate, (7–)9–15(–22) × (2.5–)4–6(–10) cm, drying deep red-brown or sometimes green-brown; secondary veins (6–)8–16(–20) pairs, the axils lacking domatia or hairs or sometimes with segments of red-brown hairs along midvein and secondary veins below; tertiary veins inconspicuous, orthogonal reticulate. *Inflorescences:* panicle branched to 3–4 degrees; main axis (2.5–)5–9 cm long, the peduncle usually lacking, or 1.5–3 cm long; secondary axes in (4–)5–7(–8) ranks, the first-rank axes 2, (1–)2–6.5 cm long, the second-rank axes 2, (0.4–)1–3.5 cm long, the third-rank axes 2, (0.2–)0.6–2 cm long, the fourth-rank axes 2, (0.1–)0.2–1.5 cm long, the fifth-rank axes 2, 0.1–0.6 cm long, the sixth-rank axes 2, 0.4 cm long, the seventh-rank axes 2, 0.2 cm long, the eighth-rank axes 2, 0.1 cm long; cymes branched to 1–2 degrees. *Flowers:* corolla white, the tube 2–3 × 1.5–2 mm, the lobes lanceolate, 2–2.5 × 1 mm; stamens 5, the filaments 2.5–3 mm long in pins, 4–5 mm long in thrums; style 4–6 mm long in pins, 2.5 mm long in thrums, the branches spathulate. *Fruit* when dry ellipsoid, (6–)7–8 mm long, (4.5–)5.5–6.5(–7) mm diam., drying red-brown; persistent calyx usually a beak to 1 mm long; seed dorsal surface with 7–10 irregular longitudinal furrows, the ventral surface with 2 deep plus several irregular longitudinal furrows.

Distribution (Fig. 28). Continuous along the central cordillera from Veracruz, Mexico, to eastern Panama, at 200–2,100 m elevation, almost all above 500 m, in premontane to low montane wet forest to rainforest with usually equatorial to tropical-mountainous climate. It has been collected in flower throughout the year, primarily March–August, and in fruit throughout the year, primarily November–April.

Selected specimens examined. MEXICO. CHIAPAS: Mpio. Berriozábal, 13 km N of Berriozábal nr. Pozo Turipache and Finca El Suspiro, 1,000 m, 24 July 1972 (fr), *Breedlove 26311* (F, MEXU, MO); Mpio. La Trinitaria, E of Laguna Tzikaw, Monte Bello National Park, 1,300 m, 13 May 1973 (fl), *Breedlove 35141* (ENCB, MEXU, MO, NY); 16 Nov. 1972 (fr), *Breedlove & Dressler 29565* (MEXU, MO, NY); Mpio. Rayón, Selva Negra 10 km above Rayón Mezcalapa along rd. to Jitotol, 1,700 m, 25 Jan. 1973 (fr), *Breedlove & Smith 32414* (ENCB, MEXU, MO); Mpio. Angel Albino Corzo, nr. the Rancho Viejo of the Finca Prusia, 720 m, 23 Jan. 1968 (fr), *Ton 3581* (ENCB). OAXACA: Hwy. 175, 18.4 mi. S of Valle Nacional bridge, 1,500 m, 19 Feb. 1979 (fl), *Croat 48055* (CR, MO); Mpio. Matías Romero, 9.5 km por camino al SE del Aserradero La Floresta, 21.5 km al S de Esmeralda, 17°03′N, 94°43′W, 400 m, 25 May 1981 (fl), *Wendt et al. 3307* (MEXU); Mpio. Matías Romero, orilla N del Río Verde, 6.4 km al SE de Aserradero La Floresta sobre camino a Arroyo Amaca, 17°03′N,

94°45′W, 200 m, 30 Nov. 1981 (fr), *Wendt et al. 3555* (MEXU). PUEBLA: Mpio. de Teziutlán, Río Frío, 1,450 m, 29 Mar. 1973 (fr), *Ventura 8094* (ENCB). VERACRUZ: Mpio. San Andres Tuxtla, lado W de Cerro Mastagaga, ca. 13 km al NE de San Andres Tuxtla, 1,200 m, 29 Jan. 1972 (fr), *Beaman 5564* (F, MEXU—2 sheets, MO); Mpio. de Soteapan, lado W de la Sierra de Santa Marta cerca del Ejido de Santa Marta, 1,220 m, 28 May 1972 (fl), *Beaman 6007* (F, MEXU—2 sheets); Mpio. de Santiago Tuxtla, cima del Cerro Vigia, 950 m, 22 July 1972 (fr), *Beaman 6391* (MEXU); Mpio. Atzalán, la Calavera, carret. Altotonga a Tlapacoyan, 1,500 m, 17 May 1973 (fl), *Chazaro & Dorantes 110* (MEXU); Mpio. Soteapan, camino de Tebanca a Bastonal, 6–8 km al SE de Tebanca, 1,000–1,100 m, 26 Apr. 1982 (fl), *Lorence et al. 4238* (MEXU); Mpio. Teocelo, 19°23′N, 96°57′W, 17 Feb. 1973 (fr), *Menéndez 67* (MEXU); Mpio. Chocamán, 1 km N of Chocamán, gorge of river upstream from Chocamán–Coscomatepec hwy., 19°02′N, 97°01′W, 1,350 m, 7 Dec. 1981 (fr), *Nee 23880* (MO); Mpio. Totutla, Zochiapa, 1,280 m, 25 Apr. 1972 (fl), *Ventura 5288* (MEXU). GUATEMALA. BAJA VERAPAZ: Unión Barrios, E of km 154, 8 June 1975 (fl), *Lundell & Contreras 19396* (LL); 3 km SE of Purulha, Sierra de los Minas, cloud forest, 1,800 m, 4 Jan. 1974 (fr), *L. O. Williams et al. 43149* (F). CHIMALTENANGO: lower and middle SW slopes of Volcán Fuego, above Finca Montevideo, along Barranco Espinoza and tributary of Río Pantaleón, 1,200–1,600 m, 20 Sep. 1942 (early fr), *Steyermark 52052* (F). IZABAL: Cerro San Gil, uppermost ridges and summit, 1,200–1,300 m, 26–27 Dec. 1941 (st), *Steyermark 41968* (F). JALAPA: Volcán Jumay, N of Jalapa, 1,300–2,200 m, 1 Dec. 1939 (fl), *Steyermark 32472* (F). QUEZALTENANGO: Volcán Zunil, 1,700 m, 31 July 1934 (fl), *Skutch 890* (A, F, NY, US); lower S-facing slopes of Volcán Santa María, between Santa María de Jesús and Calahuaché, 1,300–2,000 m, 1–2 Jan. 1940 (fr), *Steyermark 33417* (F). SAN MARCOS: S-facing slopes of Volcán Tajumulco, above Finca El Porvenir, 1,400–1,700 m, 9 May 1940 (fr), *Steyermark 37415* (F); 1,300–1,500 m, 16 Mar. 1940 (fl), *Steyermark 37948* (F). HONDURAS. COMAYAGUA: bosque de Montaña La Choca cerca de Qda. El Zope, 1,500 m, 15 Apr. 1957 (fr), *A. Molina R. 8177* (F, US); Barranco Trincheras, 20 km al N de Siguatepeque, 1,400 m, 18 July 1962 (fr), *A. Molina R. 10823* (F, NY); 10 km W of Siguatepeque, pine forest, 1,200 m, 29 July 1974 (early fr), *A. Molina R. 30578* (ENCB, F, MO). DISTRITO CENTRAL: ca. 10 km N of Tegucigalpa, cloud forest, La Tigra, 16 Feb. 1972 (fr), *Clewell & M. Hernández 3039* (TEFH). FRANCISCO MORAZÁN: Mt. Uyuca, nr. Zamorano, 1,500 m, 21 Feb. 1952 (fr), *Carlson 2449* (F); Cerro de Uyuca, trail from Las Flores to La Labranza, 1,600–1,750 m, Oct.–Dec. 1948 (fl), *Standley 13377* (F). INTIBUCA: Rastrojos del Pelón de Guise a lo largo de la quebrada, 1,600 m, 9 Apr. 1956 (fr), *A. Molina R. 6370* (GH, US); Cordillera Opalaca, between Pela Naríz and Calaveras, rd. to La Esperanza, 2,000 m, 3 Sep. 1968 (fl), *A. Molina R. 22615* (NY—2 sheets). LA PAZ: Cordillera Guajiquiro 5 km a Sabanetas, 2,100 m, 21 Mar. 1964 (fl), *A. Molina R. & A. Molina 13882* (NY); Cordillera Guajiquiro, Montaña Verde, 1,900 m, 23 Mar. 1969 (fr), *A. Molina R. & A. Molina 24394* (F, NY). LEMPIRA: Montaña de Celaque, 1,900 m, 18–22 Nov. 1974 (fr), *Hazlett s.n.* (MO). NICARAGUA. BOACO: Cerro Alegre, San José de Los Remates, 12°26′N, 85°44′W, 1,100–1,180 m, 11 Feb. 1983 (fr), *P. P. Moreno 20240* (MO). CHONTALES: Cerro Oluma, 750 m, 4 Jan. 1984 (st), *Gentry et al. 43930* (MO). ESTELÍ: Laguna de Miraflor, 13°15′N, 86°15′W, 1,260–1,300 m, 29 Aug. 1982 (fl), *Grijalva 947* (MO); 29 Mar. 1983 (fr), *P. P. Moreno 21132* (MO); Cerro Quiabu, ca. 8 km NO de Estelí, 1,500–1,600 m, 19 Oct. 1979 (fr), *Grijalva & Araquistain 656* (MO—2 sheets). GRANADA: W slope of Volcán Mombacho, rd. and trail above Finca Sta. Ana, from reservoir to somewhat above Plan del Flores, 11°50′N, 85°58′W, 950–1,150 m, 1 Oct. 1977 (fl), *W. D. Stevens 4327* (MO); Volcán Mombacho, Plan del Flores to W rim, cloud forest, 11°50′N, 85°58′W, 1,100–1,220 m, 14 Nov. 1978 (fr), *W. D. Stevens 10830* (MO). JINOTEGA: 4 km al SE del Cerro Kilambé, 13°35′N, 85°40′W, 800–1,000 m, 25 Mar. 1981 (fr), *P. P. Moreno 7459* (MO). MATAGALPA: El Comején, 1 km W de la carret. a Waslala, 13°15′N, 85°34′W, 600 m, 23 Feb. 1983 (fr), *P. P. Moreno & Robleto 20569* (MO). RIVAS: Isla de Ometepe, N slope of Volcán Maderas on trail from Balgue to Laguna Maderas, 11°27′N, 85°32′W, 1,200 m, 23 Jan. 1981 (fr), *W. Hahn 510* (MO); Isla de Ometepe, N de Volcán Concepción, 11°33′N, 85°37′W, 1,100–1,150 m, 11 Mar. 1981 (fl), *Sandino 492* (MO). COSTA RICA. ALAJUELA: Sta. María National Park, 10°48′N, 85°16′W, 600 m, 8 Feb. 1978 (fr), *Liesner 5218* (CR, MO); 15 km NW of San Ramón by air, Cerro Azahar, headwaters of Río San Pedro, 10°09′N, 84°34′W, 1,400–1,500 m, 14 May 1983 (fr), *Liesner et al. 15563* (CR, MO); Zapote, 1,400 m, 17 Aug. 1938 (fl), *A. Smith 1103* (A, F, MO); region of Zarcero, 1,600 m, 6 July 1937 (fl), *A. Smith 4224* (F). GUANACASTE: Los Ayotes, nr. Tilarán, 600–700 m, 21 Jan. 1926 (fr), *Standley & Valerio 45433* (US). HEREDIA: Volcán Barba, nr. San José de la Montaña, 1,600 m, 19 June 1965 (fl), *Hatheway 1460* (US). PUNTARENAS: rd. to Las Alturas, 8°56′N, 82°51′W, 1,400 m, 10 July 1972 (fl, early fr), *Lent 2727* (CR, F, MO). SAN JOSÉ: Pacific slope of Cerro Chirripó massif, 2,000 m, 7 Apr. 1969 (fl), *Davidse & Pohl 1668* (F, MO, NY); vic. Sta. María de Dota, 1,500–1,800 m, 26 Dec.–Jan. 1926 (fr), *Standley & Valerio 44098* (US). PANAMA. CHIRIQUÍ: trail from Bambito to Cerro Punta, along Río Chiriquí Viejo, 6 Apr. 1937 (fl, fr), *Allen 308* (A, F, GH—2 sheets, MO—2 sheets, US); vic. "New Switzerland," central valley of Río Chiriquí Viejo, 1,800–2,000 m, 6–14 Jan. 1939 (fl), *Allen 1387* (F, GH, MO, NY, US); SO del campamento Fortuna, propriedad del IRHE, 8°45′N, 82°15′W, 1,000–1,200 m, 25 Sep. 1976 (early fr), *M. Correa A. et al. 2796* (CR, MO); on NW side of Cerro Pando cloud forest, 21 July 1971 (fl), *Croat 15990* (MO—2 sheets); 21 July 1971 (early fr), *Croat 15993* (MO); Boquete, Cerro Horqueta, 1,500–1,800 m, 8 Aug. 1967 (fr), *Dwyer & Hayden 7693* (DUKE, F, MO, NY); along Río Colorado, 8°50′N, 82°43′W, 1,200–1,400 m, 11 July 1983 (st), *Hamilton & Krager 3773* (MO); Nueva Suiza, 8°52′N, 82°40′W, ca. 1,300 m, 21 Aug. 1982 (early fr), *Hamilton et al. 763* (CR, MO); Sta. Clara region, 27 km NW of El Hato del Volcán, finca of R. Hartman, 1,500–1,600 m, 18 July 1975 (early fr), *Mori & Bolten 7190* (MO). COCLÉ: foothills of Cerro Pilón, nr. El Valle, ca. 900 m, 5 Oct. 1967 (early fr), *Duke & Correa 14672* (MO—2 sheets); 7 km N of El Copé, lumber camp, ca. 900 m, 11 Jan. 1977 (fl, fr), *Folsom 1202* (MO); Coclesito rd., 20 Apr. 1978 (fr), *Hammel 2558* (MO); 15–20 km NE of La Pintada towards Toabre, 600–1,000 m, 15 Feb. 1981 (fl), *Sytsma & D'Arcy 3643* (MO). COLÓN: Cerro Santa Rita, ca. 6 mi. from the Transisthmian Hwy., 250 m, 13 Sep. 1979

(early fr), *Antonio 1804* (ENCB, MO); Santa Rita Ridge lumber rd., 11 Jan. 1968 (fr), *M. Correa A. & Dressler 600* (DUKE, GH, MO); Santa Rita Ridge, 23 Jan. 1968 (fr), *Dwyer & Correa 8423* (DUKE, MO—2 sheets, NY). DARIÉN: headwaters of Río Tuqueza, between Qda. Venado and Peje Swamp, 28 June 1967 (fl), *Bristan 1051* (MO). PANAMÁ: Cerro Jefe, Feb. 1968 (fr), *Gómez-Pompa et al. 3065* (MEXU, MO); El Llano–Cartí Rd., 8–11 km from Inter-American Hwy., 300–400 m, 13 Aug. 1975 (fl), *Mori 7734* (MO, US); Cerro Campana, ca. 10 km SE of Capira, trail to summit, 870–1,000 m, 7 Dec. 1974 (fr), *Mori & Kallunki 3556* (MO—2 sheets). VERAGUAS: rd. between Escuela Agricola Alto Piedra and Río Dos Bocas, ca. 10 km from escuela, 530–620 m, 26 July 1974 (fl), *Croat 25878* (DUKE, F—2 sheets, GH, MO, NY); "Cerro Tute" ridge up from former Escuela Agricola, Santa Fe, 8°35′N, 81°05′W, 800–1,000 m, 20 Feb. 1983 (fr), *Hamilton & Dressler 2986* (CR, MO); NW of Sante Fe, 1 km from Escuela Agricola Alto de Piedra, 24 Feb. 1975 (fr), *Mori & Kallunki 4785* (ENCB, MO).

The morphologies of *P. grandistipula* Standl., *P. yunckeri*, *P. molinae*, and *P. durilancifolia* fall well within the broad range of *P. panamensis* var. *panamensis*, so these former species are merged with var. *panamensis*.

Psychotria panamensis var. *panamensis* shows great variation within its range, including the following: leaves from Veraguas, Panama, are narrower and more coriaceous than those from elsewhere; leaves from Colón, Panama, are unusually large; secondary veins are more numerous in material from Guatemala, Honduras, and Colón and fewer in material from Chiapas, Mexico, and from Coclé, Panamá, and Veraguas provinces in Panama; secondary vein angle of divergence is greatest in leaves from Chiriquí, Panama; secondary veins are brochidodromous in Nicaraguan specimens; inflorescences are largest in specimens from Panama and Costa Rica; flowers are generally larger in Costa Rican material; and the corolla tubes from Honduras are narrowest (1.5 mm).

45. Psychotria sarapiquensis Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1360. 1938. TYPE: Costa Rica. Heredia: Vara Blanca de Sarapiquí, 1,500 m, July–Sep. 1937 (fl), *Skutch 3330* (holotype, US; isotypes, GH, K, MO). Figure 31.

Tree 2–10 m tall; young stems glabrous, the bark smooth; stipules sheathing, lanceolate, 11–45 × 2–5 mm, glabrous, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles (0.5–)1–2.5(–3.5) mm, glabrous, grooved above; blades membranous to subcoriaceous, oblanceolate to narrowly (or rarely broadly) elliptic to lanceolate, the apex short-acuminate, the base attenuate to cuneate, 6.5–15(–18) × 2–4.5(–8.5) cm, glabrous above and below, drying green-brown to red-brown; secondary veins 6–9(–11) pairs, diverging 30°–60°(–70°), eucamptodromous to brochidodromous, constantly arcuate to straight, prominulous below, glabrous, the axils lacking domatia or hairs; tertiary veins inconspicuous, orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of cymes; panicle branched to 3–4 degrees; main axis (2–)5–13 cm long, the peduncle lacking or 3–4.5 cm long; secondary axes in (3–)4–5 ranks, the first-rank axes 2, (1–)1.5–5.5 cm long, the second-rank axes 2, (0.3–)1–2.5 cm long, the third-rank axes 2, (0.1–)0.5–1.4 cm long, the fourth-rank axes 2, 0.3–0.8 mm long, the fifth-rank axes 2, 0.1 mm long; cymes branched to 1–2 degrees; bracts not evident; bracteoles irregular, ca. 0.5 mm long, fringed. *Flowers* pedicellate, the pedicels 1–3 mm long; calyx often drying paler than the pedicel, cup-shaped, the tube 0.3–0.5 mm long, the lobes not evident, glabrous; corolla green-white, the tube cylindrical, 2.5–3 × 2 mm, white pubescent in throat, the lobes 5, lanceolate, 2–3.5 × 1.2 mm; stamens 5, the filaments 2.5–3 mm long in pins, 4 mm long in thrums, the anthers 1.2–1.5 mm long; style 4–4.5 mm long in pins, 2.5 mm long in thrums, the branches short. *Fruit* when dry ellipsoid to slightly obovoid, 7–8 mm long, 4–5.5 mm diam., maturing red, drying black to red-brown; persistent calyx often a minute beak; seed dorsal surface with 4–5 irregular often plus several shallow irregular longitudinal furrows, the ventral surface with 2 deep plus several shallow irregular longitudinal furrows.

Distribution (Fig. 31). Disjunct, occurring in Veracruz, Mexico, at 400–900 m elevation, and along the cordillera in Costa Rica and Panama, at 600–1,600 m, in tropical moist to premontane wet forest with equatorial-mountainous to usually tropical-equatorial climate. *Psychotria sarapiquensis* has been collected in flower in January, February, May, and August and in fruit July–March.

Selected specimens examined. MEXICO. VERACRUZ: Mpio. Catemaco, cerro al E de Coyame, 900 m, 13 Dec. 1971 (fr), *Beaman 5307* (MEXU); Estación de Biología Tropical Los Tuxtlas, 400 m, July 1975 (fr), *Chazaro 417* (ENCB, MEXU); Estación de Biología Tropical Los Tuxtlas, Cerro "El Vigia," 18 Mar. 1971 (fr), *Flores 50* (MEXU); Mpio. Catemaco, highest point on rd. from Catemaco to Sontecomapan, 18°29′N, 95°04′W, 510 m, 14 Jan. 1981 (fr), *Schatz & Nee 233* (F). COSTA RICA. GUANACASTE: Los Ayotes, nr. Tilarán, 600–700 m, 21 Jan. 1926 (fr), *Standley & Valerio 45344* (US). HEREDIA: Vara Blanca de Sarapiquí, 1,500–1,750 m, July–Sep. 1937 (fl), *Skutch 3282* (A, K, MO, US). PUNTARENAS: Monteverde, 1,600 m, 20 May 1981 (fl), *Haber 531*

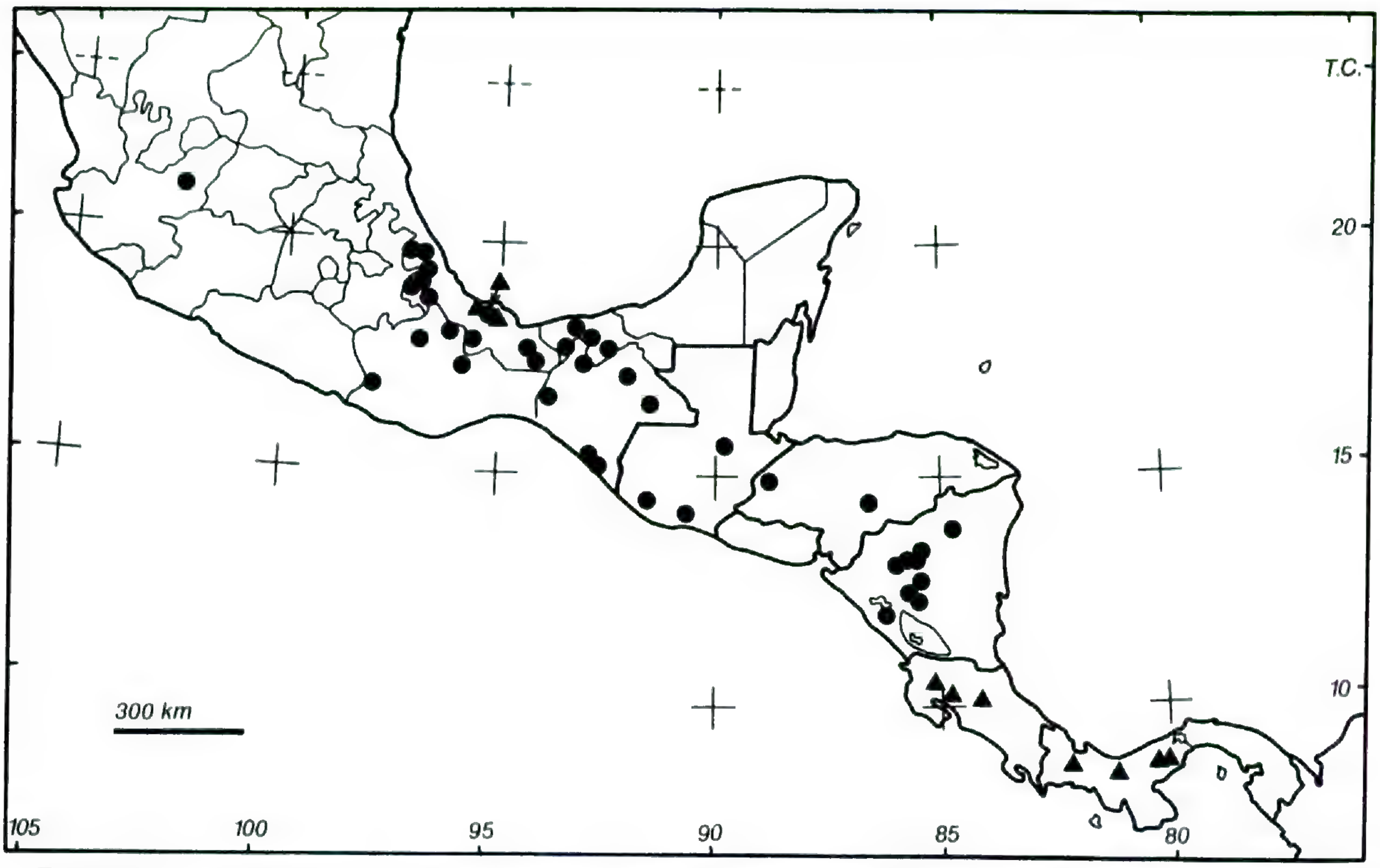

FIGURE 31. Distributions of *Psychotria sarapiquensis* (triangles) and *P. trichotoma* (circles) in Mesoamerica.

(MO). PANAMA. CHIRIQUÍ: Fortuna dam site, 1,200–1,400 m, 15 Sep. 1977 (fr), *Folsom et al. 5505* (MO—2 sheets); 1,400–1,600 m, 15 Sep. 1977 (fr), *Folsom et al. 5569* (MO); Qda. Aleman, 8 mi. N of Los Planes de Hornito IRHE Fortuna Hydroelectric Project, 8°45′N, 82°12′W, 1,200 m, 13 Mar. 1982 (early fr), *Knapp et al. 4153* (MO). COCLÉ: base of Cerro Pilón above El Valle, 9 Jan. 1972 (early fr), *Gentry 3648* (MO, NY). PANAMÁ: Cerro Campana above Su Lin Motel, 25 May 1971 (fl), *Croat 14780* (GH, MO, NY); 800–1,000 m, 11 Mar. 1981 (fr), *Sytsma & D'Arcy 3725* (MO). VERAGUAS: 5 mi. W of Santa Fe on rd. past Escuela Agricola Alto Piedra on Pacific side of divide, 800–1,200 m, 18 Mar. 1973 (fr), *Croat 23037* (MO); above Santa Fe on slopes of Cerro Tute, 1,200–1,400 m, 28 Sep. 1972 (early fr), *Gentry 6275* (F, GH, MO, NY); Alto Piedra, Santa Fe, 1,200 m, 27 Sep. 1972 (fr), *Lao 519* (MO); N of Santa Fe, 0–2 km N of Escuela Agricola Alto de Piedra, 16 Oct. 1974 (fr), *Mori & Kallunki 2510* (GH, MO); 16 Oct. 1974 (fr), *Mori & Kallunki 2519* (GH, MO); 18 Oct. 1974 (fr), *Mori & Kallunki 2638* (GH, MO); 26 Feb. 1975 (fl, fr), *Mori & Kallunki 4868* (MO—2 sheets); 29 Mar. 1975 (fr), *Mori & Kallunki 5325* (MO).

Psychotria sarapiquensis may be recognized by its usually narrow (length/width = 3) leaves with few (6–9[–11]) secondary veins and its large (7–8 mm long) ellipsoid to often obovoid fruit drying black or dark red-brown.

Mexican material is noteworthy for having lanceolate leaves with secondary veins diverging 60°–70°. Collections from the Fortuna and El Valle areas in Panama have large (to 18 cm long) broadly elliptic leaves with ca. 11 secondary veins, but they fit this species concept in other respects. Three of the Costa Rican collections—*Dryer 1539* (not cited above), *Skutch 3282*, and *Haber 531*—have subcoriaceous leaves drying red-brown and pedunculate inflorescences. *Psychotria sarapiquensis* is the most variable and/or the most problematic species in this treatment; it is conceivable that additional material from throughout its range will reveal it to be two or perhaps three different taxa.

46. Psychotria stockwellii C. Hamilton, Phytologia 64: 235. 1988. TYPE: Costa Rica. Alajuela: region of Zarcero, 1,800 m, 18 Oct. 1937 (fl, early fr), *A. Smith 543* (holotype, US; isotype, F). Figures 7i, 30.

Tree or shrub, (1–)2–10 m tall; young stems puberulent, the bark pale, ridged longitudinally; stipules sheathing, ovate, 9–15 × 3.5–9 mm, glabrous, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 0.5–2(–2.5) cm long, glabrous, terete; blades membranous, obovate or elliptic, the apex acuminate, the base attenuate, (8.5–)9–19 × (2–)3–7 cm, glabrous above and below, the midvein sometimes minutely puberulent below, drying dark brown above, slate brown or pale brown below; secondary veins (11–)14–17 pairs, diverging 60°–75°(–80°), eucamptodromous to sometimes brochidodromous, constantly arcuate, prominulous below, glabrous or minutely

puberulent below, the axils lacking domatia or hairs; tertiary veins conspicuous to evident, orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, spreading panicles of cymes (Fig. 7i); panicle branched to 3–4 degrees; main axis (7–)9–12 cm long, the peduncle (4–)5–9 cm long; secondary axes in 4–5 ranks, usually diverging over 90°, the first-rank axes 2, 1.8–5 cm long, the second-rank axes 2(4), 1–2.5 cm long, the shorter pair when present 0.4 cm long, the third-rank axes 2, 0.7–1.5 cm long, the fourth-rank axes 2, 0.4–0.6 cm long, the fifth-rank axes 2, 0.3 cm long; cymes branched to 1–2 degrees; bracts and bracteoles triangular, 0.5–2 mm long, ciliate. *Flowers* on pedicels 0.5–1.5 mm long; calyx cup-shaped, the tube 0.8 mm long, the lobes 5, triangular, often reflexed, 0.7 mm long, puberulent; corolla cream, the tube cylindrical, 4–5 × 1.5–2 mm, white pubescent in throat, minutely puberulent without, the lobes 5, ovate, 2 × 1 mm; stamens 5, the filaments 3.5–4 mm long in pins, 4.5–5.5 mm long in thrums, the anthers 1–1.2 mm long; style 6–7 mm long in pins, 3–4 mm long in thrums, the branches clublike or linear. *Fruit* when dry ellipsoid, 5–6 mm long, 4.5–5 mm diam., maturing red, drying dark red-brown; persistent calyx not evident or a beak or ring drying pale brown; seed dorsal surface with 6–10 irregular longitudinal furrows, the ventral surface with 2 deep regular plus sometimes several irregular longitudinal furrows.

Distribution (Fig. 30). Known from Alajuela, Costa Rica, and western Chiriquí, Panama, at 1,000–2,200 m elevation in regions of low montane rainforest with equatorial-mountainous climate. *Psychotria stockwellii* has been collected in flower January–October, primarily January–March, with immature fruit July–October, and in fruit January–March.

Additional specimens examined. COSTA RICA. ALAJUELA: region of Zarcero, 1,800 m, 18 Jan. 1937 (fl), *A. Smith 165* (F, MO). PANAMA. CHIRIQUÍ: Las Nubes, ca. 2,000 m, 7 Aug. 1974 (fl, early fr), *Croat 26450* (MO); Bajo Chorro, 1,800 m, 22 Jan. 1938 (fl), *Davidson 172* (F, MO); 2 Mar. 1938 (fl, fr), *M. Davidson 363* (A, F, MO); end of rd. to Bajo Mono, 21 Mar. 1977 (fl), *Folsom et al. 2250* (MO); E slopes of Cerro Pando, 8°55′N, 82°44′W, 2,000–2,300 m, 15 Oct. 1981 (fr), *Knapp 1646* (MO); vic. Las Nubes, 2.7 mi. NW of Río Chiriquí Viejo W of Cerro Punta, 2,200 m, 27 Feb. 1973 (fl, fr), *Liesner 293* (F, MO—2 sheets, NY); Las Nubes, 5 km NW of Cerro Punta, 1,800–1,950 m, 19 July 1975 (early fr), *Mori & Bolten 7240* (MO—2 sheets); Cerro Pando, nr. Panama–Costa Rica border, 2,000–2,482 m, 21 July 1975 (fl, early fr), *Mori & Bolten 7328* (MO, US); NW side of Cerro Punta beyond Las Nubes, 2,250 m, 15 Jan. 1971 (fl, fr), *Wilbur et al. 13211* (DUKE—2 sheets, MO); above San Ramón nr. Bajo Mono, 4 mi. NW of Boquete, 1,800 m, 22 Jan. 1971 (fl, fr), *Wilbur et al. 13544* (DUKE).

Psychotria stockwellii may be recognized readily by its inflorescence, whose secondary axes diverge over 90° from the main axis and whose tertiary axes diverge likewise from the secondary axes, and so forth, a character state unique in the subgenus. In addition, *P. stockwellii* differs from *P. panamensis* in having a larger corolla tube (4–5 vs. 2–3 mm long), long-pedunculate inflorescences, and conspicuous to evident (vs. inconspicuous) tertiary veins.

Reproductive organs at both levels are longer in the pin morph than in the thrum.

47. Psychotria trichotoma M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11: 227. 1844. *Uragoga trichotoma* (M. Martens & Galeotti) Kuntze, Revis. Gen. Pl. 2: 963. 1891. TYPE: Mexico. Veracruz: Jalapa et Mirador, 900–1,200 m, Aug. 1840 (fl), *Galeotti 7092* (holotype, G, n.v., photo, MO). Figure 31.

Shrub or small tree 1.5–6 m tall; young stems glabrous or rarely minutely puberulent, the bark smooth or longitudinally furrowed; stipules sheathing, lanceolate, (10–)20–30 × 3–5 mm, glabrous, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 1–4(–5.5) cm long, glabrous, flat above; blades membranous, ovate to elliptic, the apex acuminate, the base attenuate to cuneate, (10.5–)13–23(–26) × (5.5–)6.5–12(–15) cm, glabrous above and below, drying usually green-brown or sometimes red-brown, the veins usually drying paler; secondary veins (12–)14–18(–20) pairs, diverging 45°–60°, brochidodromous with secondary loops near margin, straight or sometimes slightly arcuate, elevated below, glabrous, the axils lacking domatia or hairs; tertiary veins evident to inconspicuous, orthogonal reticulate to percurrent. *Inflorescences* terminal or pseudoaxillary, panicles of cymes: panicle branched to 4–5 degrees; main axis (4–)7–16 cm long, the peduncle usually absent or 5–9 cm long; secondary axes in 5–7 ranks, the first-rank axes 2(4), equal, 4–8.5 cm long, the second-rank axes 2, 2–4.5 cm long, the third-rank axes 2, 1–3 cm long, the fourth-rank axes 2, 0.5–1.5 cm long, the fifth-rank axes 2, 0.2–1 cm long, the sixth-rank axes 2, 0.3–0.4 cm long, the seventh-rank axes 2, 0.2 cm long; cymes branched to (1)2 degrees; bracts and bracteoles not evident. *Flowers* pedicellate, the pedicels 0.5–1 mm long; calyx cup-shaped, the tube 0.2–0.5 mm long, the lobes (4)5, trian-

gular to barely evident, glabrous; corolla white, the tube cylindrical, 2.5 × 1.5 mm, white pubescent in throat, the lobes (4)5, lanceolate, 2–2.5 × 1 mm; stamens (4)5, the filaments 2–2.5 mm long in pins, 3–3.5 mm long in thrums, the anthers 0.8–1.3 mm long; style 4 mm long in pins, 2 mm long in thrums, the branches short. *Fruit* when dry obovoid, (5–)6–8 mm long, (4–)4.5–5.5 mm diam., maturing red, drying usually black or sometimes red-brown; persistent calyx inconspicuous or a broad beak ca. 0.5 mm long; seed dorsal surface with 4–5 irregular often plus several irregular shallow longitudinal furrows, the ventral surface with 2 deep regular and often 2–4 irregular longitudinal furrows.

Distribution (Fig. 31). Southern Mexico through Nicaragua, at 100–1,600 m elevation in regions of mostly evergreen forest with usually tropical-mountainous climate. *Psychotria trichotoma* occurs also in Venezuela and Ecuador. It has been collected in flower April–July and December–January, and in fruit throughout the year, primarily August–March.

Selected specimens examined. MEXICO. CHIAPAS: Mpio. Solusuchiapa, 3–5 km above Solusuchiapa along rd. to Tapilula, 450 m, 26 July 1972 (fl), *Breedlove 26461* (ENCB, MEXU, MO); Mpio. Ocosingo, adjacent to Laguna Ocotal Grande, 800 m, 6 Feb. 1973 (fr), *Breedlove 33093* (MEXU, MO); Mpio. Cintalapa de Figueroa, nr. microwave station of La Mina, 12 km S of Hwy. 190 nr. Rizo de Oro, 1,000 m, 16 Oct. 1971 (fr), *Breedlove & Thorne 20640* (MEXU, MO, NY); Mpio. Mapastepec, along Río Testecapa 10 km SE of Mapastepec, 180 m, 24 Dec. 1972 (fl), *Breedlove & Thorne 30660* (MEXU); Escuintla, Esperanza, 14 Apr. 1947 (fl), *Matuda 16461* (F, MEXU); nr. Tumbala, 1,200–1,650 m, 20 Oct. 1895 (fr), *E. Nelson 3299* (F, US). JALISCO: W of San Sebastian, Hda. del Ototal, Arroyo de los Palos Blancos, 1,500 m, 9 Mar. 1927 (fr), *Mexia 1846* (A, F, GH, MO, NY, US). OAXACA: Dto. de Putla, 3 km al NE de Putla, sobre el Río Cuchara, 970 m, 20 June 1982 (fl), *Cedillo & Torres 1487* (ENCB, MEXU, MO); Dto. Cuicatlán, De La Raya al Faro, 600 m, 4 Nov. 1919 (fr), *Conzatti 3807* (GH, US); Tuxtepec, Chiltepec, 12 June 1965 (fl), *G. Martínez C. 34* (ENCB, MEXU, MO, NY); Dto. Choapan (Santiago Choapan), Monte Negro de Lalana, 17°32′N, 95°40′W, 150 m, 3 May 1939 (fl), *Schultes & Reko 757* (F). TABASCO: Nacajuca, a 6 km carret. a Tecoluta, 26 m, 9 Oct. 1978 (fr), *Calzada 4965* (ENCB, MEXU); Mpio. Huimanguillo, km 12.6 de la desviación de Huimanguillo hacia Francisco Rueda, 10 Oct. 1980 (fr), *Cowan & Magaña 3267* (ENCB, MEXU); Mpio. Macuspana, along Arroyo Hular, S of Macuspana, 28 Sep. 1944 (fr), *Gilly & E. Hernández X. 339* (GH, MEXU); a 11.5 km de Villahermosa, por la carret. a Escárcega, 18 Jan. 1966 (fr), *González & Pérez P-546* (ENCB). VERACRUZ: Mpio. Huatusco, entre "La Victoria" y Chavaxtla, 19°09′N, 96°53′W, 650 m, 3 Oct. 1979 (fr), *Avendaño & Calzada 516* (ENCB, F, MEXU); Teocelo, El Olmo, 11 Oct. 1980 (fr), *Barrera et al. 298* (MEXU); Mpio. Hidalgotitlán, Benito Juárez segundo, 17°47′N, 94°39′W, 100 m, 2 Nov. 1978 (fr), *Castillo 358* (F); km 3 carret. Playa Vicente a Santa Cecilia, 6 Oct. 1971 (fr), *Chavelas et al. ES-4245* (MEXU); orillas de la Laguna de Catemaco, camino a Coyame, 14 Apr. 1969 (fr), *Nevling & Gómez-Pompa 903* (F, GH, MEXU); swamps nr. Jalapa, 1,200 m, 19 May 1899 (fl, fr), *Pringle 8198* (A, F, GH, K, MEXU—2 sheets, MO, NY, US—2 sheets); Mpio. Hidalgotitlán, brecha Hermanos Cedillo–La Escuadra, 17°17′N, 94°38′W, 150 m, 3 June 1974 (fl), *M. Vázquez et al. 779* (ENCB, F, MEXU); Zongolica, por el camino a Zongolica a Nacaxtla, 1,610 m, 10 Nov. 1976 (fr), *V. Vázquez T. 541* (ENCB—2 sheets); Mpio. Atzalan, Napoala, 950 m, 23 Nov. 1969 (fr), *Ventura 103* (ENCB); Mpio. de Totutla, el Mirador, 1,000 m, 3 May 1976 (fl, fr), *Ventura 12723* (MEXU). GUATEMALA. ALTA VERAPAZ: nr. Finca Sepacuite, 9 Apr. 1902 (st), *Cook & Griggs 540* (US). ESCUINTLA: Río Guacalata, 600 m, 16 Dec. 1938 (fr), *Standley 60207* (F). SUCHITEPÉQUEZ: nr. Santo Domingo, S of Mazatenango, 300 m, 5 Mar. 1941 (fr), *Standley 88882* (F). HONDURAS. COPÁN: cerca de Dulce Nobre, 1,200 m, 30 Mar. 1963 (fr), *A. Molina R. 11760* (F—2 sheets). OLANCHO: Montaña del Chifiringó, 20 km S de Campamento, 1,000 m, 6 Sep. 1979 (fr), *C. Nelson 5339* (TEFH). NICARAGUA. BOACO: entre Cerro Alegre y el Roblar, San José de los Remates, 12°36′N, 85°43′W, ca. 1,000 m, 11 Feb. 1983 (fr), *P. P. Moreno 20193* (MO); summit and upper SW slope of Cerro Mombachito, 12°24′N, 85°33′W, 950–1,020 m, 18 Jan. 1981 (fr), *W. D. Stevens & Hahn 18943* (MO). JINOTEGA: along rd. from Hwy. 3 to La Fundadora, 13°03′N, 85°54′W, 1,200–1,400 m, 31 Oct. 1979 (fr), *W. D. Stevens & Grijalva 15443* (MO). MANAGUA: ca. 5.4 km NE of El Crucero, ridge of Sierra de Managua nr. Hda. Palmira, 12°01′N, 86°16′W, 800–900 m, 25 Aug. 1977 (fr), *W. D. Stevens 3466* (MO). MATAGALPA: camino al Cerro La Carlota, a 2 km de la carret. al Tuma, 12°58′N, 85°52′W, 1,040–1,100 m, 5 Mar. 1982 (fr), *P. P. Moreno 15666* (MO); ridge along rd. between La Danta and La Luna, E of Esquipulas, 12°40′N, 85°43′W, 960–1,000 m, 25 Jan. 1979 (fr), *W. D. Stevens 11801* (MO); Macizos de Peñas Blancas, drainage of Qda. El Quebradón, slopes N and W of Hda. San Martín, 13°14–15′N, 85°38–39′W, 1,000–1,400 m, 18–20 Jan. 1982 (fr), *W. D. Stevens et al. 21144a* (MO); rd. to La Fundadora, N of Sta. María de Ostuma, 1,300–1,500 m, Feb. 1963 (fr), *L. O. Williams et al. 24803* (GH, NY, US). ZELAYA: El Hormiguero, caño above camp, 13°45′N, 84°59′W, 800–1,000 m, 17 Mar. 1980 (fr), *Pipoly 6182* (MO).

The name *Psychotria trichotoma* has been used to misidentify specimens of most of the species in Group 6 plus *P. tenuifolia*, *P. limonensis*, *P. carthagenensis*, *P. quinqueradiata*, and *P. chagrensis*.

Psychotria trichotoma may be recognized by its fairly wide (length/width = 2) leaf blades drying usually green-brown with veins drying paler; secondaries usually 14–18 pairs, straight and making arches near margin; large inflorescences (usually 7–16 cm long) with no peduncle; and large (usually

6–8 mm long) obovoid fruit often drying black. The pedunculate inflorescences are found in some material from Oaxaca and Veracruz, Mexico, where the basal secondary axes may have been aborted. Specimens from Oaxaca show also minute puberulence on the inflorescence axes.

Reproductive organs at both levels are longer in the pin morph that in the thrum.

NEW SPECIES AND OTHER TAXONOMIC MATTERS IN THE NEW WORLD MEMECYLEAE (MELASTOMATACEAE)

Thomas Morley[1]

ABSTRACT

Four new species of *Mouriri* and one of *Votomita* are described and illustrated. *Mouriri coibensis* is reduced to a variety of *M. gleasoniana*. The relation of *Votomita* to *Mouriri* is discussed in the light of new information on seed structure; no change in generic boundaries is recommended for the present. Supplementary descriptions and drawings of *M. longifolia* and *V. pubescens* are provided.

Recent collections and older ones recently identified correctly to genus have yielded five new species of the tribe Memecyleae DC. (Melastomataceae). Four of these are members of the genus *Mouriri*: one from the Osa Peninsula of Costa Rica, one from western Venezuela in the state of Táchira, a third from southern Venezuela in Amazonas, and the fourth from northeastern Peru and adjacent Brazil. Also in *Mouriri*, new collections of *M. gleasoniana* from the Panama mainland, from Costa Rica, and from the island of Coiba revealed much intraspecific variation and require reassessment of the status of its close ally, *M. coibensis*. A recent flowering collection of *M. longifolia* permits the completion of its description and illustrations and allows its sectional placement. The fifth new species is a *Votomita* from Roraima of Brazil, the eighth known member of that small genus. The specimens of this species, as well as those of another collection of *V. pubescens*, bear ripe fruit, so that it is now possible to compare more accurately the seeds of *Votomita* and *Mouriri*. Previously, mature seeds were known only from *V. monantha* of Cuba. A discussion of ovule and seed structure and of generic relations therefore follows the description of *V. roraimensis*. More collections of *V. pubescens* make possible the completion of the descriptions and illustrations for that species.

References in the descriptions to the "type" of stomatal crypt refer to the forms described on pages 6 and 7 of Morley (1976).

Mouriri osaensis Morley, sp. nov. TYPE: Costa Rica. Peninsula de Osa, Llorona. Arbol común; solamente con frutos; con aprox. 7 m de alt. y 30 cm DAP. Madera pesada y muy resistente, usada para timones y ejes de carretas, macetas para pilar arroz, plumas o palancas etc., al rajarla al acha se va en capas y al quebrarla quedan chuzos muy punzantes. Nombre regional: *Huesillo & Quiebracho*. 19 Sep. 1975, *L. J. Poveda & Chrys y Adelaida Vaughan s.n.* (holotype, MIN). Figure 1.

Arbor usque 7 m alta trunco 30 cm diametro; petioli 3–5 mm longi; laminae grandes, basi rotundata usque truncata usque subcordata incisura usque 1 mm profunda; cryptae stomatophorae nullae; hypodermis absens; scleredes terminales foliorum irregulariter stellatae usque columnares; pedunculi ut videtur 1-flori, 1–3 in quoque later ad nodos aphyllos ramulorum 3.5–4 mm crassorum; fructus atropurpureus, globosus vel depresso-globosus, sine lobis; cicatrix hypanthii 7–11 mm diametro, 1.5–2 mm alto; loculi 2–5; semina 2–5.

Tree to 7 m tall and 30 cm in diam., glabrous except for the inflorescence; crown at times dense and elongate; young twigs terete or with 4 rounded angles; bark light gray, exfoliating in very small sheets; wood heavy and very resistant. Petioles 3–5 mm long; blades somewhat shiny on the face, 16–27 cm long, 5.6–9 cm wide, elliptic to ovate-elliptic or with an oblong tendency, abruptly acuminate at the apex, rounded to truncate to shallowly cordate at base, when cordate the notch to 1 mm deep; midrib grooved above at least in the lower half, prominent and rounded below; lateral nerves conspicuous when dry. Midrib xylem tubular, depressed in the center above; stomatal crypts none; upper epidermis mostly 1 cell thick but oc-

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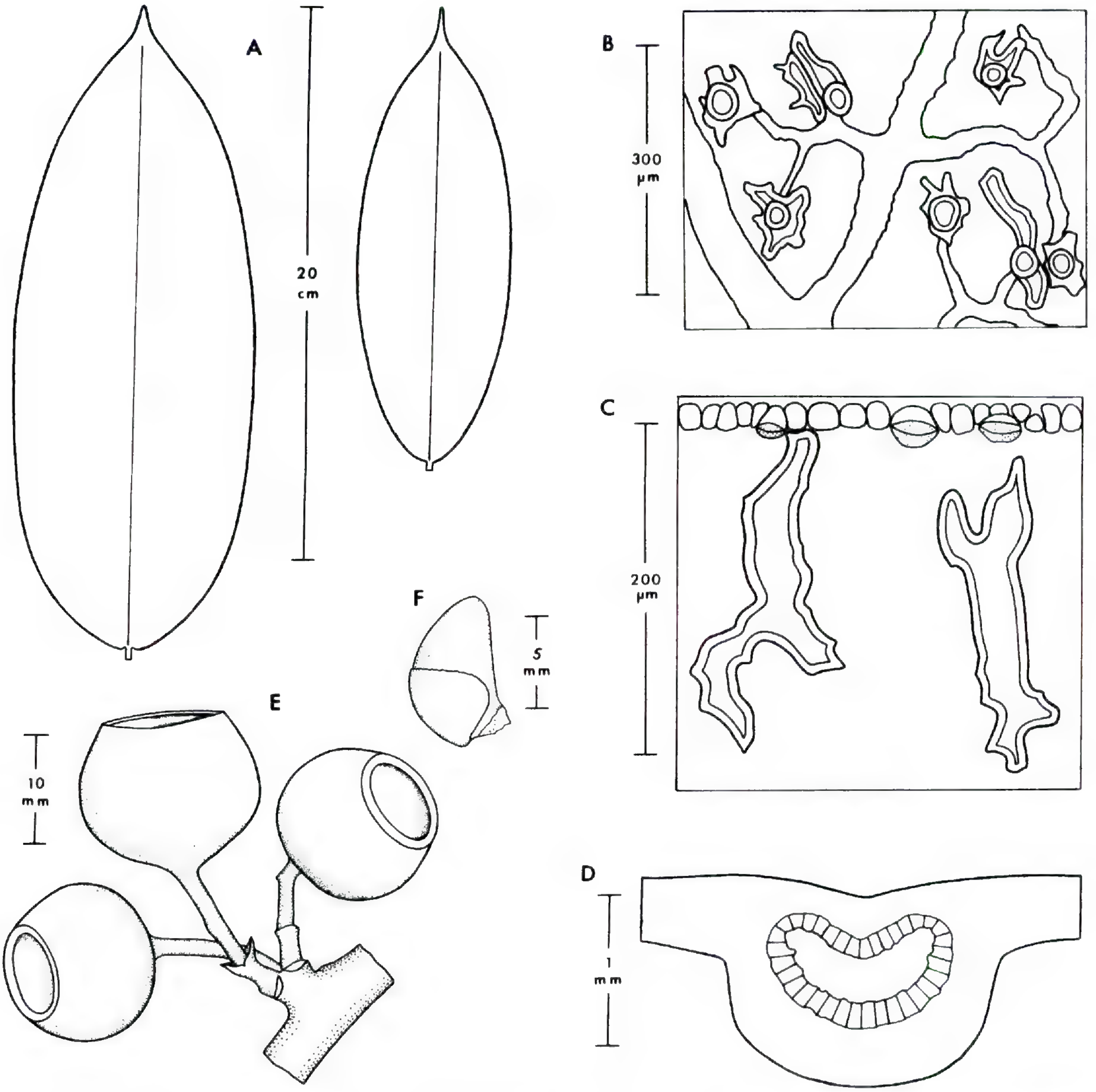


FIGURE 1. *Mouriri osaensis* (*Poveda & C. & A. Vaughan s.n.*).—A. Leaves.—B. Cleared portion of leaf blade showing veins and terminal sclereids.—C. Cross section of leaf blade showing sclereids and upper epidermis.—D. Cross section of leaf midrib.—E. Fruit cluster.—F. Seed (perhaps not fully mature).

casionally 2 cells thick at scattered places in the same leaf, mucilaginous walls occasional to frequent in the single cells and in the inner of the doubled cells; hypodermis none; terminal sclereids irregularly stellate with a strong columnar tendency, most with columnar arms, many entirely columnar. Flowers borne at leafless nodes of twigs 3.5–4 mm thick, in clusters of 1–3 per side, the peduncles 1-flowered, ca. 4.5 mm long to base of pedicel with 2 internodes in that length; bracts triangular, 2 mm long. True pedicels 7–9 mm long in fruit, very minutely puberulent. Flowers unknown. Fruits dark purple at maturity, globose to depressed-globose, not lobed, 12.2–16.5 mm high including hypanthium rim, 12–17 mm diam. when dry, bearing a circular rim of the circumscissile hypanthium 7–11 mm diam. and 1.5–2 mm high, 2–5-locular, 2–5-seeded. Seeds 8–8.7 mm high, 6.5–7.7 mm wide, 5–5.2 mm thick, irregularly ovoid, with a light brown slightly thickened portion 6–6.5 mm high in the lower half, the rest dark brown; hilum basal, whitish, rough, 1.5–3 × 3 mm.

Distribution. Known only from the type locality in the western part of the Osa Peninsula on the southwest coast of Costa Rica.

The new species appears to belong in subg. *Mouriri* sect. *Olisbea*. The characteristics suggesting this alignment are the large leaves, absence

of stomatal crypts, simple upper epidermis with mucilaginous walls, stellate terminal sclereids, and lack of a hypodermis. Within the section, the new species is closest to *M. completens*, on the basis of the former's similar leaves with a cordate tendency, very similar upper epidermis and foliar sclereids, and above all, the circumscissile hypanthium as seen on the fruit. The absence of flower characters of course detracts from understanding the relationships, but I still regard this alignment as reasonably certain. *Mouriri osaensis* differs from *M. completens* in leaf, fruit, and seed characters. The leaf blade is less cordate than in *M. completens*; the fruit is purple instead of greenish, lacks a broad stipe at base, and is not abruptly narrowed to the hypanthium at the apex, nor is it lobed according to the seed number; the hypanthium on the fruit is 7–11 mm in diameter rather than 4.5–7 as in *M. completens* and is only 1.5–2 mm deep instead of 3.8–4.5 mm. The seeds are a bit smaller and differ in shape, best compared in the illustrations.

Mouriri papillosa Morley, sp. nov. TYPE: Venezuela. Táchira: 10 airline km E of La Fundación, 13–23 km by road, around Represa Dorada, primary evergreen forest with patches of secondary vegetation. Soils tending to be sandy, derived from metamorphic rock (schist or gneiss), 600–900 m, 7°47–48′N, 71°46–47′W, 4 m tree, petals and anthers pinkish. 30 Apr. 1981, *R. Liesner & M. Guariglia 11616* (holotype, US; isotypes, MIN, MO). Figure 2.

Arbor usque 15 m alta; laminae 4.7–11.5 cm longae, 2.3–5.5 cm altae, elliptico-ovatae usque ellipticae, basi truncata vel subcordata; pagina inferior costae mediae rotundata ad basem, 2-angulata ¼–½ distantiae versus apicem; cryptae stomatophorae Typi II, tecto saepe depresso; epidermis supera stratiis 2–3 cellularum, cellulae interiorae plerumque parietibus mucilaginis aureis, parietes lamellis 5–9; calyx ovarium inferum includens 6–7 mm longus, ovarium papillosum; calyx 1.4–1.8 mm findens inter lobos sub anthesi; antherae 3.6–4 mm longae; ovarium 4–5-loculare; ovula 12–16.

Tree to 15 m high, glabrous except for the inflorescence; young twigs terete to 2-channeled to 4-angled. Petioles 1.5–3 mm long; blades 4.7–11.5 cm long, 2.3–5.5 cm wide, elliptic-ovate to seldom elliptic, abruptly short- to medium-acuminate at apex, rounded to a truncate or slightly cordate base, the basal notch up to 1 mm deep; midrib plane above, prominent below, rounded at base, becoming 2-angled ¼–½ of the way to the apex, then becoming plane near the apex; lateral nerves slightly visible above and below when dry. Midrib xylem tubular; stomatal crypts Type II, averaging in a leaf ca. 45 μm diam., 35 μm high, 57 per mm² (extremes 35–55 μm diam., 30–40 μm high, 45–69 per mm²), the roof often depressed in the center; upper epidermis 2 or 3 cells thick, the upper 1 or 2 layers without mucilaginous walls, the cells of the inner layer mostly with golden mucilaginous walls ⅓–¾ the height of the cell and containing 5–9 lamellae, these cells enlarged and together resembling a hypodermis, aligned or not with the cells of the outer layers; terminal sclereids stellate-columnar, crowded. Inflorescences in the lower leaf axils and at leafless nodes of twigs up to 5 mm thick, 1–3 per side, each 1–3-flowered, 1.5–3.5 mm long to base of farthest pedicel measured along the axes with 2 internodes in that length, the internodes very minutely puberulent; bracts 1–1.5 mm long, ovate-triangular, often deciduous by anthesis. True pedicels 1–4 mm long; calyx including inferior ovary 6–7 mm long, campanulate, it and the pedicels very minutely puberulent, the ovary papillose, the papillae enlarging into rounded wartlike bumps crowded on the immature fruit; free hypanthium 2.5–2.8 mm long; calyx lobes before anthesis low-triangular, 0.7–0.8 mm long, 2–2.1 mm wide, 1.8–2.4(–2.8) mm long when measured from the stamen attachment, the calyx splitting between the lobes at anthesis a distance of 1.4–1.8 mm. Petals pinkish, 5.5–6 mm long, 5.5–6 mm wide, triangular, erose, clawed at base. Mature filament length unknown; anthers pinkish, 3.6–4 mm long; thecae 3–3.5 mm long, dehiscing by apical slits; gland 0.4–0.6 mm long, 2.6–2.9 mm from apex of anther when measured from center of gland; cauda ca. 0.45 mm long, scarcely noticeable externally. Ovary 4–5-locular; ovules axile-basal, produced only outwardly from each placenta, 12–16 in all; style ca. 15 mm long. Persistent calyx red on immature green fruit. Ripe fruit and seed unknown.

Paratype. VENEZUELA. TÁCHIRA: Distr. Uribante. In forest along road from La Siberia to entrance to Las Cuevas Represa. Evergreen forest with much bamboo and *Scleria secans*, ±1,100 m (immature fr), 8 July 1983, *H. van der Werff & A. González 5123* (US, MO).

Distribution. Evergreen forests of far western Venezuela in south-central Táchira State SE of San Cristóbal at 600–1,100 m.

This species is best placed in the sect. *Mouriri* (Morley, 1976: 36) on the basis of its tubular midrib xylem, small Type II stomatal crypts, hypodermis, acuminate leaf apex, axile-basal placentation, and relatively short thecae. Section *Litophyllum* is very similar, differing only in its lack of a hypoderms. The hypodermis of sect. *Mouriri*

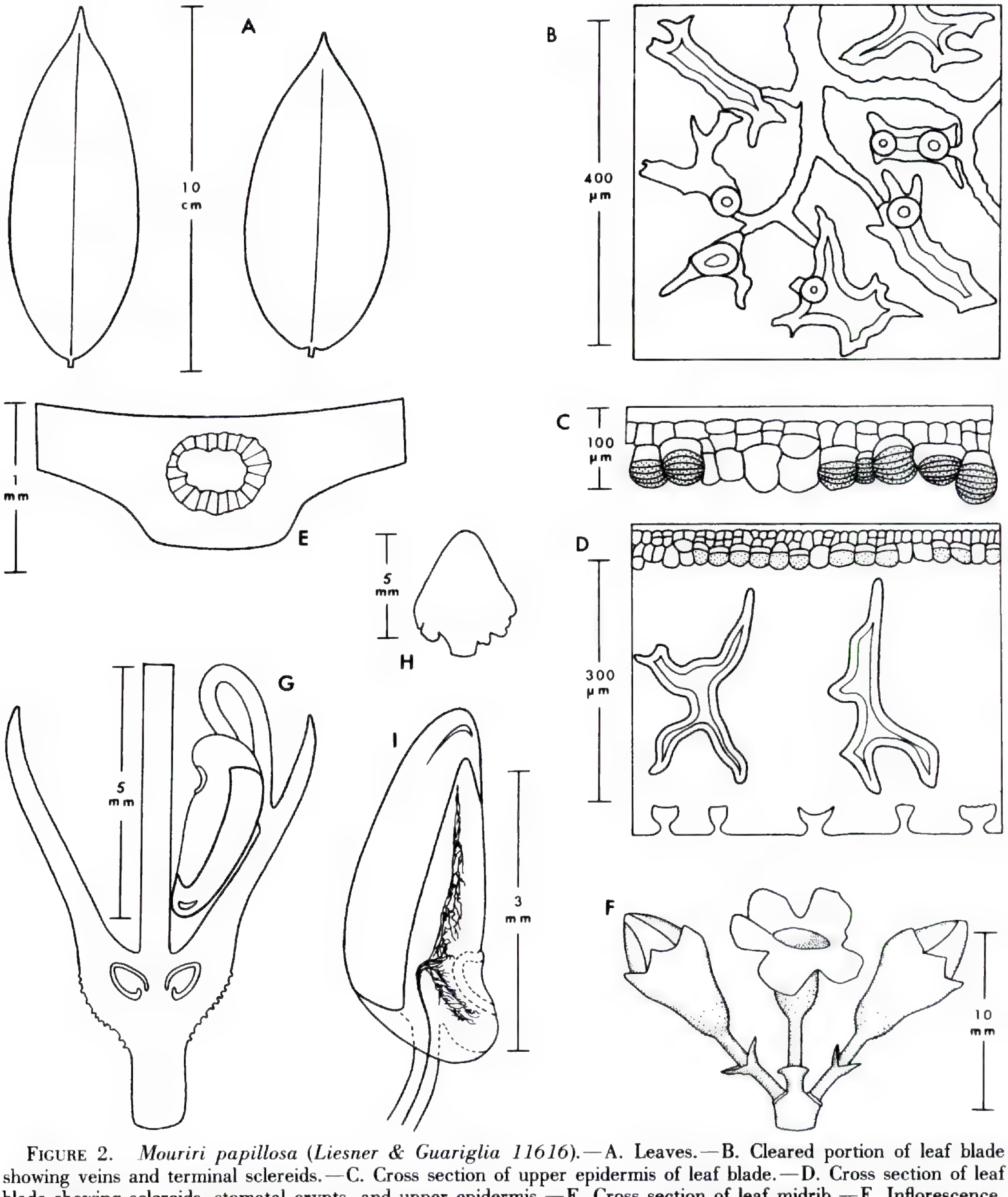


FIGURE 2. *Mouriri papillosa* (*Liesner & Guariglia 11616*).—A. Leaves.—B. Cleared portion of leaf blade showing veins and terminal sclereids.—C. Cross section of upper epidermis of leaf blade.—D. Cross section of leaf blade showing sclereids, stomatal crypts, and upper epidermis.—E. Cross section of leaf midrib.—F. Inflorescence.—G. Longisection of flower before anthesis.—H. Petal.—I. Anther, shown cleared except for the thecae.

appears to be derived from the inner layer of a double or triple epidermis, judging by the presence in its cells of mucilage walls and the occasional alignment of the hypodermal cells with cells or groups of cells in the epidermis. In *M. papillosa* the alignment is rather frequent, as seen in section view; however, as seen in face view, the cells are most often unaligned. Thus the inner layer of cells appears to be sufficiently modified to justify considering it a hypodermis like those of the other species of sect. *Mouriri*, and not simply as the inner layer of a multiple epidermis.

Section *Mouriri* contains three species in addition to *Mouriri papillosa*: *M. guianensis*, *M. domingensis*, and *M. barinensis*. From all three, *M. papillosa* differs in having a papillose ovary, a larger ovary plus calyx, and a longer free hypanthium, anthers, thecae, and splitting distance

between calyx lobes. It further differs from *M. barinensis* in having short petioles.

The curious multiple lamellations in the mucilage walls of *M. papillosa* I have noted elsewhere only in two collections of *M. barinensis*. Since this character varies in the latter species, it is possible that it will also prove to be a variable in *M. papillosa*.

Although plants of sect. *Litophyllum* lack a hypodermis, in other respects some of them resemble rather closely the members of sect. *Mouriri*. Most similar is *M. gleasoniana*, including its var. *coibensis*. From this, *M. papillosa* differs in its lack of a two-winged lower midrib and in its papillose ovary and longer ovary plus calyx, longer anthers and thecae, and greater splitting distance between the calyx lobes.

Mouriri latihila Morley, sp. nov. TYPE: Venezuela. Amazonas: Selva alta pluvial, a 7–9 km de Yavita hacia Pimichín, lat. 2°55′N, long. 67°25–30′W. Altura: 125 metros. Tree 3 m tall; leaves subchartaceous, dark green above, pale green below; fruit orange red. 22 Apr. 1970, *Julian A. Steyermark & George Bunting 102927* (holotype, VEN; isotype, MICH). Figure 3.

Arbor 3 m alta; cryptae stomatophorae Typi II; epidermis supera strata uno cellularum; sclerides terminales foliorum plerumque columnares; flores tetrameri, axillares, solitarii; calyx omnino clausus usque ad anthesem, tum ad lineas conjunctionis loborum rumpens; semen 1, lateribus 2, hilum latissimum, partem majoram lateris uni seminis occupans.

Tree 3 m high, glabrous; young twigs narrowly 4-winged. Leaves subchartaceous, dark green above, pale green below; petioles 1–2.5 mm long; blades 6.5–11.5 cm long, 3.3–5.7 cm wide, ovate-elliptic or ovate-oblong to ovate, abruptly acute to abruptly acuminate at apex, broadly acute to broadly rounded at base; midrib slightly grooved above, prominent and rounded below; lateral nerves prominent above and below when dry. Midrib xylem tubular; stomatal crypts Type II, averaging in a leaf ca. 55 μm diam., 31 μm high, 50 per mm² (extremes 40–75 μm diam., 25–38 μm high, 33–66 per mm²); upper epidermis 1 cell thick, the cells with mucilage walls ⅔–¾ of the cell height; hypodermis none; upper palisade layer clear, not filled with tannin compounds, but most of the other mesophyll cells so filled; terminal sclereids mostly columnar, narrow, often slanting and weaving somewhat, sometimes branching in the spongy parenchyma, the ends there sometimes horizontal. Flowers single in the leaf axils, borne on peduncles 0.2–1 mm long bearing 2–3 pairs of bracts, the bracts 0.7–1.2 mm long, triangular. True pedicels 0.5–1.3 mm long; flowers tetramerous; calyx including inferior ovary 3 mm long when immature, mature length unknown, ellipsoid or slightly obovoid, conical at each end; calyx lobes fused to the apex of the flower in bud, splitting apart regularly at anthesis, each then triangular and acute, 1.8–2.4 mm long, 1.2–1.4 mm wide, 2–2.4 mm long when measured from the stamen attachment; free hypanthium ca. 1 mm long. Petals, stamens, and ovary at anthesis unknown. Fruit orange-red, depressed-globose, ca. 9 mm long, 12 mm diam., bearing the calyx lobes and the remains of the style. Seed 1, ca. 7.5 mm high, 10.5 mm wide, 4.6 mm thick, oblongish with an apical notch as seen in face view, one face and most of the edges with polished surfaces, these curved over onto the opposite side at 4 places, 2 above, 2 below, the irregularly roughened hilum occupying most of the opposite side of the seed.

Distribution. Known only from the type locality in tropical rainforest near the west-central border of Amazonas, Venezuela, between the headwaters of the Guainía and Atabapo rivers.

Mouriri latihila clearly falls within subg. *Mouriri* on the basis of its tubular midrib xylem and its seed with a large polished area. The new species is very distinctive, standing apart on the combination of its tetramery, closed calyx, and small Type II stomatal crypts. Its sectional relation is uncertain; it is here placed tentatively in sect. *Litophyllum* because of its tubular midrib xylem, small crypts, leaf shape, small flower, and lack of a hypodermis (Morley, 1976: 36). When placed here, it weakens further the already weak sectional boundaries. From this position the new species appears to have ties with sect. *Megacrypta*, whose two species also have tetramery, closed calyces, and columnar sclereids. The new plant differs widely from these two, however, in its much smaller leaves and small Type II stomatal crypts, as well as in its shorter pedicels and calyces. Within sect. *Litophyllum*, no species appear very similar to *M. latihila*, although two are tetramerous and have short one-flowered peduncles like the new species: *M. exadenia* and *M. lancifolia*. *Mouriri latihila* differs from *M. exadenia* in having Type II crypts, columnar sclereids, a closed calyx, and a different seed shape; from *M. lancifolia* it differs in its broader leaves, presence of stomatal crypts, columnar sclereids, and closed calyx.

Mouriri retentipetala Morley, sp. nov. TYPE: Brazil. Amazonas: Rio Javari, behind Palmei-

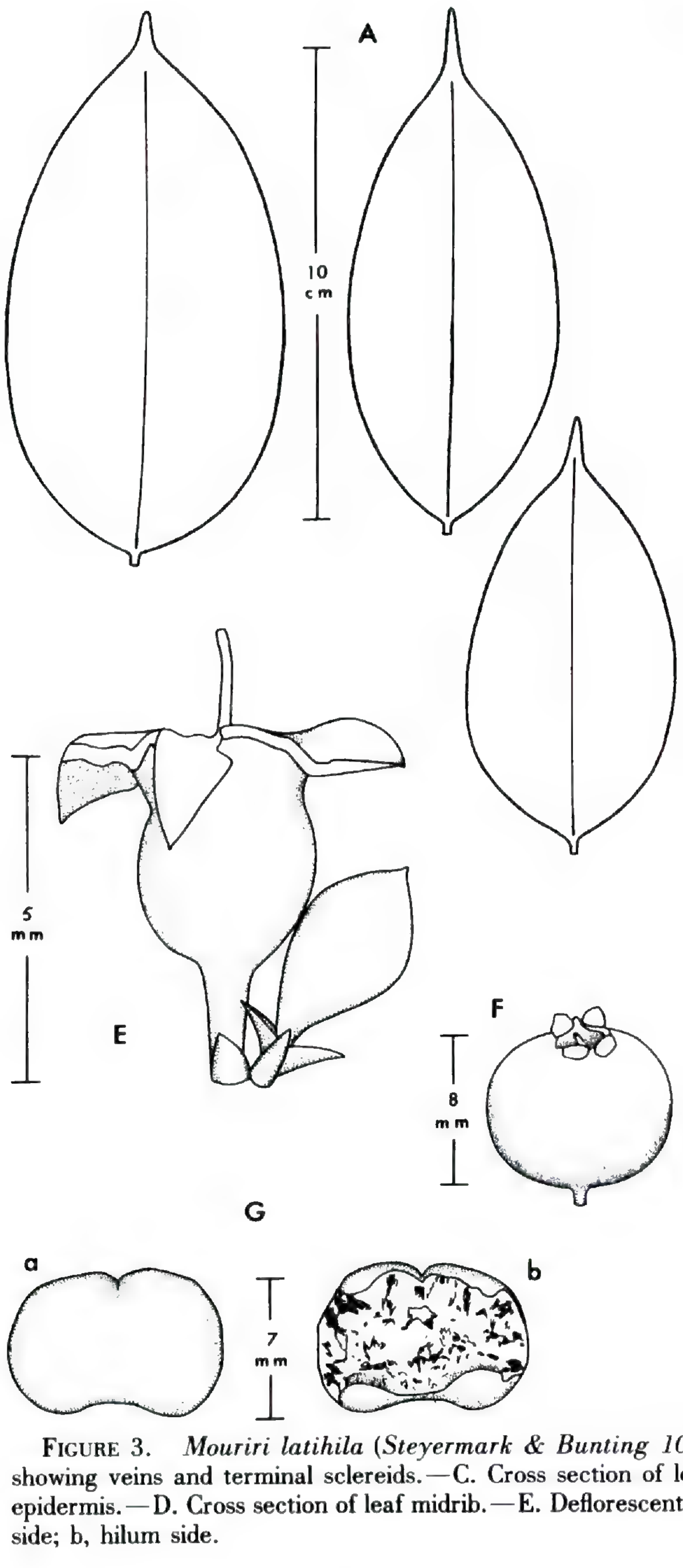
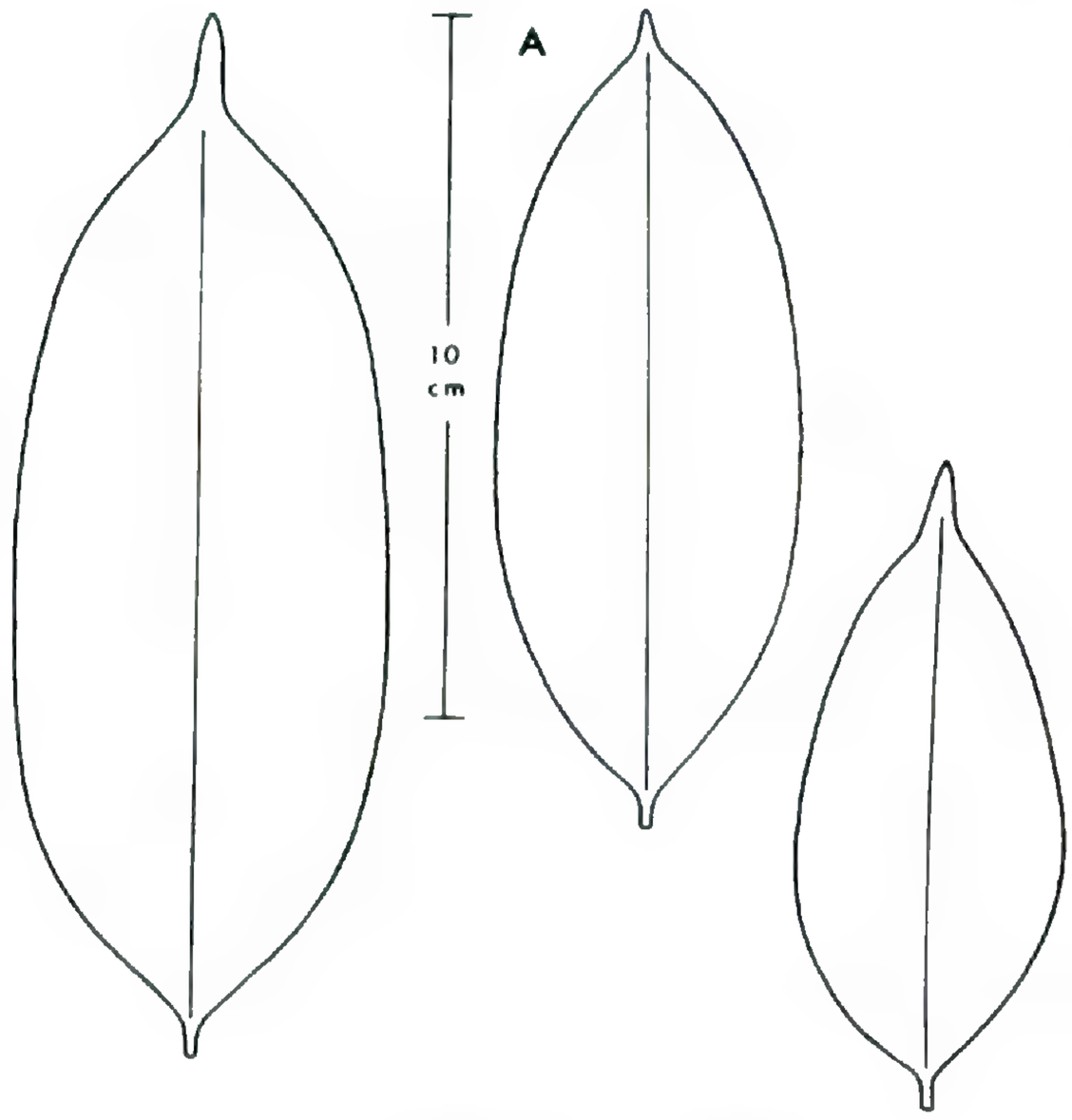


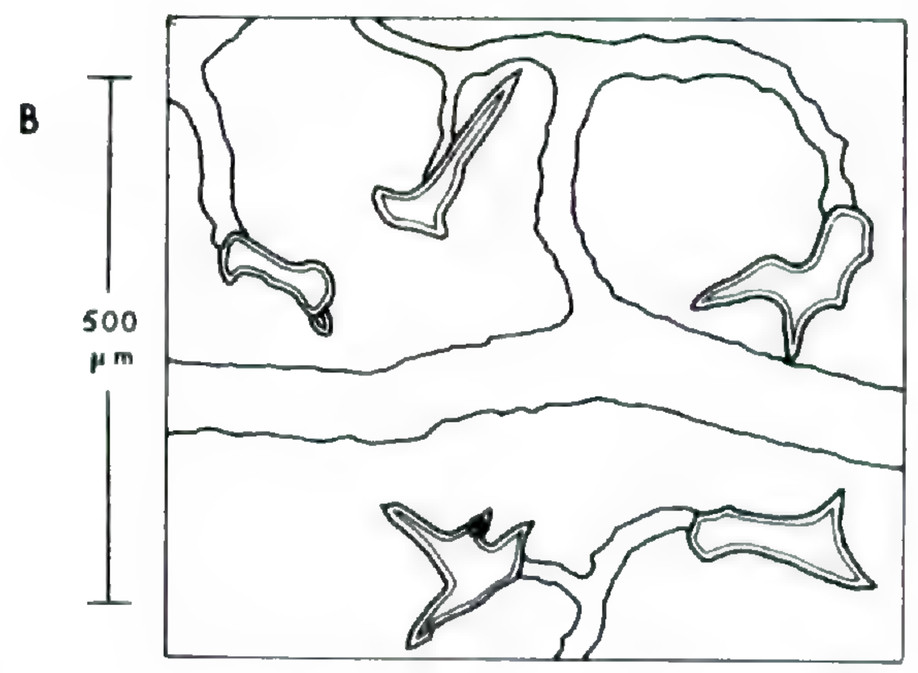
FIGURE 3. *Mouriri latihila* (*Steyermark & Bunting 102927*).—A. Leaves.—B. Cleared portion of leaf blade showing veins and terminal sclereids.—C. Cross section of leaf blade showing sclereids, stomatal crypts, and upper epidermis.—D. Cross section of leaf midrib.—E. Deflorescent flower and flower bud.—F. Fruit.—G. Seed: a, polished side; b, hilum side.

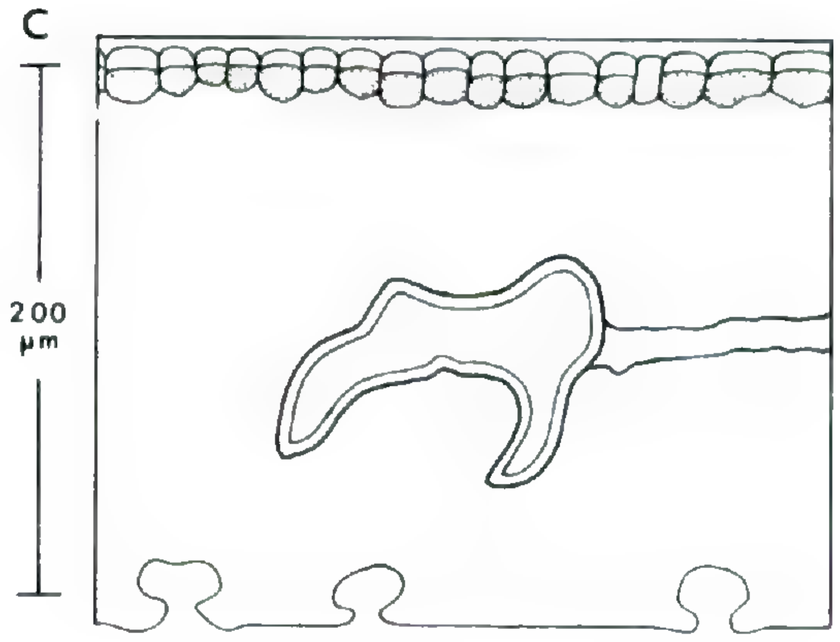
ras Army Post, 72°49′W, 5°8′S. Forest on terra firme. Treelet, 3 m tall. Fruit green, 1 Aug. 1973, *E Lleras, W. C. Steward, J. C. Ongley, D. F. Coelho, J. F. Ramos & J. F. Lima P16980* (holotype, NY; isotypes, CAS, G, INPA, MIN). Figure 4.

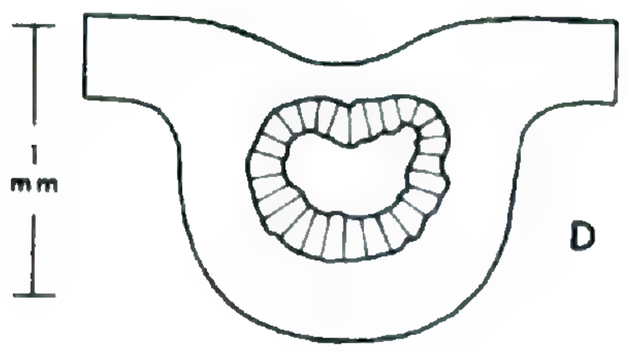
Arbor parva; laminae 7.8–16 cm longae; cryptae stomatophorae simplices; sclerides terminales foliorum stellatae; flores axillares, solitarii, tetrameri; calyx ovarium inferum includens 2.5–3.4 mm longus; lobi calycis in alabastro separati; petala persistentes in fructu immaturo; thecae antherae ambae poro unico apicali dehiscentes; glandula nulla; ovarium 1-loculare, ovula 4; semen 1.

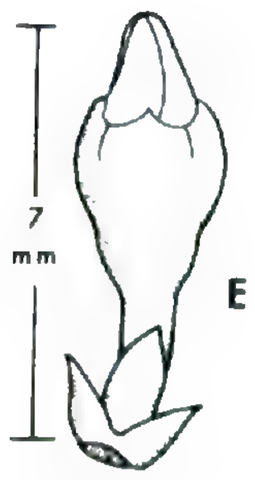
Small tree, 3 m the only cited height, the plants glabrous except for the flower; young twigs rounded. Petioles 1.5–4 mm long; blades 7.8–16 cm long, 3.1–7 cm wide, ovate to elliptic or these oblong, abruptly acuminate to short caudate at apex, medium acute at base; midrib moderately grooved above, prominent and rounded below; sec-

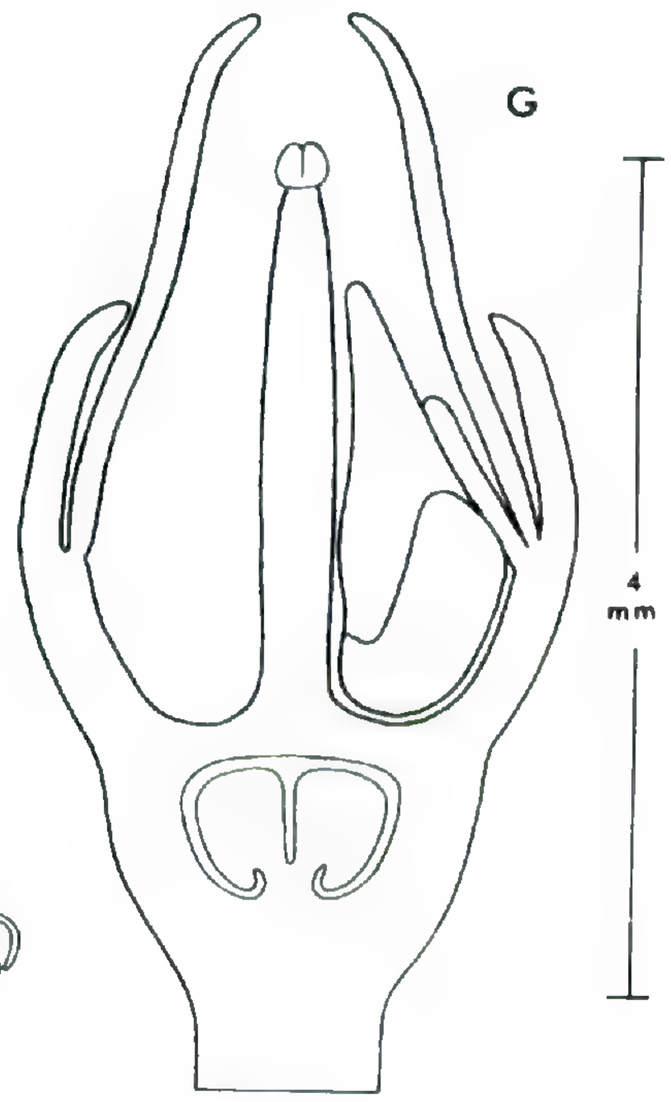


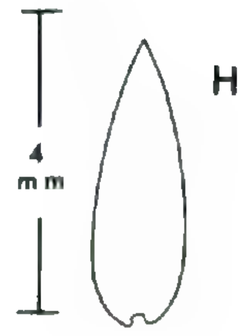


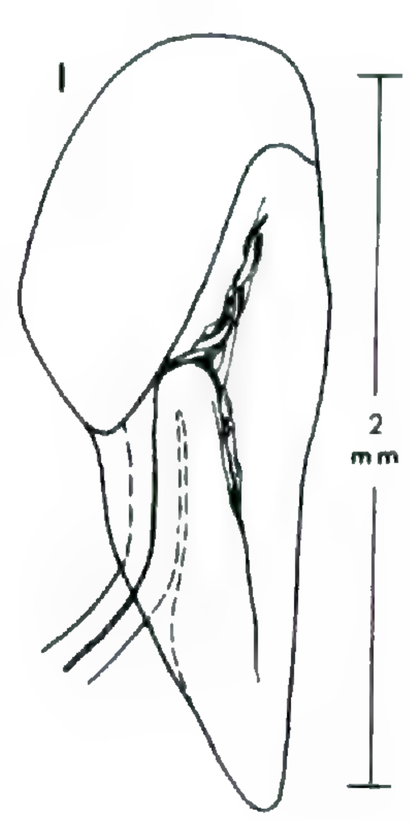


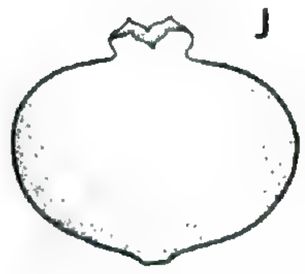


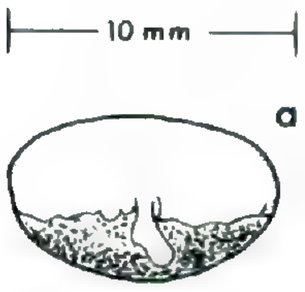


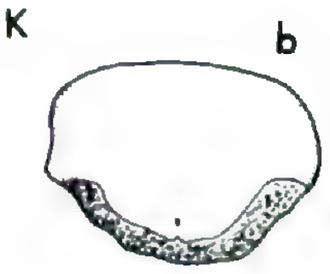












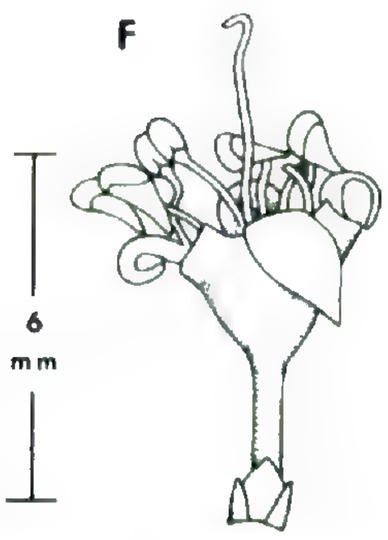


FIGURE 4. *Mouriri retentipetala.*—A. Leaves (both collections).—B. Cleared portion of leaf blade showing veins and terminal sclereids.—C. Cross section of leaf blade showing sclereids, stomatal crypts, and upper epidermis.—D. Cross section of leaf midrib.—E. Flower before anthesis.—F. Flower at anthesis.—G. Longisection of flower before anthesis.—H. Petal.—I. Anther.—J. Fruit.—K. Seed: a, funiculus side; b, micropyle side. (B–I, *Lleras et al. P16980*; J, K, *Bernardi s.n.*)

ondary and smaller nerves prominent above and below when dry. Midrib xylem tubular; stomatal crypts Type II, averaging in a leaf 31–50 μm diam., 18–25 μm high, 27–54 per mm²; superficial stomata numerous; upper epidermis 1 cell thick, nearly all the cells with thick mucilaginous walls; hypodermis none; terminal sclereids stellate, the central body sometimes isodiametric with 4–5 arms, more often 2–6 times as long as wide with 1–3 large arms. Flowers tetramerous, single in the leaf axils on sessile pedicels 2–2.5 mm long with 1 or 2 pairs of ovate-triangular bracts 1–1.6 mm long at base of pedicel. Calyx including inferior ovary 2.5–3.4 mm long, campanulate, the surface scattered-mealy with loose inflated hairs, these white on the outer surface of the calyx lobes, golden on the inner surface; free hypanthium ca. 0.7 mm long; calyx lobes 0.2–0.4 mm long, 1.1–1.4 mm wide, broadly triangular or slightly apiculate, splitting apart a distance of 0.5–0.7 mm at anthesis. Petals protruding from the calyx early in the bud, narrowly ovate-elliptic, 3–3.6 mm long, 1.1–1.5 mm wide, minutely glandular-hairy mostly on the apical third, persistent on the unripe fruit. Antesepalous filaments 1.2–1.4 mm long, antepetalous ones 1.7–1.9 mm long; anthers 1.6–2.2 mm long; thecae 0.9–1.2 mm long, dehiscing by a single apical pore; gland none; cauda 0.8–1 mm long. Ovary 1-locular with 4 ovules arranged around a short central and basal placenta; style ca. 5 mm long, sharply curved at tip, with a sharply demarcated 4-lobed stigma. Fruits subglobose, ca. 6.5–7.5 mm high, 8–9 mm thick, crowned with the persistent calyx. Seed 1, ca. 5.5–5.8 mm high, 7–7.5 mm wide, 4–5 mm thick, medium brown and polished except for a basal hilum as wide as the seed, the funiculus visible as a hardened and polished irregular stalk extending below the main polished part of the seed.

Paratype. PERU. LORETO: Arboreti Jenaro Herrera (Amazoniae Peruvianae, Prov. Requena, ad flumen Ucayali, silva uda aequinotiali, 73°45′W, 4°55′S, ca. 120 m alt.). Specimina lecta vel selecta praecipue a *Luciano Bernardi* illuc misso a COTESU (Cooperation Technique Suisse) VIII–IX. 1976. 6-R-83 (Parcela Marmillod) (G).

Distribution. Tropical forests in the drainages of the Ucayali and Javari rivers in NE Peru and adjacent Brazil at about the latitude of Requena, Peru.

This species, like the foregoing one, falls in subg. *Mouriri*, its tubular midrib xylem, anatropous ovules, and polished seed being the determining features. The tetramery, monoporous and eglandular anthers, and persistent petals of this entity make it very distinctive. This is only the second species of the genus to be found with monoporous anthers, and persistent petals have not been noted before. The petals were persistent on the green but nearly ripe fruits of the type collection; they were gone from the ripe fruit of the paratype. It is impossible to know if they had dropped naturally or were broken off during collection in the latter case. Within its subgenus the new species is most similar to three species in sect. *Litophyllum*: *M. exadenia*, *M. latihila*, and *M. monopora*. Probably *M. retentipetala* is most closely related to these three and belongs with them in sect. *Litophyllum*.

The characteristics of *M. retentipetala* suggesting the three species named are: small simple stomatal crypts, a one-layered upper epidermis, small flowers, tetramery, monoporous eglandular anthers, a one-locular ovary with few ovules, and a large hilum on the seed. Some of these characters are not found in all three of the presumed allies, and several have not yet been investigated in *M. latihila* owing to lack of material.

Mouriri retentipetala differs from *M. exadenia* in having higher, more numerous stomatal crypts, pedicellate flowers, persistent petals, monoporous caudate anthers, and a large hilum on the seed. From *M. monopora* the new species departs in its tetramery, triangular calyx lobes, and eglandular anthers with a longer cauda and straight thecae. From *M. latihila*, *M. retentipetala* varies in having stellate foliar sclereids, short calyx lobes so that the petals protrude from the calyx early in the bud, and persistent petals.

Mouriri gleasoniana Standley ex Standley & Steyermark var. **coibensis** (Morley) Morley. *Mouriri coibensis* Morley, Fl. Neotropica 15: 143–145. 1976.

Recent collections of *M. gleasoniana* from Costa Rica and Panama require reassessment of the status of *M. coibensis*, a close relative of the former species from the island of Coiba off the southwest coast of Panama. When *M. coibensis* was described, *M. gleasoniana* was known only from Honduras to Mexico, and the differences between the two taxa as then known were sharp. The new material partly bridges the gap between them and seriously weakens their separation. I believe realities are best served by viewing both as part of a single variable species. As presently known, the island plants are still distinguishable and are retained as a variety. Six major variables are involved, as shown in Table 1. Plants of the complex are yet to be found in Nicaragua.

TABLE 1. Geographic variation in six characters of *Mouriri gleasoniana*.

			Anthers			
	Foliar Sclereids	Stomatal Crypts	Theca Length (mm)	Gland Length (mm)	Distance from Theca Base to Anther Base on Gland Side (mm)	Ovule Numbers
Central Panama	roundish	Type II	2.7–3.0	0.8–0.9	1.0–1.2	29–33
Coiba Island	roundish	mostly Type III	1.9–2.2	0.2–0.5	1.2–1.4	18–20
Northeastern Costa Rica	roundish to columnar	mostly Type II	2.2–2.7	0.5–0.7	0.9–1.2	23–33
Honduras–Mexico	columnar tendency	mostly Type II	2.0–3.0	0.4–0.9	0.7–0.8	15–24

Ovule numbers are relatively large in plants of Costa Rica and the Panama mainland. In the one flowering collection from Panama (*Knapp & Huft 4424*) and one of the two Costa Rican collections (*Hammel 9317*), the large number of ovules apparently results in an unusual placentation in that the ovules in each locule are arranged on all sides of the axile-basal placenta. These are the only known examples of such an arrangement in sections 4 through 9 of subg. *Mouriri*.

A transition from a large number of ovules to a small one raises the question of which state, if either, represents the primitive condition. A similar trend was found in *M. guianensis*, where the conclusion was that the greater number was primitive (Morley, 1983). In *M. gleasoniana* the presence of the larger numbers close to South America, where the genus appears to have originated, with the smaller numbers to the north, where the environment gradually becomes more extreme, suggests that the same interpretation should be made in this species. Throughout the range, the fruits are 1–4(–5)-seeded; as in *M. guianensis*, many ovules must therefore abort when a large number is present before fertilization. Accordingly, those plants with fewer ovules in the flower and thus less wastage would be regarded as better adapted and, in this case, more specialized. It would appear that in increasingly extreme environments the demand for floral economy becomes greater.

Mouriri longifolia (HBK) Morley. Until recently, this species was known only from fruiting material. A flowering collection has now been made, so that the following addendum to the description of the species can be given, with illustrations (Fig. 5).

Inflorescences at leafless nodes of twigs 4–7 mm thick, 1 or 2 per side, each 1–5-flowered, 2.5–7.7 mm long to base of farthest pedicel measuring along the axes and with 2 or 3 internodes in that length; bracts 1.4–2.5 mm long, triangular or narrowly so, mostly present at anthesis, deciduous later. Axes of inflorescence, ovary, and calyx minutely puberulent. True pedicels 7–15 mm long; calyx including inferior ovary 6.2–8.5 mm long, campanulate; free hypanthium 2.2–2.7 mm long; calyx lobes just before anthesis 2.1–2.4 mm long, 2.5–3 mm wide, 3.8–4.1 mm long from the stamen attachment, triangular with inverse-curved sides, the calyx splitting 0–0.5 mm between the lobes at anthesis. Petals ovate-oblong, ca. 10 mm long including a basal claw ca. 3 mm long, 7 mm wide, broadly acute at apex, erose toward the base. Filaments 11–14 mm long; anthers 3–3.3 mm long; thecae 2.8–3 mm long, dehiscing by apical slits; gland 0.8–1 mm long, 2.1–2.3 mm from apex of anther when measured from center of gland; cauda 0.6–0.8 mm long. Ovary 5-locular; placentae basal in each locule, the ovules borne on all sides of a short basal column, ca. 5 per placenta, ca. 25 in all; style 17–22 mm long.

With the flowering material in hand it now becomes apparent that *M. longifolia* belongs in sect. *Apirangia*. Specifically, the characters that place it there are the tubular midrib xylem, filiform sclereids, Type III crypts like those of *M. apiranga*, the lack of a hypodermis, the free calyx lobes with the petals protruding from them early in the bud, the anther shape which generally agrees with that of the other species, the proximate position of the placentae which are not widely separated, and the position of the ovules on all sides of each placenta.

Additional collections examined. VENEZUELA. AMAZONAS: Estación Experimental de Sta. Bárbara del Orinoco, 1–2 km al sur de Trapichote, 26 Feb.–2 Mar. 1976 (st), *Berry & Chesney 2083* (US); 28 Mar. 1976 (defl.), *Berry & Chesney 2179* (US); Tayari, 1 Nov. 1975 (fl), *Lissot s.n.* (US).

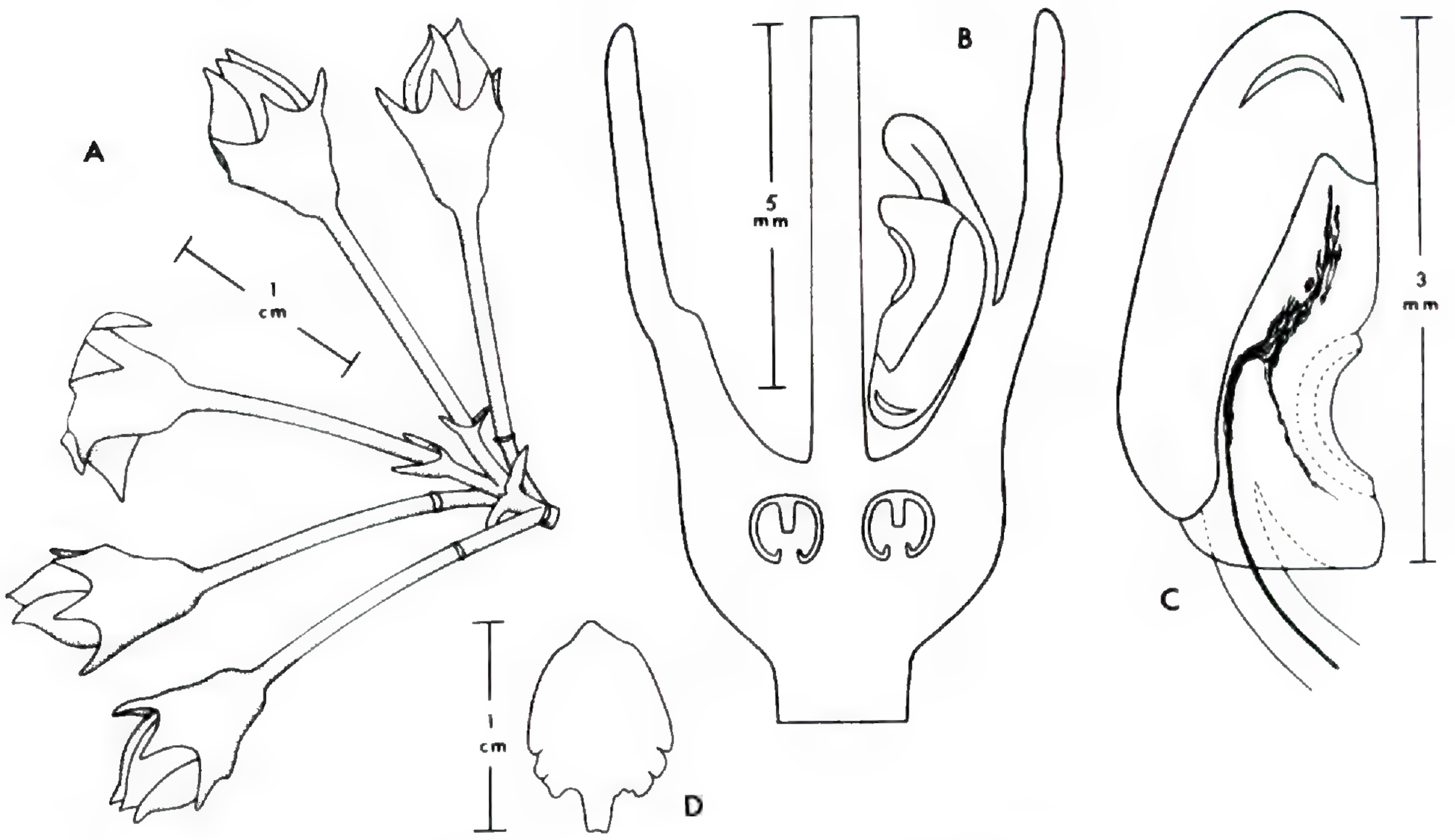


FIGURE 5. *Mouriri longifolia* (*Lissot. s.n.*).—A. Inflorescence.—B. Longisection of flower before anthesis.—C. Anther, shown cleared except for the thecae.—D. Petal.

Votomita roraimensis Morley, sp. nov. TYPE: Brazil. Roraima: BR 174, Manaus–Caracaraí, km 523, 1°20′N, 60°43′W. In damp water-logged woodland. Straggling tree to 5 m, 2 June 1986, *Hopkins, Pereira de Lima, Guedes de Oliveira & Lowy 502* (holotype, INPA; isotypes, K, MIN, NY, US). Figure 6.

Arbor usque 5 m alta; costa media folii subta lateribus papillosa; cryptae stomatophorae unaquaeque cavitatibus 2–5; ovarium 4-loculare placentis axialibus; ovula 3–4 undique circum quamque placentam genita, in recta verticilla; fructus 6.7–9.5 mm diametro, stylo persistenti; semen 1, vitta angusta laeve ⅔ circumdatum.

Tree to 5 m, glabrous except for the leaf midrib; young twigs terete. Petioles 1.5–2.5 mm long; blades 6.1–10.2 cm long, 2.3–4 cm wide, elliptic to elliptic-ovate, acuminate at the apex, medium acute at base; midrib flat to slightly rounded above, narrowly winged below for its length, the sides with papillae 20–35 μm long; lateral nerves not visible above or below when dry. Midrib xylem tubular; stomatal crypts multiple, each branched above the mouth into 2–5 small cavities, with prominent papillae on the central roof, the multiples 60–125 μm total diam., 55–75 μm high, averaging ca. 28 per mm²; upper epidermis mostly 1(2) cell(s) thick, a deep hypodermis present with walls tending to align with the epidermal cells above, the hypoderm cells commonly with mucilaginous walls; foliar sclereids terminal, thick-columnar with large dendroid branches at each end. Peduncles terminal and at leafless nodes of twigs up to 5 mm thick, 1–2 per side, 1-flowered, 2–11 mm long to base of farthest pedicel including 1 or 2 internodes; bracts narrowly triangular, 0.7 mm long, deciduous before anthesis. True pedicels 3–5 mm long; flowers 4-merous; calyx including inferior ovary ca. 4.5 mm long, campanulate; calyx lobes 0.4 mm long, 1.4 mm wide, rounded-triangular and mucronulate, stretching and splitting irregularly between lobes as bud enlarges. Immature petals ovate, sessile, 4.7 mm long, 2 mm wide. Stamens lightly connate in the lower third, 2.9–4.2 mm long; filaments 0.3–0.4 mm long; anthers 2.6–2.8 mm long; thecae 1.2–1.3 mm long; gland terminal, concave, 0.6–0.7 mm long, Ovary 4-locular with axile placentation, each locule with 3–4 ovules in a vertical whorl, the ovules 15–16 in all; style 6 mm long. Fruit medium brown when dry, spheroid with persistent style, 7–9.3 mm high excluding style and calyx, 7.7–9.4 mm wide, 6.7–8.9 mm thick. Seed 1, spheroid, light brown with dark brown markings, 5.9–6.8 mm high, 7.4–8.2 mm wide, 7–7.9 mm thick, with a narrow, smooth but unpolished tan band encircling ⅔ of the seed, extending from a small projection near the broken chalazal vascular strand where the band is narrowest to the micropylar end where it is widest, the width here 2.7–3 mm; remainder of surface rugose.

Distribution. Known only from the type locality in tropical forest in SW central Roraima, Brazil, east of the Rio Branco.

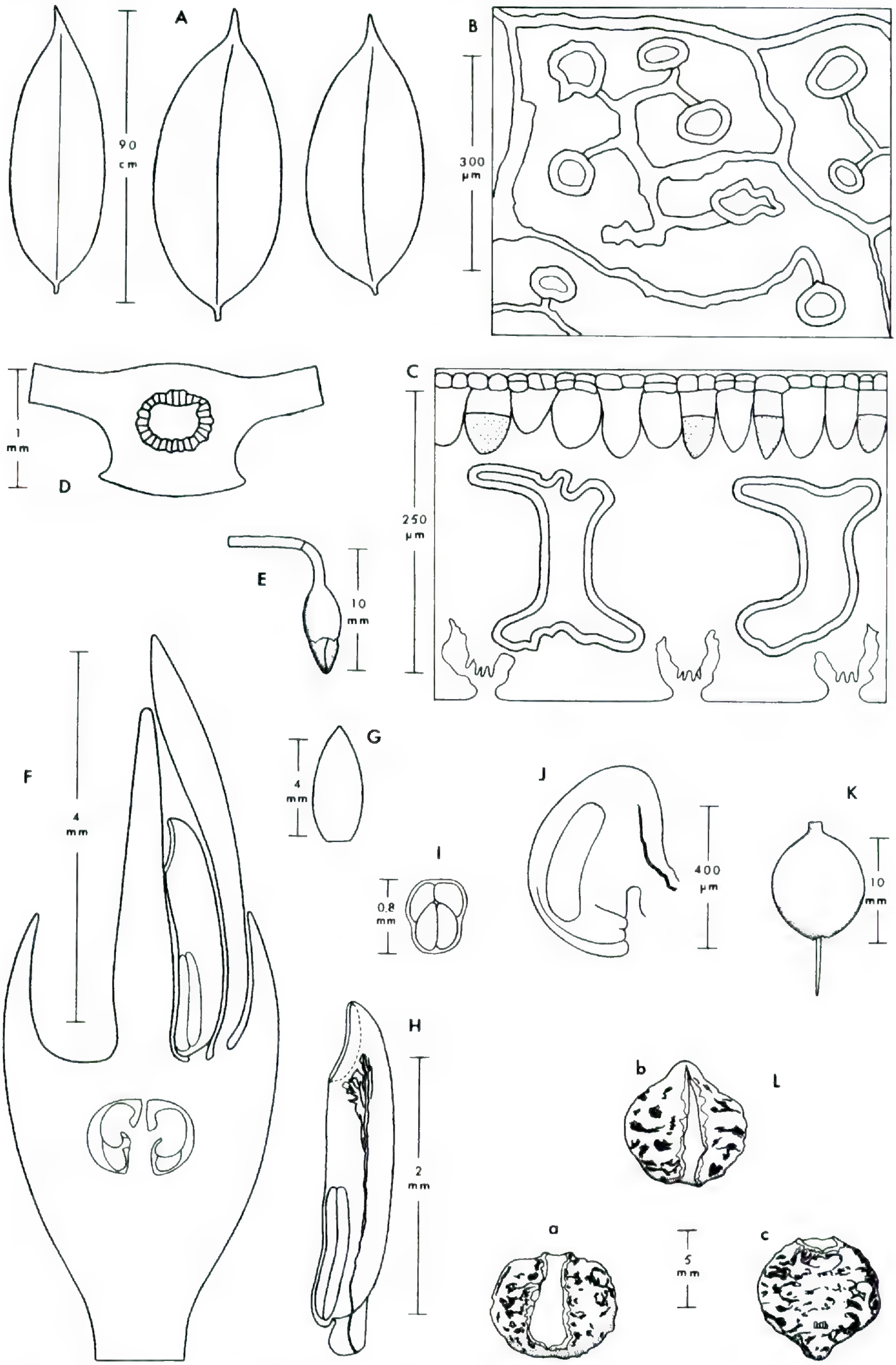


FIGURE 6. *Votomita roraimensis* (*Hopkins et al. 502*).—A. Leaves.—B. Cleared portion of leaf blade showing veins and terminal sclereids.—C. Cross section of leaf blade showing sclereids, stomatal crypts, and upper epidermis.—D. Cross section of leaf midrib.—E. Flower before anthesis.—F. Longisection of flower.—G. Petal.—H. Anther, shown cleared.—I. Cluster of ovules in one locule as seen from abaxial side.—J. Ovule.—K. Fruit.—L. Seed: a, abaxial view; b, view from top; c, underside.

This species is identified more by its combination of features than by any unusual characters. It is allied to the other four species that have four locules or placentas, numerous ovules, and (with one exception) hairs on the midrib. Its laterally fused stamens occur in two members of this group of four, *V. plerocarpa* and *V. monadelpha*. From all of these the new species differs in having much smaller leaves and flowers and only 15–16 ovules. Three of the other four, *V. monadelpha*, *V. orbinaxia*, and *V. plerocarpa*, have 36–48 ovules. The fourth, *V. pubescens*, is closest in ovule number with 20–26, but the new species differs greatly from that species by having small nearly glabrous leaves, a nonindurated ovary wall, laterally fused stamens, four locules, and a persistent style. The remaining three species in the genus, *V. guianensis*, *V. orinocensis*, and *V. monantha*, have one-locular ovaries with 8–10 ovules and glabrous midribs. Because of its small leaves, small flowers, and geographic proximity, a close relation of *V. roraimensis* to *V. orinocensis* and the related Cuban species *V. monantha* seems likely, although the floral structure mostly does not sustain this view. The small leaves, deep hypoderm, and persistent style of the new species in particular suggest *V. monantha*, although the hypoderm of the former differs in having abundant mucilage walls.

Ovules in *Votomita* and *Mouriri* vary from a campylotropous type in which the ovule is bent at a sharp angle from a short, broad placental attachment at the chalazal end to half-anatropous, and fully anatropous forms occur in *Mouriri*. In *V. pubescens* and *V. roraimensis*, the ovules are half-anatropous and are borne on an axile placenta, the only known examples of such a combination in the two genera. In *Mouriri*, half-anatropous ovules occur only on axile-basal, free central, or basal placentas. In *V. pubescens*, the ovules are sessile laterally with extruded inner integuments that appear to serve as internal stigmas (Fig. 7D).

Seeds are known in three species of *Votomita*: *V. monantha*, *V. pubescens*, and *V. roraimensis*. In *V. monantha*, which has free-central placentation, the angular distance on the seed between the micropyle and the broken chalazal strand is about 94°, while in *V. roraimensis* and *V. pubescens*, with axile placentation, the angles are 60° and 50° respectively.

In *V. monantha* the whole abaxial (outer) surface of the seed is smooth, whereas in *V. roraimensis* and *V. pubescens* the smooth part is narrow and is broadest at or near the micropylar end (Figs. 6L, 7F). In none of these seeds is the smooth part polished. Seeds of the latter two species resemble superficially seeds found in *Mouriri* sect. *Brevipedillus*; however, in that section the smooth area is narrowest at the micropylar end and is usually conspicuously widened at the opposite end nearest the broken chalazal strand. I have no explanation for the difference in shape.

The reason for the smooth area is unknown; it may be that this is the part of the ovule first pushed against the ovary wall as enlargement begins.

The Genus Question

Partial generic differences between *Votomita* and *Mouriri* in ovule and seed structure are suggested by the above and may be summarized thusly: (1) half-anatropous ovules on an axile placenta occur only in some species of *Votomita*; (2) the smooth area of the seed is unpolished in *Votomita* but is polished in almost all species of *Mouriri*; (3) in no known species of *Votomita* does the smooth area cover all of the seed except for the hilum, as it does in seeds of the subgenus *Mouriri*; and (4) seeds of *Votomita* most closely resembling those of *Mouriri* are found only in sections *Acutiflos* and *Brevipedillus* of *Mouriri* subg. *Taphroxylon*. Seeds of *V. monantha* somewhat resemble those of sect. *Acutiflos* but lack the polished face and rugose surrounding area of the seeds of that section. Seeds of *V. pubescens* and *V. roraimensis* have narrow smooth areas with surrounding rugose surfaces as in *Mouriri* sect. *Brevipedillus*, but the smooth parts differ in shape as described above.

The above considerations may affect present generic divisions. The seed structure in *V. roraimensis* and *V. pubescens* maintains the difference between *Votomita* and *Mouriri* subg. *Mouriri* but increases the resemblance between *Votomita* and *Mouriri* subg. *Taphroxylon*.

It may be that the New World Memecyleae should be regarded as consisting of three genera or subgenera: *Votomita*, *Mouriri*, and *Taphroxylon*. Absolute differences exist between all three groups, the most between *Votomita* and subg. *Taphroxylon*, the fewest between subgenera *Taphroxylon* and *Mouriri*, thus supporting the present disposition of these groups. Between *Votomita* and subg. *Taphroxylon* the differences are those of midrib xylem form, flower mery, hypanthium development with accompanying features of stamen form, and the presence or absence of free stone cells in the petals. Between *Votomita* and subg. *Mouriri* the differences are the presence or absence of free stone cells in the petals, and seed structure; between subgenera *Taphroxylon* and *Mouriri* the single absolute difference is that of

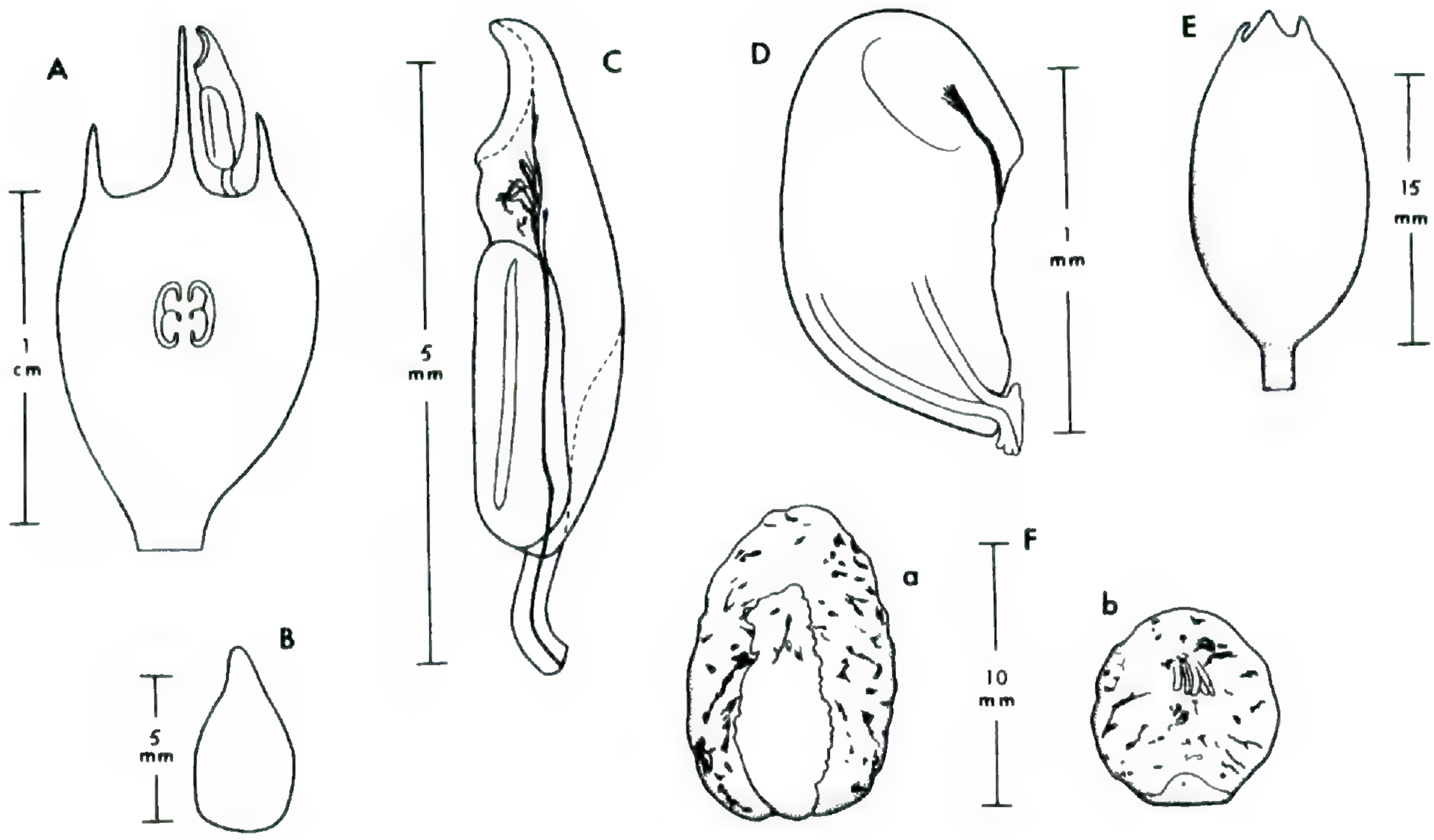


FIGURE 7. *Votomita pubescens*.—A. Longisection of flower (ovules copied from Morley, 1985, *Lao 22*).—B. Petal.—C. Anther, shown cleared (*Bernardi s.n.*, tree 5-145).—D. Ovule (*Lao 22*).—E. Immature fruit.—F. Seed: a, lengthwise view showing smooth face; b, underside. (A, B, E, F, *Bernardi s.n.*, tree 2/168.)

seed structure. On this basis *Votomita* is overall more like subg. *Mouriri* than subg. *Taphroxylon*, even though seed structure in *Votomita* is more like that of the latter.

Because the above differences do not negate the present arrangement of genera, I think any serious effort to reconsider the generic divisions must await more evidence. Seeds of more species of *Votomita* should be examined, and detailed comparative studies of wood anatomy, karyotypes, and phytochemistry may be expected to aid in the evaluation. When the similarities and dissimilarities between the three are well known it can then be decided how many of them should be assigned generic status.

Votomita pubescens Morley. Several more collections of this species have been made from the same area as the type. Among these are specimens with petals, stamens, fruit, and seed—all lacking from the type. An extended and illustrated (Fig. 7) description of the species is therefore presented, omitting the anatomical features, which are not modified.

Tree to 16 m high. Petiole 4–6.5 mm long; leaf blades 10.5–15.5 cm long, 3.6–6.5 cm wide, elliptic or slightly elliptic-ovate, abruptly caudate at the apex with a cauda 11–13 mm long, medium acute at base, glabrous above, pubescent beneath; midrib nearly plane above but with a slight groove down the center, prominent below, the underside rounded at the petiole but abaxially soon 2-angled with 2 very narrow wings for its length, pubescent on the sides; lateral nerves not visible above or below when dry. Peduncles axillary, 1 or 2 per side, each 2–9-flowered, 19–53 mm long to base of farthest pedicel measured along the axes and with 1–3 internodes in that length; bracts unknown, deciduous before anthesis. True pedicels 8–11 mm long; flowers 4-merous, white or yellow; calyx including inferior ovary 10.3–13.3 mm long, 7.8–9 mm thick, glabrous, shrinking only slightly on drying, when dry with a hard, smooth, somewhat polished olive-green to brown outer layer, the ovary widest ½–⅔ of the way above the base; calyx lobes separate, 0.9–2 mm long, 2.4–2.7 mm wide, triangular and slightly apiculate, not separating further at anthesis. Immature petals oblong-ovate, 6.5 mm long, 3.5–3.7 mm wide. Stamens 4–5.5 mm long; filaments 1.2–1.5 mm long; anthers coherent, apparently not truly fused, 3.6–4.5 mm long; thecae 2–2.5 mm long; gland terminal, concave, 0.8–1.2 mm long. Ovary 2-locular, each locule with 2 axile placentas and an irregular very incomplete ridge running down the outer wall representing a missing partition; ovules sessile with an extruded inner integument, 5–7 per placenta, 20–26 in all; style ca. 5 mm long. Fruit maturing red, ellipsoid, ca. 20–24 mm long, 14–18 mm wide. Seed 1, light brown, ovoid-ellipsoid, 12–15 mm high, 8–10 mm wide, 7.5–8 mm thick, with a narrowly ovate, slightly elevated, rather smooth, slightly pebbled, unpolished face (the enlarged outer face of the ovule) extending ¾ of the length of the seed

from the base, the widest end of the face down and turned under opposite the broken chalazal strand, the micropyle in the underturned end; remainder of seed surface rugose.

Vernacular name. Lanza caspi.

Additional collections examined. PERU. LORETO: Prov. Requena, Ucayali River, Arboreti Jenaro Herrera, *Bernardi L. 15608* (G), *s.n.* trees 2/39, 2/168, 5/145 (G); *Diaz M. 59-A, 76-A* (G); slightly disturbed moist forest NW of Arboretum Jenaro Herrera, *D. C. Daly et al. 5641* (MIN, NY); Jenaro Herrera, 73°45′W, 4°50′S, ca. 170 m, bosque primario, *R. Vasquez, K. Young & N. Jaramillo 2057* (US).

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STUDY OF THE FLORA OF RUCAMANQUE, CAUTIN PROVINCE, CHILE[1]

Carlos Ramírez,[2] *Enrique Hauenstein,*[3] *José San Martín*[4] *and Domingo Contreras*[3]

ABSTRACT

The flora of forest, scrub, and grass communities was studied in Rucamanque, located near the city of Temuco, Cautín Chile, in the central valley of south central Chile. Forty-six vegetation samples were made, and plants were collected intensively outside the sample areas. A catalog was written for 203 plants species, which were analyzed for systematics, phytogeographics, life forms, the biological spectrum that they compose, the frequency and relative importance of each in the different vegetational communities, and their uses in industry, crafts, and medicine.

Rucamanque, "The House of the Condor" in Mapudungun, the language of the indigenous people of this region (Ramírez-Sánchez, 1985), is a valley located 12 km northwest of the city of Temuco, capital of the IX Region of the Araucanía, Chile (Fig. 1). The primitive forest vegetation of this valley escaped destruction during last century's process of colonization of central southern Chile (Donoso, 1983) because it was protected as an early watershed area for the drinking water for Temuco (Magofke, 1985).

With the increase in population, water for the city had to be drawn from other sources, principally subterranean, so the state lost its interest in Rucamanque and offered it for sale in March of 1986. Because of its value as a forest relict and its scientific interest, several state and private institutions and ecological organizations intervened to preserve it from exploitation. Finally, the University of the Frontera in Temuco became the legal owner, saving the relict forest for science, education, and the general public.

The present catalog of the flora of Rucamanque was made during the time that the land was for sale.

STUDY AREA

Rucamanque is a small river valley oriented southeast–northwest to the south of the Ñielol-Huimpil hills (Magofke et al., 1986). Through it runs Chivilcán Creek, which receives the water of two small unnamed streamlets. Its elevation ranges from 300 to 530 m. The area occupies about 525 ha, including some of the adjacent forests that belong to private owners. The basin and slopes of Rucamanque Valley are covered by native forest, which is evergreen in the lower areas and partially deciduous at higher elevations. In several places the forest has been destroyed and secondary scrub replaces it. In the higher slopes, originally of deciduous forest, permanent grasslands of human origin can be found. Small bogs, which we include in the grassland formation, appear in open areas on the edges of streams at the bottom of the valley.

The climate of the area is humid and temperate with a Mediterranean influence (Di Castri & Hajek, 1976). The average annual rainfall is 1,400 mm and the median annual temperature is 12°C. Rainfall is abundant in winter, and summers often have one to two dry months, as shown in the climatic diagram in Figure 1. Winter and spring frosts are frequent. To this climate corresponds a subtropical semideciduous forest type as natural vegetation (Schmithüsen, 1956).

The Ñielol-Huimpil hills comprise a tectonic unit characteristic of the central valley of Chile and do not connect with either the Coastal Ranges or with the Andes. The red clay soil does show similarity to the Coastal Range soils (Weinberger & Binsack, 1970). When cultivated or grazed, this soil is subject to erosion.

METHODS

The catalog of plant species of Rucamanque was made from 46 vegetation samples taken using the

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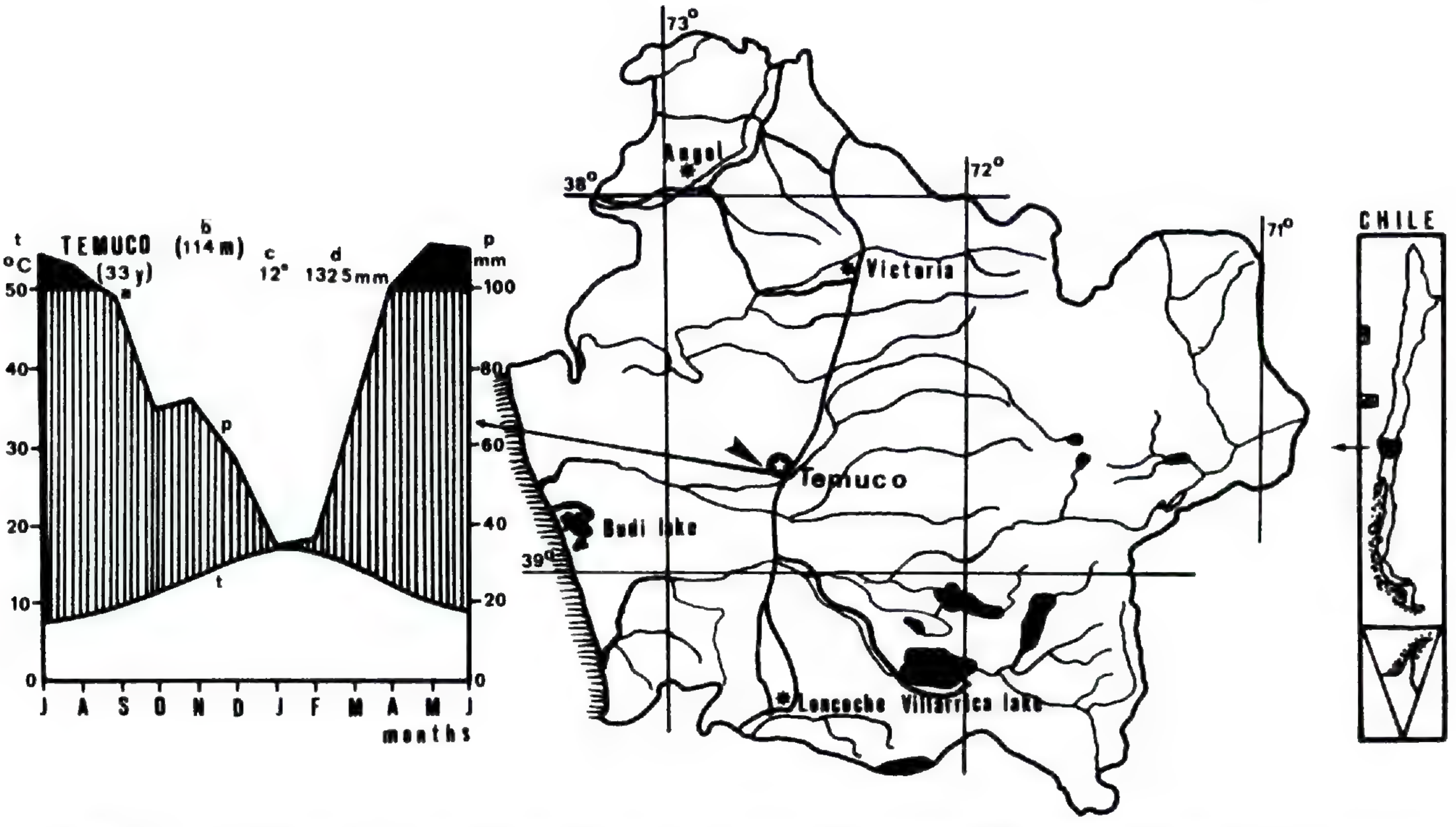

FIGURE 1. Ninth Region of Chile. Climate diagram of Temuco according to Hajek & Di Castri (1975): a = years of observation, b = altitude, c = year average temperature, d = year average precipitation, p = precipitation, t = temperature. Black areas = surplus of precipitation.

Braun-Blanquet (1964) phytosociological method for the study of the local vegetation. Other plants, collected outside the study quadrats, were added to the collection. Eighteen samples were taken in the forest, 20 in scrub vegetation, 6 in pastures, and 2 in bogs. The vegetation contains the following associations: *Lapagerio–Aextoxiconetum punctatii*, *Nothofago–Perseetum linguae*, *Fuchsio–Chusqueetum quilae*, *Rhaphithamno–Aristotelietum chilensis*, *Chusqueetum coleu*, *Aristotelio–Rubetum constrictae*, *Hyperico–Agrostidetum castellanae*, and *Juncetum procerii* (Oberdorfer, 1960; Ramírez, 1982; Hilldebrand, 1983).

The frequency of each species was estimated in each plant association. The relative importance value was calculated adding this frequency and the average cover expressed in relative percentage of each species in the different associations according to the Wikum & Shanholtzer (1978) method. This value was not determined for species collected outside the quadrats.

Nomenclature and phytogeographic origin of the taxa were based on Marticorena & Quezada (1985) and the family nomenclature on Cronquist (1981). The common names are according to Muñoz (1966). Introduced species were classified using the German flora by Rauh & Senghas (1968). The collected species were kept in the herbarium of the Institute of Botany, Austral University of Chile (VALD).

Life forms follow the Raunkiaer system (Ellenberg & Mueller-Dombois, 1966). Vines, epiphytes, and parasites were included under phanerophytes. The interpretation of the biological spectrum was based on Cain (1950).

Information was added on the present and potential uses of the plants.

Results and Discussion

The flora of the study area is made up of 203 species, of which 190 were inventoried in the 46 vegetation samples taken in the forest, scrub, and grassland formations (Appendix I). The other 13 species were collected outside the sample quadrats. The 203 species are distributed among 161 genera, 84 families, and 6 classes (Table 1). The class with the greatest number of taxa was Magnoliopsida (dicotyledons), which include almost 69% of the species present in Rucamanque. Following these are the Liliopsida (monocotyledons) with 42 species (21%), and the Polypodiopsida (Filicinae) with 16 species (8%).

The best-represented family of the Magnoliopsida was the Asteraceae, with 18 genera and 25 species, amounting to 12% of the total. Next came the Fabaceae with 4 genera and 9 species, the Apiaceae with 6 genera and species, the Lamiaceae and Rosaceae with 5 species each, and the Myrtaceae, Proteaceae, and Scrophulariaceae with 4

TABLE 1. Taxonomic distribution of the flora of Rucamanque.

Classes	Families	Genera	Species (%)
Bryopsida	3	3	3 (1.47)
Equisetopsida	1	1	1 (0.49)
Polypodiopsida	7	9	16 (7.88)
Pinopsida	1	1	1 (0.49)
Magnoliopsida	60	115	140 (68.96)
Liliopsida	12	32	42 (20.68)

TABLE 2. Phytogeographic origin of the flora of Rucamanque, distributed by class. Percentages in parentheses.

Classes	Native	Introduced	Total
Bryopsida	3	0	3
Equisetopsida	1	0	1
Polypodiopsida	16	0	16
Pinopsida	1	0	1
Magnoliopsida	96 (68.6)	44 (31.4)	140
Liliopsida	30 (71.4)	12 (28.6)	42
Total	147 (72.41)	56 (27.58)	203

species each. Outstanding among the Liliopsida are the Poaceae, with 16 genera and 18 species, the Cyperaceae with 5, and the Juncaceae with 4 species. Among the ferns, the Hymenophyllaceae presented 6 species, all of which were epiphytes in the forest formation.

ORIGIN

Of the 203 species, 147 (72.41%) are native and 56 (27.58%) are introduced (Table 2). This high percentage of introduced weeds indicates a strong human influence on the vegetation (Sukopp, 1969). The introduced species only belong to the classes Magnoliopsida and Liliopsida, and make up 31.4% and 28.6% of each group, respectively. Of course the greatest percentage of introduced species is found in the shrub grassland formations, of anthropic and therefore secondary, origin (Ramírez, 1982). The evergreen forest of *Aextoxicon punctatum* is the association least invaded by weeds. The majority of the introduced species are originally European and of little grazing value (Montaldo, 1975; Añazco et al., 1981).

LIFE FORMS

The biological spectrum of the study area was constructed from 200 species; the remaining three were mosses. In the epiphytic synusia that were not considered, mosses are very abundant (Riveros & Ramírez, 1978). The most-represented life form was the phanerophytes with 80 species, representing 40% of the total. This life form abounds in forest and scrub formations, occupying different strata in the vegetation. Chamaephytes and cryptophytes were the scarcest, with eight species (4%) each. Hemicryptophytes appeared in about the same numbers as phanerophytes, with 78 species, or 39%. Therophytes were represented by 26 species, or 13%. The latter two herbaceous life forms were abundant in grassy and scrub formations (Table 3).

The biological spectrum here described (Fig. 2) corresponds to a phanerophytic phytoclimate, typical of intermediate latitudes in temperate zones (Cain, 1950). The relative abundance of hemicryptophytes and therophytes is related to the degree of anthropic intervention suffered by the original vegetation. In the original vegetation, these life forms certainly were not as important.

This is confirmed by separating the native elements from the introduced for each life form (Table 4, Fig. 3). Only one of 80 phanerophytes is exotic. The cryptophytes are all native. Among the chamaephytes and hemicryptophytes, the percentage of introduced species is much higher, reaching 37.5% and 38.5%, respectively. Cryptophytes are not very frequent, unlike the hemicryptophytes, which contribute 30 exotic species. These perennial cespitose herbs and rosettes are plants that accompany man and do not characterize any particular phytoclimate (Le Blanc, 1963). Their abundance is due to destruction of forest and to grazing, which impedes their replacement by more aggressive woody species (Pessot & Montaldo, 1974).

The therophytes constitute a special case of plants typical of dry climate or weeds of cultivated areas. They act as pioneers in uncovered soil (Cain, 1950). Only 15% of the therophytes present in the study area are native. This life form was scarce in the original vegetation but invaded anthropogenic grasslands formed on eroded soils, where the vegetational cover never reaches 100%. Thus, therophytes are not typical of Rucamanque.

The phanerophytes, therefore, make up the most

TABLE 3. Biological spectrum of the flora of Rucamanque.

Life Forms	Species	Percentage
Phanerophytes	80	40%
Chamaephytes	8	4%
Hemicryptophytes	78	39%
Cryptophytes	8	4%
Therophytes	26	13%
Total	200	100%

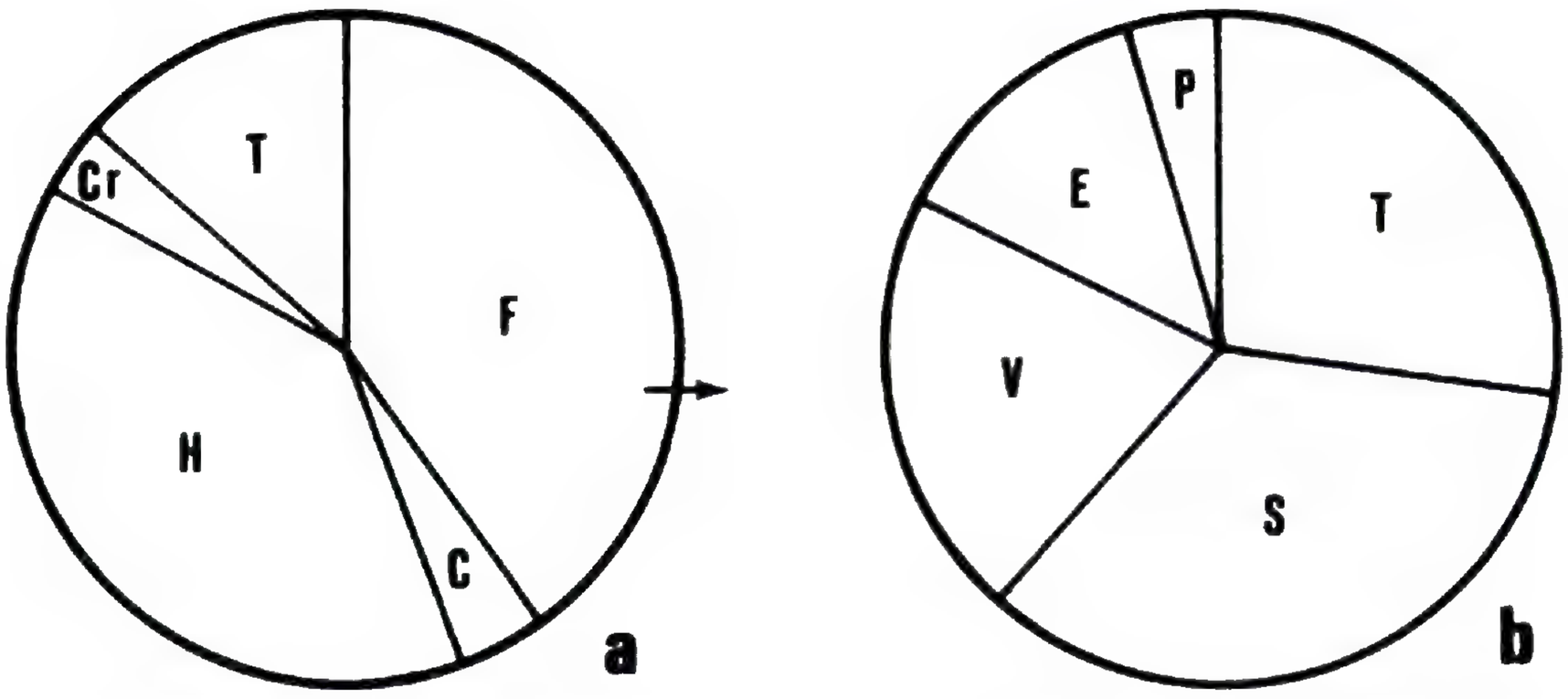

FIGURE 2.—a. Biological spectrum of Rucamanque. F = phanerophytes, C = chaemaephytes, H = hemicryptophytes, Cr = cryptophytes, T = therophytes.—b. Distribution of phanerophytes: T = trees, S = shrubs, V = vines, E = epiphytes, P = parasites.

abundant and representative life form of the research area, including trees, shrubs, epiphytes, and parasites (Table 5). Shrubs were very abundant, with 28 species, 35% of all the phanerophytes. This life form dominates the secondary scrub and tends to invade degraded and abandoned pastures or grassy areas (Ramírez et al., 1984a, 1985). Twenty-two species of trees were present, or 27% of the total.

Sixteen climbing plants flourish in Rucamanque, making up 20% of the total. The most robust of these, *Hydrangea serratifolia*, can have a stem diameter of up to 15 cm. Climbers are typical of forest and proliferate in secondary scrub where more light penetrates. The epiphytes, principally filmy ferns of the Hymenophyllaceae, presented 11 species, or 13.5%. Only three parasitic species were present.

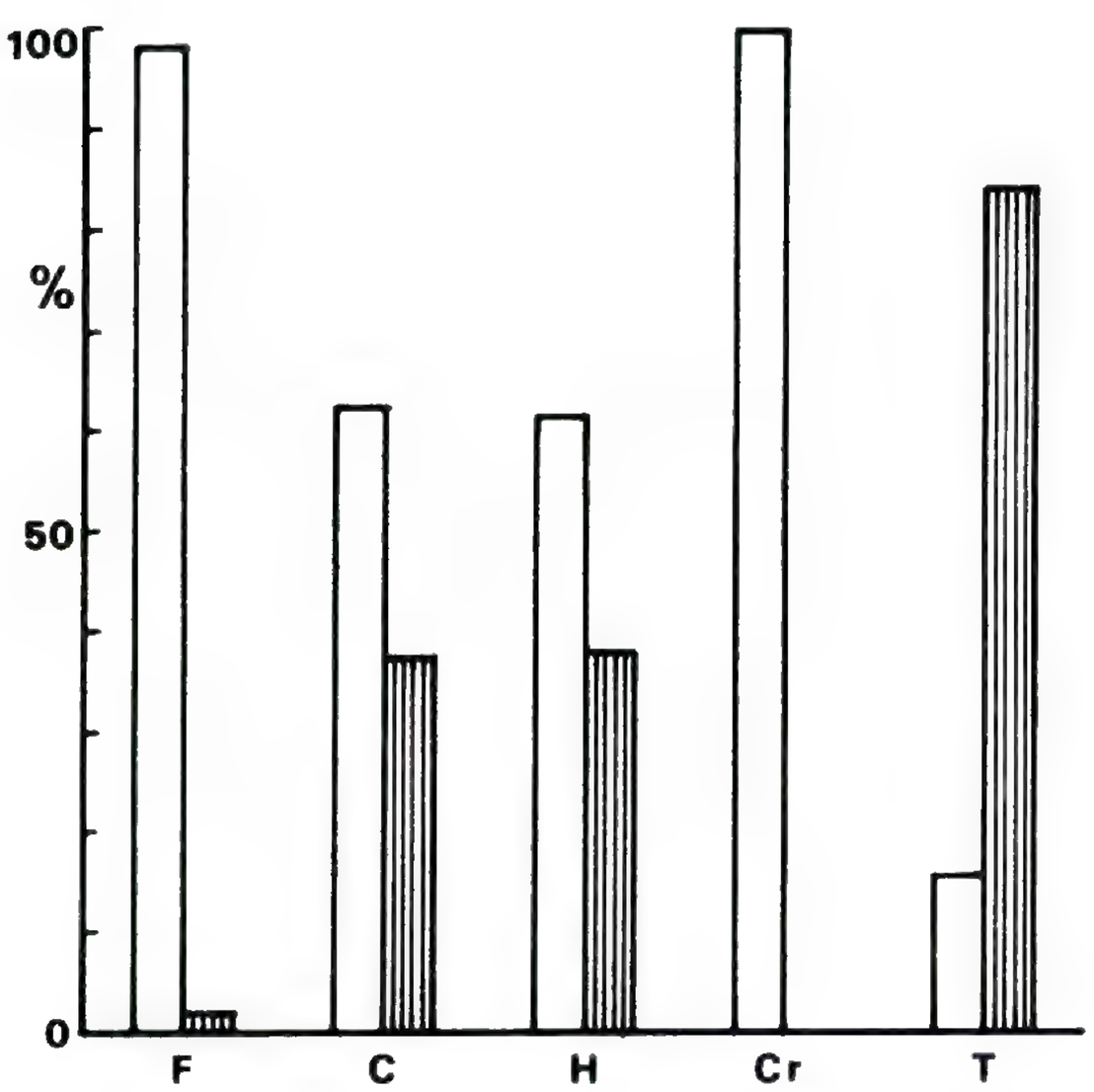

FIGURE 3. Native vs. introduced species in the biological spectrum of Rucamanque. F = phanerophytes, C = chamaephytes, H = hemicryptophytes, Cr = cryptophytes, T = therophytes. White bars = percentage of native species. Hatched bars = percentage of introduced species.

FREQUENCY IN THE PLANT ASSOCIATION

Only two species were present in each of the eight studied plant associations: *Rubus constrictus* and *Prunella vulgaris* (Table 6). These are European weeds, the first a spiny, semiclimbing shrub, and the second, a chamaephytic herb. Both have wide ecological ranges, colonizing any disturbed site in central-southern Chile. Another European species, *Holcus lanatus*, was found in seven of the eight associations studied. In six associations, *Plantago lanceolata*, another European herb, was found along with *Aristotelia chilensis* and *Eucryphia cordifolia*, two native woody species.

Native species with a frequency of five, that is, which occur in five associations, are: *Aextoxicon punctatum*, *Luma apiculata*, *Baccharis racemosa*, *Lapageria rosea*, *Cissus striata*, *Boquila trifoliolata*, and *Blechnum hastatum*. The first two are arboreal species of forests and scrubland; the third is a small shrub fairly frequent in the south of Chile. The remaining three are vines that

TABLE 4. Phytogeographic origin of the plant species of Rucamanque distributed by life form. Percentages in parentheses.

Life Forms	Native	Introduced	Total
Phanerophytes	79 (98.75)	1 (1.25)	80
Chamaephytes	5 (62.50)	3 (37.50)	8
Hemicryptophytes	48 (61.53)	30 (38.47)	78
Cryptophytes	8 (100)	0 (0)	8
Therophytes	4 (15.38)	22 (84.62)	26

TABLE 5. Habits of phanerophytes present in the flora of Rucamanque.

Habits of Phanerophytes	Numbers of Species	Percentage
Trees	22	27.50
Shrubs	28	35.00
Vines	16	20.00
Epiphytes	11	13.75
Parasites	3	3.75
Total	80	100.00

form large populations in secondary brush, and the last is a fern tolerant of a wide range of luminosity, as Godoy et al. (1981) demonstrated. The exotic hemicryptophyte herbs having the same frequency (5) are *Agrostis castellana* and *Rumex acetosella*. The former dominates the grassy vegetation in the study area (Oberdorfer, 1960) and the latter thrives on worn-out soils.

IMPORTANCE VALUES

Chusquea quila, a climbing bamboo, was found to be the most important species in the vegetation of Rucamanque (Table 6). It grows in areas of moist soil (Ramírez et al., 1984b) and prefers light in forest clearings. It forms extensive and impenetrable secondary scrub, locally called "quilantales." Following it with slightly less importance is the blackberry (*Rubus constrictus*), which colonizes all of the vegetational communities in Rucamanque. This blackberry forms scrubby areas called "murrales" when it invades degraded meadows and hedges (Hildebrand, 1983). It is an aggressive, woody plant whose control poses a serious problem in the study region (Ramírez, 1973). The importance of these two shrubs, which belong to disclimax communities, indicates the degree of anthropic intervention found in the vegetation of Rucamanque. They invade areas when the forest has been cut, and in this case make difficult the regeneration of the original forest community (Ramírez et al., 1985).

Third in order of importance is "olivillo" (*Aextoxicon punctatum*), a tall tree that forms evergreen forests in the lowest and deepest parts of Rucamanque Valley. *Aristotelia chilensis* and *Nothofagus obliqua* show similar importance values. The former dominates in shrub communities and the latter in partially deciduous forests of the *Nothofago–Perseetum*. The next-lowest values were found for *Agrostis castellana*, *Chusquea coleu*, and *Juncus procerus*, these dominant in grassy areas, scrub, and bogs, respectively.

TABLE 6. Frequencies in the plant associations, and importance values of the main species of Rucamanque.

Species	Frequencies	Importance Values
Chusquea quila	4	11.69
Rubus constrictus	8	9.33
Aextoxicon punctatum	5	7.92
Aristotelia chilensis	6	6.96
Nothofagus obliqua	4	6.66
Agrostis castellana	5	5.61
Chusquea coleu	2	5.03
Juncus procerus	1	2.93
Blechnum chilense	4	2.81
Eucryphia cordifolia	6	2.46
Prunella vulgaris	8	2.39
Holcus lanatus	7	2.30
Persea lingue	4	2.25
Trifolium repens	4	2.17
Senecio yegua	4	2.00
Plantago lanceolata	6	1.95
Leontodon taraxacoides	2	1.95
Peumus boldus	3	1.91
Cynosurus echinatus	4	1.90
Baccharis racemosa	5	1.88
Conium maculatum	2	1.88
Lapageria rosea	5	1.79
Vulpia bromoides	3	1.77
Baccharis concava	3	1.74
Cissus striata	5	1.64
Leucanthemum vulgare	3	1.62
Blechnum hastatum	5	1.49
Luma apiculata	5	1.49
Boquila trifoliolata	5	1.49
Rumex acetosella	5	1.49

APPLICATIONS

The flora of Rucamanque offers many uses, some of which are employed by the Araucarian Indians (Mapuche) who populate Cautin Province. *Chusquea coleu* and *C. quila* are used in crafts and for the construction of furniture and household articles. To fasten pieces of these bamboos, "voquis" (*Boquila trifoliolata* and *Campsidium valdivianum*) serve as ties. *Juncus procerus* is used to make mats. From *Luma apiculata*, tool handles are cut, and the wood of *Embothrium coccineum* is carved.

Applications as construction materials are important for tree species, including *Aextoxicon punctatum*, *Laurelia sempervirens*, *Persea lingue*, *Nothofagus obliqua*, *N. dombeyi*, and *Weinmannia trichosperma*. Tannins for the leather tanning industry are obtained from the barks of *Persea lingue* and *Weinmannia trichosperma*. Many individuals of the latter species can presently be

found with the bark cut off, resulting from excessive exploitation. *Eucryphia cordifolia* is valued for domestic firewood, and for this reason the tree is being cut so extensively that it risks local extirpation. Edible fruits grow on *Lapageria rosea*, Chile's national flower. "Maqui cider" is made from the berries of *Aristotelia chilensis*. Edible fruits also grow on *Gevuina avellana, Ribes trilobum, Fragaria chiloensis, Ugni molinae, Fuchsia magellanica*, and *Peumus boldus*. The fruits of *Rubus constrictus* are used to make jams.

The bark of *Dasyphyllum diacanthoides* allegedly regulates blood sugar; *Boquila trifoliolata* is applied for eye infections; *Peumus boldus* is used for stomachaches and liver illnesses; an infusion of *Tristerix tetrandrus* is thought to reduce cholesterol in the blood. *Solanum gayanum* is a reputed febrifuge; *Buddleja globosa* allegedly helps heal ulcers; and *Equisetum bogotense* is used as a diuretic. The following introduced plants have applications in popular medicine: *Urtica urens* as an antirheumatic, *Hypericum perforatum* as a vulnerary, and *Mentha rotundifolia* and *M. pulegium* for the stomach.

The rhizomes of *Dioscorea brachybotrya* are edible and high in starch. *Maytenus boaria* and *Chusquea quila* provide excellent winter forage.

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APPENDIX I. Scientific names, families, local names, life forms (Lf), origins (O), frequencies (F), and importance values (I.V.) of the flora of Rucamanque (Cautín, Chile).

Scientific Name	Family	Local Name	Lf	O	F	I.V.
BRYOPHYTAE						
Dendrolygotrichum dendroides (Hedw.) Brot.	Polytrichaceae	Musgo pinito		n	1	0,29
Hypopterigium thouinii Bridges	Hypopterygiaceae	Paragua de sapo		n	1	0,29
Rygodium implexum Schwaegr.	Brachytheciaceae	Lana del pobre		n	2	0,59
EQUISETATAE						
Equisetum bogotense H.B.K.	Equisetaceae	Limpiaplata	Cr	n	1	0,29
POLYPODIATAE						
Adiantum chilense Kaulf.	Adiantaceae	Patita negra	H	n	3	0,89
Asplenium dareoides A. N. Desv.	Aspleniaceae	Apio del monte	F	n	2	0,59
Asplenium trilobum Cav.		Calahuala	F	n	2	0,59
Blechnum blechnoides (Bory) Keyserl.	Blechnaceae	Helecho	H	n	2	0,59
Blechnum chilense (Kaulf.) Mett.		Quil-Quil	H	n	4	2,81
Blechnum hastatum Kaulf.		Palmilla	H	n	5	1,49
Ctenitis spectabilis (Kaulf.) Kunkel	Aspidiaceae	Unknown	H	n	2	0,59
Hymenoglossum cruentum (Cav.) K. Presl	Hymenophyllaceae	Helecho película	F	n	1	0,29
Hymenophyllum caudiculatum Mart.			F	n	1	0,29
Hymenophyllum dentatum Cav.			F	n		col
Hymenophyllum krauseanum Phil.			F	n	1	0,29
Hymenophyllum pectinatum Cav.			F	n		col
Hymenophyllum plicatum Kaulf.			F	n	2	0,59
Hypolepis rugosula (Labill.) J. E. Sm.	Dennstaedtiaceae	Unknown	H	n	2	0,59
Polypodium feuillei Bert.	Polypodiaceae	Hierba del lagarto	F	n	3	0,89
Polystichum chilense (Christ) Diels	Aspidiaceae	Helecho palmita	H	n	1	0,29
PINATAE						
Podocarpus salignus D. Don	Podocarpaceae	Mañio hoja larga	F	n	1	0,90
MAGNOLIATAE						
Acaena ovalifolia R. et P.	Rosaceae	Cadillo	H	n	3	0,89
Aextoxicon punctatum R. et P.	Aextoxicaceae	Olivillo	F	n	5	7,92
Anagallis arvensis L.	Primulaceae	Pimpinela escarlata	T	f	1	0,29
Anmannia coccinea Roth	Lythraceae	Unknown	T	f	1	0,29
Aristotelia chilensis (Mol.) Stuntz	Elaeocarpaceae	Maqui	F	n	6	6,96
Aster bellidiastrum Nees ex Walp.	Asteraceae	Unknown	H	n	1	0,50
Azara integrifolia R. et P.	Flacourtiaceae	Aromo	F	n	2	0,66
Azara lanceolata Hook. f.		Corcolén	F	n	3	0,89
Azara microphylla Hook. f.		Chin-chín	F	n	1	0,29
Baccharis concava (R. et P.) Pers.	Asteraceae	Chilca	F	n	3	1,74
Baccharis confertifolia Bert. ex Colla			F	n		col
Baccharis linearis (R. et P.) Pers.			F	n	3	0,89
Baccharis racemosa (R. et P.) DC.			F	n	5	1,88
Baccharis rosmarinifolia Hook. et Arn.		Romerillo	F	n		col
Boquila trifoliolata (DC.) Dcne.	Lardizabalaceae	Pil-pil voqui	F	n	5	1,49
Buddleja globosa Hope	Buddlejaceae	Palguín, matico	F	n	1	0,29
Calcluvia paniculata (Cav.) D. Don	Cunoniaceae	Tiaca	F	n	1	0,29
Callitriche stagnalis Scop.	Callitrichaceae	Estrella de agua	H	f	1	0,81
Carduus pycnocephalus L.	Asteraceae	Cardo	T	f	1	0,29
Centaurea calcitrapa L.		Unknown	T	f	1	0,29
Centella triflora (R. et P.) Nannf.	Apiaceae	Centella	H	n	1	0,29
Cerastium arvense L.	Caryophyllaceae	Cerastio	C	f	3	0,89
Chevreulia sarmentosa (Pers.) Blake	Asteraceae	Unknown	H	n	1	0,94
Chrysosplenium valdivicum Hook.	Saxifragaceae		H	n	1	0,29
Cichorium intybus L.	Asteraceae	Achicoria	H	f	1	0,29
Cirsium vulgare (Savi) Ten.		Cardo negro	T	f	4	1,19
Cissus striata R. et P.	Vitaceae	Voqui-naranjillo	F	n	5	1,64
Citronella mucronata (R. et P.) D. Don	Icacinaceae	Huilli-patagua	F	n	3	0,98
Conium maculatum L.	Apiaceae	Cicuta	T	f	2	1,88

APPENDIX I. Continued.

Scientific Name	Family	Local Name	Lf	O	F	I.V.
Coniza bonariensis (L.) Cronq.	Asteraceae	Coniza	T	f	4	1,19
Crepis capillaris (L.) Wallr.		Crepis	T	f	2	0,59
Cryptocarya alba (Mol.) Looser	Lauraceae	Peumo	F	n	1	0,29
Cynanchum pachyphyllum (Dcne.) Schum.	Asclepiadaceae	Voqui	F	n	2	0,59
Dasyphyllum diacanthoides (Less.) Cabr.	Asteraceae	Palo santo	F	n	2	0,59
Daucus carota L.	Apiaceae	Zanahoria silvestre	T	f	4	1,32
Dichondra sericea Sw.	Convolvulaceae	Oreja de ratón	H	n	1	0,29
Digitalis purpurea L.	Scrophulariaceae	Cartucho	T	f	1	0,29
Discaria serratifolia (Vent.) B. et H.	Rhamnaceae	Chacay	F	n	1	0,29
Disopsis glechomoides (A. Rich.) Muell.-Arg.	Euphorbiaceae	Unknown	H	n	1	0,60
Echium vulgare L.	Boraginaceae	Viborera	T	f	1	0,29
Ecremocarpus scaber R. et P.	Bignoniaceae	Chuplin	F	n	1	0,29
Elytropus chilensis (A. DC.) Muell.-Arg.	Apocynaceae	Quilmay	F	n	2	0,59
Embothrium coccineum J. R. et G. Forster	Proteaceae	Notro	F	n	1	0,29
Epilobium puberulum Hook. et Arn.	Onagraceae	Epilobio	H	n	1	0,29
Ercilla volubilis A. H. L. Juss.	Phytolaccaceae	Voqui-auca	F	n	1	0,29
Eryngium paniculatum Cav. et Domb.	Apiaceae	Cardoncillo	H	n	1	0,29
Escallonia alpina Poepp. ex DC.	Escalloniaceae	Siete camisas	F	n	3	1,19
Eucryphia cordifolia Cav.	Eucryphiaceae	Ulmo	F	n	6	2,46
Flourensia thurifera (Mol.) DC.	Asteraceae	Incienso	F	n		col
Fragaria chiloensis (L.) Duch.	Rosaceae	Frutilla	H	n	1	0,29
Francoa appendiculata Cav.	Saxifragaceae	Llaupangue	H	n	1	0,29
Fuchsia magellanica Lam.	Onagraceae	Chilco	F	n	3	1,33
Gamochaeta americana (Mill.) Wedd.	Asteraceae	Vira-vira	H	n	2	0,59
Gamochaeta spicata (Lam.) Cabr.		Unknown	H	n	1	0,40
Geranium robertianum L.	Geraniaceae	Core-core	T	f	4	1,19
Gevuina avellana Mol.	Proteaceae	Avellano	F	n	3	0,89
Hydrangea serratifolia (H. et A.) F. Phil.	Hydrangeaceae	Pehuelden	F	n	4	1,21
Hydrocotyle poeppigii DC.	Hydrocotylaceae	Tembladerilla	H	n	3	0,89
Hypericum brevistylum Choisy	Hypericaceae	Ñanco	H	n	1	0,19
Hypericum perforatum L.		Hierba de San Juan	H	f	5	1,63
Hypochaeris radicata L.	Cichoriaceae	Hierba del chancho	H	f	4	1,19
Lardizabala biternata R. et P.	Lardizabalaceae	Voqui-cógüil	F	n	2	0,59
Lathyrus hookeri D. Don	Fabaceae	Clarincillo	T	n	1	0,29
Laurelia philippiana Looser	Monimiaceae	Tepa	F	n	2	1,23
Laurelia sempervirens (R. et P.) Tul.		Laurel	F	n	4	1,32
Leontodon taraxacoides (Vill.) Mérat	Cichoriaceae	Chinilla	H	f	2	1,95
Leptocarpha rivularis DC.		Palito negro	F	n	3	0,89
Leucanthemum vulgare Lam.		Margarita	H	f	3	1,62
Linum usitatissimum L.	Linaceae	Lino	T	f	4	1,19
Loasa acanthifolia Desr.	Loasaceae	Ortiga caballuna	H	n	3	0,89
Lobelia tupa L.	Lobeliaceae	Tabaco del diablo	H	n	1	0,29
Lomatia dentata (R. et P.) R. Br.	Proteaceae	Piñol	F	n	4	1,19
Lomatia ferruginea (Cav.) R. Br.		Huinque	F	n	1	0,29
Lotus corniculatus L.	Fabaceae	Lotera	H	f	1	0,29
Lotus uliginosus Schkuhr		Alfalfa chilota	H	f	2	1,2
Luma apiculata (DC.) Burret	Myrtaceae	Arrayán	F	n	5	1,49
Margyrycarpus pinnatus (Lam.) O.K.	Rosaceae	Perlilla	C	n	1	0,29
Matricaria perforata Mérat	Asteraceae	Manzanilla	H	f	1	0,29
Maytenus boaria Mol.	Celastraceae	Maitén	F	n	1	0,56
Mentha pulegium L.	Lamiaceae	Poleo	C	f	3	0,89
Mentha rotundifolia (L.) Hudson		Menta alemana	H	f	1	0,29
Mimulus bridgessii (Benth.) Clos	Scrophulariaceae	Berro	H	n	1	0,29
Misodendrum brachystachyum DC.	Misodendraceae	Injerto	F	n		col
Mitraria coccinea Cav.	Gesneriaceae	Botellita	F	n	3	1,16
Muehlenbeckia hastulata (J. E. Sm.) Johnst.	Polygonaceae	Voqui-quilo	F	n	4	1,34
Mutisia retusa Remy	Asteraceae	Clavel del campo	F	n	1	0,29

APPENDIX I. Continued.

Scientific Name	Family	Local Name	Lf	O	F	I.V.
Myoschilos oblonga R. et P.	Santalaceae	Orocoipo	F	n	2	0,59
Myrceugenia exsucca (DC.) Berg	Myrtaceae	Pitra	F	n		col
Myrceugenia planipes (H. et A.) Berg		Picha	F	n	2	1,06
Nertera granadensis (Mutis ex L. f.) Druce	Rubiaceae	Rucachucao	H	n	1	0,29
Nothanthera heterophylla (R. et P.) D. Don	Loranthaceae	Quintral del boldo	F	n	1	0,29
Nothofagus dombeyi (Mirb.) Oerst.	Fagaceae	Coigüe	F	n	1	0,36
Nothofagus obliqua (Mirb.) Oerst.		Roble	F	n	4	6,66
Osmorhiza chilensis H. et A.	Apiaceae	Asta de cabra	H	n	2	0,59
Oxalis araucana Reiche	Oxalidaceae	Vinagrillo	T	n	4	1,19
Persea lingue (R. et P.) Nees	Lauraceae	Lingue	F	n	4	2,25
Peumus boldus Mol.	Monimiaceae	Boldo	F	n	3	1,91
Plantago hirtella H.B.K.	Plantaginaceae	Llantencillo	H	f	1	0,29
Plantago lanceolata L.		Siete venas	H	f	6	1,95
Prunella vulgaris L.	Lamiaceae	Hierba mora	C	f	8	2,39
Pseudopanax valdiviensis (Gay) Seem. ex Reiche	Araliaceae	Curaco	F	n	3	0,91
Ranunculus minutiflorus Bert. ex Phil.	Ranunculaceae	Botón de oro	H	n	4	1,19
Relbunium hypocarpium (L.) Hemsl.	Rubiaceae	Relbún	C	n	4	1,19
Rhammus diffusus Clos	Rhamnaceae	Murta negra	F	n	2	0,59
Rhaphanus sativus L.	Brassicaceae	Rabanito silvestre	T	f	1	0,29
Rhaphithamnus spinosus (A. L. Juss.) Mold.	Verbenaceae	Huayún	F	n	4	1,22
Ribes trilobum Meyen	Grossulariaceae	Zarzaparrilla	F	n	3	0,89
Rubus constrictus Muell. et Lef.	Rosaceae	Zarzamora	F	f	8	9,33
Rumex acetosella L.	Polygonaceae	Romacilla	H	f	5	1,49
Rumex sanguineus L.		Romaza	H	f	2	0,59
Sanguisorba minor Scop.	Rosaceae	Pinpinela	H	f	1	0,29
Sanicula crassicaulis Poepp. ex DC.	Apiaceae	Pata de guanaco	H	n	1	0,59
Sarmienta repens R. et P.	Gesneriaceae	Medallita	F	n	2	0,59
Satureja multiflora (R. et P.) Briq.	Lamiaceae	Menta de árbol	F	n	1	0,29
Senecio chilensis Less.	Asteraceae	Palo de yegua	F	n	3	0,89
Senecio otites Kunze ex DC.		Tutuco	H	n	3	1,08
Senecio yegua (Colla) Cabr.		Palpalén	F	n	4	2,00
Sherardia arvensis L.	Rubiaceae	Unknown	T	f	1	0,29
Solanum gayanum (Remy) Reiche	Solanaceae	Natri	F	n	3	0,89
Solanum nigrum L.		Tomatillo	T	f	3	0,89
Solanum valdiviense Dunal		Yaguecillo	F	n	3	0,89
Soliva sessilis R. et P.	Asteraceae	Dicha	H	n		col
Stachys grandidentata Lindl.	Lamiaceae	Unknown	C	n	1	0,29
Stellaria cuspidata Willd.	Caryophyllaceae	Quilloi-quilloi	C	n	2	0,59
Taraxacum officinale Weber	Cichoriaceae	Diente de león	H	f	1	0,29
Trifolium dubium Sibth.	Fabaceae	Trébol enano	T	f	3	0,99
Trifolium polymorphum Poir.		Trébol	H	f	1	0,29
Trifolium repens L.		Trébol blanco	H	f	4	2,17
Tristerix tetrandrus (R. et P.) Mart.	Loranthaceae	Quintral del álamo	F	n	2	0,59
Tropaeolum ciliatum R. et P.	Tropaeolaceae	Espuela de galán	Cr	n	2	0,59
Ugni molinae Turcz.	Myrtaceae	Murtilla	F	n	2	1,44
Urtica urens L.	Urticaceae	Ortiga	H	f	3	0,89
Valeriana floribunda Phil.	Valerianaceae	Valeriana	H	n	3	0,89
Verbascum thapsus L.	Scrophulariaceae	Hierba de paño	H	f	1	0,29
Veronica anagallis-aquatica L.		No me olvides del campo	H	f	1	0,29
Vestia foetida (R. et P.) Hoffmanns.	Solanaceae	Huevil	F	n		col
Vicia macraei H. et A.	Fabaceae	Arvejilla	T	n		col
Vicia sativa L.			T	f	1	0,29
Vicia vicina Clos			T	n	2	0,59
Weinmannia trichosperma Cav.	Cunoniaceae	Tineo	F	n	2	1,28

APPENDIX I. Continued.

Scientific Name	Family	Local Name	Lf	O	F	I.V.
LILIATAE						
Agrostis castellana Boiss. et Reuter	Poaceae	Chépica	H	f	5	5,61
Aira caryophyllea L.		Aira	T	f	1	1,68
Alstroemeria pulchra Sims	Alstroemeriaceae	Amancay	Cr	n	2	0,59
Arachnitis uniflora Phil.	Corciaceae	Flor de la araña	Cr	n	1	0,29
Arrhenatherum elatius (L.) P. Beauv.	Poaceae	Pasto cebolla	H	f	3	0,89
Bomarea salsilla (L.) Herb.	Amaryllidaceae	Copihuito	Cr	n	1	0,29
Briza minor L.	Poaceae	Tembleque	T	f	1	0,29
Bromus unioloides H.B.K.		Pasto lanco	H	n	1	0,59
Carex acutata Boott	Cyperaceae	Cortadera	H	n	1	0,29
Carex fuscula D'Urv.			H	n	1	0,29
Chloraea cylindrostachya Poepp.	Orchidaceae	Pico de loro	Cr	n	1	0,29
Chusquea culeou Desv.	Poaceae	Colihue	F	n	2	5,03
Chusquea quila Kunth		Quila	F	n	4	11,69
Codonorchis lessonii (D'Urv.) Lindl.	Orchidaceae	Azucena del campo	Cr	n		col
Cynosurus echinatus L.	Poaceae	Cola de ratón	T	f	4	1,90
Dactylis glomerata L.		Pasto ovillo	H	f	3	1,02
Dioscorea andina Phill.	Dioscoreaceae	Papa del monte	Cr	n		col
Dioscorea brachybothrya Poepp.		Papa cimarrona	F	n	2	0,59
Eragrostis lugens Nees	Poaceae	Unknown	H	f	1	0,29
Fascicularia bicolor (R. et P.) Mez	Bromeliaceae	Chupalla	F	n	1	0,29
Gavilea odoratissima Poepp.	Orchidaceae	Orquidea	Cr	n		col
Holcus lanatus L.	Poaceae	Pasto dulce	H	f	7	2,37
Juncus capillaceus Lam.	Juncaceae	Unknown	H	n	1	0,29
Juncus dombeyanus J. Gay. ex Lah.		Junquillo	H	n	1	0,29
Juncus microcephalus H.B.K.			H	n	1	0,29
Juncus procerus E. Mey.			H	n	1	2,93
Lapageria rosea R. et P.	Philesiaceae	Copihue	F	n	5	1,79
Libertia chilensis (Mol.) Gunckel	Iridaceae	Calle-Calle	H	n		col
Libertia coerulescens Kunth et Bouché		Calle-Calle azul	H	n	1	0,29
Libertia ixioides Gay			H	n	3	0,89
Lolium multiflorum Lam.	Poaceae	Ballica italiana	H	f	1	0,29
Lolium perenne L.		Ballica inglesa	H	f	1	0,29
Luzuriaga radicans R. et P.	Philesiaceae	Coralito	C	n	2	0,59
Nasella excerta Phil.	Poaceae	Pasto quila	H	n	1	0,29
Paspalum distichum L.		Unknown	H	f	2	0,94
Polypogon chilense (Kunth) Pilger		Cola de zorro	H	n	1	0,43
Sagittaria montevidensis Cham. et Schlecht.	Alismataceae	Rosa de agua	H	n	1	0,29
Scirpus cernuus Vahl	Cyperaceae	Can-cán	H	n	1	0,43
Stipa poeppigiana Trin. et Rupr.	Poaceae	Quilmén	H	n	1	0,29
Uncinia erinacea (Cav.) Pers.	Cyperaceae	Unknown	H	n	3	0,89
Uncinia phleoides (Cav.) Pers.		Clin-clin	H	n	4	1,19
Vulpia bromoides (L.) S. F. Gray	Poaceae	Cepilla	T	f	3	1,77

NOVELTIES IN THE ORCHID FLORA OF SOUTHERN VENEZUELA[1]

Gustavo A. Romero[2,3]
and Germán Carnevali[2,4]

ABSTRACT

Six new orchids from the Venezuelan Guayana are described and illustrated, including three species, *Coryanthes cataniapoënsis*, *Catasetum gomezii*, and *Catasetum parguazense*, one natural hybrid, *Catasetum* ×*dunstervillei*, and two new natural hybrids previously described as species, *Catasetum* ×*roseo-album* (Hook.) Lindley and *Catasetum* ×*wendlingeri* Foldats. These three hybrids involve four sympatric *Catasetum* species with overlapping flowering seasons that share *Eulaema cingulata* (Fabricius) as their main pollinator.

This paper and others in preparation precede the publication of a comprehensive treatment of the Orchidaceae of southern Venezuela for J. A. Steyermark's *Flora of the Venezuelan Guayana* (Carnevali et al., in prep.). The taxa described here belong to two of the most complex genera in the Orchidaceae, *Coryanthes* Hook. and *Catasetum* Rich. Species in these two genera are extremely variable, and in the Venezuelan Guayana many closely related species are sympatric or syntopic, share pollinators, and have overlapping flowering seasons; natural hybrids are common.

Half of the taxa proposed here are natural hybrids. The parentage of these nothospecies was inferred from pollination data, phenological data, and morphological characters. This approach has its limitations, but one can postulate safely parent species if a large number of specimens of the suspected hybrid are examined, because, as Hurst (1902) indicated, "In orchid hybrids of the first generation single specific characters are inherited in all degrees of blending, forming, on the whole, a perfect series between the respective characters of the two parents." In *Catasetum* ×*wendlingeri* Foldats, the parentage was confirmed by artificial hybridization experiments (A. Pardo, pers. comm., 1988).

Coryanthes cataniapoënsis G. Romero et Carnevali, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Departamento Atures, Río Gavilán, alrededores de Cucurital, 9 May 1987, *G. A. Romero 1307* (holotype, VEN; isotype, K). Figure 1A–C.

Planta *C. macranthae* (Hook.) Hook. affinis sed hypochilo antice producto campanulato et mesochilo subaequilongo differt.

Plant epiphytic in ant gardens. Rhizomes short; pseudobulbs ovoid to narrowly ovoid, grooved, bifoliate at the apex, to 11 cm long, surrounded at the base by scarious sheaths. Leaves oblong-elliptic, acuminate, to 34 cm long, including the short, sulcate petiole; lamina to 9 cm wide and 31 cm long, plicate, with 3 conspicuous nerves beneath. Inflorescence from the base of the pseudobulbs, pendulous, elongate, 1- or 2-flowered at the apex; peduncle slender, to 18 cm long, with short remote tubular-infundibuliform sheaths. Ovary pedicellate, elongate, slender, ca. 15 cm long, almost 4 times as long as the concave, scarious subtending bract. Flowers white, densely spotted and blotched with dark red-maroon. Sepals and petals membranaceous; dorsal sepal ovate, obtuse, ca. 4.3 cm long and 5 cm wide; lateral sepals obliquely oblong-ovate, retrorse, ca. 9 cm long and 6 cm wide, margins involute; petals narrowly oblong-lanceolate, falcate, obtuse, ca. 5 cm long and 1.3 cm wide near the base, margins shallowly undulate.

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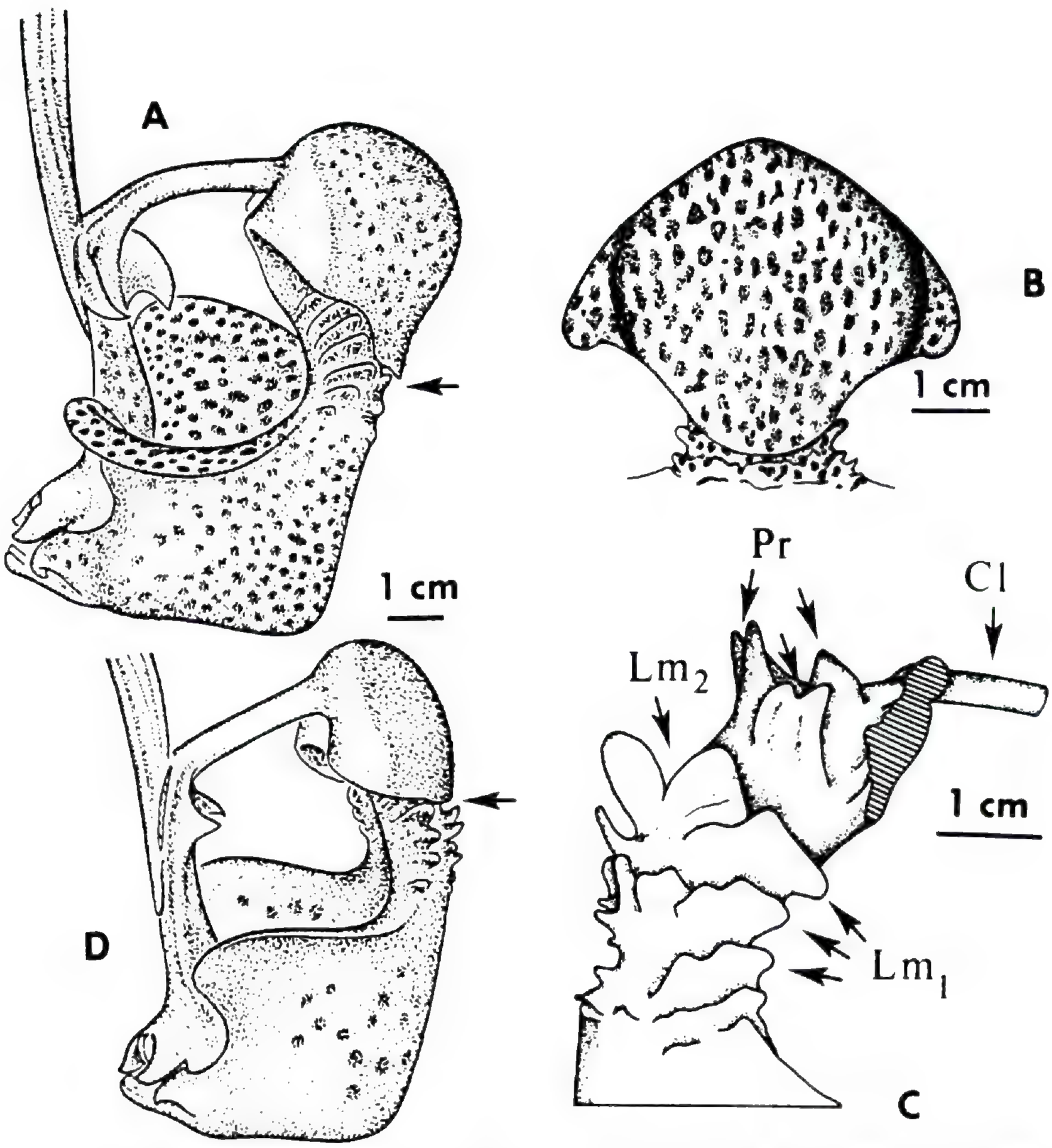

FIGURE 1.—A–C. *Coryanthes cataniapoënsis*. A. Side view of labellum. B. Front view of hypochile. C. Side view of mesochile, after removing hypochile, showing the labellum claw (Cl), the transverse ridges (Lm_1 and Lm_2), and the projections (Pr) near the base (Lm_2 and Pr not visible unless the hypochile is removed).—D. *Coryanthes macrantha* (Hook.) Hook. shown for comparison. A, B from *G. A. Romero 1307*; C from *C. Gomez s.n.*; D from *G. Bergold s.n.* (VEN).

Lip fleshy, divided into 3 parts, the clawed, semispherical hypochile 4.5–5 cm wide; the semitubular mesochile ca. 4–4.5 cm long, with 5–6 transverse ridges, bilobed to multilobed, decreasing in size from the base, with 3 toothlike projections near the base (these seen only after removing the hypochile), 8–13 mm high; the deeply saccate epichile bucketlike, with a 3-lobed apex, the lateral lobes uncinate at the apex, the middle lobe lingulate, shallowly obcordate. Column gradually dilated toward the apex, recurved near the apex, bialate, ca. 2.5 cm long, with a pair of shallowly falcate, fluid-producing glands at the base. Pollinia 2, waxy, yellow.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Departamento Atures, Río Gavilán, alrededores de Cucurital, June 1985, *G. A. Romero 1273* (AMES); Río Cataniapo, entre la boca del Río Gavilán y los Raudales de Rabipelado, Jan. 1985, *C. Gomez s.n.* (TFAV).

Etymology. Named for the Río Cataniapo, where the species was first found.

This species differs from *Coryanthes macrantha* (Hook.) Hook. in the globose hypochile with the anterior margin that almost reaches the epichile, and in the toothlike projections near the base of the mesochile. It flowers from January to June and is pollinated around Puerto Ayacucho, T. F. Amazonas, Venezuela, by *Eulaema cingulata* (Fabricius) and, less frequently, by *E. meriana* (Olivier) (G. A. Romero, unpubl. data).

Catasetum gomezii G. Romero et Carnevali, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Departamento Atures, Río Cataniapo, cerca de la desembocadura del Río Gavilán, 30 June 1987, *G. A. Romero & C. Gomez 1333* (holotype, VEN; isotypes, K, TFAV). Figure 2A–B.

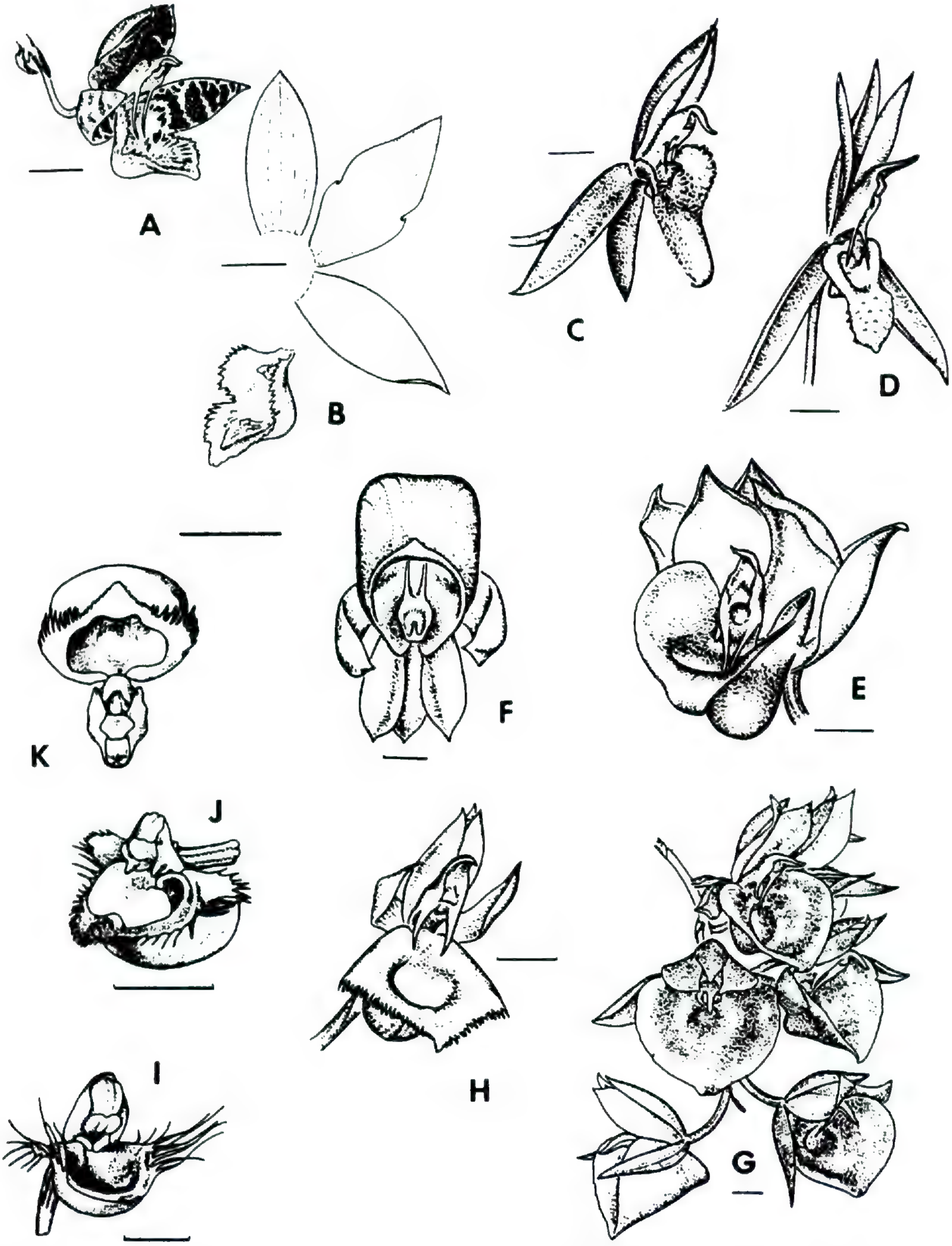

FIGURE 2.—A, B. *Catasetum gomezii*. A. Staminate flower. B. Detail of staminate flower.—C. *Catasetum paraguazense*.—D. *Catasetum callosum*.—E. *Catasetum* ×*wendlingeri*.—F. *Catasetum planiceps*.—G. *Catasetum pileatum*.—H. *Catasetum* ×*dunstervillei*.—I. *Catasetum* ×*roseo-album*.—J. *Catasetum longifolium*.—K. *Catasetum discolor*. Scale bars = 1 cm. A, B from *G. A. Romero & C. Gomez 1333*; C from *E. Rutkis 185*; D redrawn from Foldats, 1970: 59; E from *G. A. Romero & L. Rojas 1201*; H from *G. A. Romero & A. Cortez 914*; I, K redrawn from the plates accompanying the original descriptions (Hooker, 1840, and Lindley, 1834, respectively); and J from Saunders, 1882.

Planta inter *C. barbatum* Lindley et *C. ochraceum* Lindley quasi intermedia, sed ab ambas labello saccatissimo marginibus dentatis differt.

Plant epiphytic, indistinguishable vegetatively from other members of the genus. Staminate inflorescence lightly arcuate to pendent, racemose, to 9-flowered, originating from the base of the fully developed pseudobulb, to 18 cm long. Staminate flowers resupinate. Tepals light green, densely spotted with maroon on their inner surface, less so on their outer surface; dorsal sepal slightly concave, oblanceolate, acute, margins entire, 11–12 mm

wide, 25–26 mm long; lateral sepals slightly concave, oblong-lanceolate, acute or shortly apiculate, slightly oblique, margins entire, 12–13 mm wide, 27–28 mm long; petals narrowly ovate, acute, margins entire or finely serrate with 1 indentation and a flush falcate tooth on each side at the widest point, 10–11 mm wide, 24–25 mm long. Labellum fleshy, rigid, yellowish green, spotted with maroon in the margins, deeply concave, deltate in general outline, with 2 lateral indentations midway between the base and the apex, thus slightly trilobulate, 12 mm deep, 22 mm long, 22 mm wide between the spread basal lobes, margins crenate to dentate in the middle lobe, dentate to fimbriate in the lateral lobes, the base with a transverse, tricuspid callus, the apex with a V-shaped, verrucose callus. Column yellowish green, with maroon dots in the inner surface near the base, densely spotted with maroon on the outer surface, semiterete, stout, straight, apically thickened, conspicuously rostrate, the clinandrium apiculate and slightly incurved at the apex; antennae bilaterally symmetrical, slightly convergent, 8 mm long. Anther white, the margins spotted with maroon. Pollinia 2, cleft, waxy, compressed, more than twice as long as wide, attached to a light yellowish green stipe with a white, adhesive viscidium. Pistillate inflorescence unknown.

Etymology. Named in honor of Carlos Gomez, the discoverer of this species.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Departamento Atures, Río Cataniapo, entre el Milagro y San Pablo, 1 Sept. 1987, *G. A. Romero, C. Gomez & P. L. Beer-Romero 1365* (AMES, TFAV).

This showy species resembles *Catasetum ochraceum* Lindley (Lindley, 1844) but differs in the epiphytic habit, pendulous inflorescence and labellum with dentate to fimbriate margins. It is also similar to *C. cornutum* Lindley (Lindley, 1840) and the recently described *C. semicirculatum* Miranda (Miranda, 1986), but the new species is distinguished by the deeply concave labellum with a frontal, V-shaped callus. It flowers from May to September.

Catasetum parguazense G. Romero et Carnevali sp. nov. TYPE: Venezuela. Bolívar: Distrito Cedeño, Río Parguaza, 12 May 1967, *E. Rutkis 1985* (holotype, VEN). Figure 2C.

Planta *Cataseto calloso* Lindley et eius affinitatis proxima, sed labello basi subcordato et callo basali truncato differt.

Plant epiphytic, indistinguishable vegetatively from other members of the genus. Staminate inflorescence lightly arcuate to pendulous, racemose, to 8-flowered, originating from the developing leaf growth, to 15 cm long. Staminate flowers resupinate. Tepals tinged green with maroon, or maroon entirely; dorsal sepal narrowly elliptic or narrowly obovate, acute or acuminate, somewhat concave, margins entire or slightly ciliolate, 29–31 mm long, 7–10 mm wide; lateral sepals similar to dorsal sepal but slightly oblique, 9–10 mm wide; petals narrowly elliptic to narrowly obovate-elliptic, acute or shortly acuminate, margins entire or finely denticulate to ciliolate, 26–31 mm long, 7–9 mm wide. Labellum green with maroon dots or maroon entirely. Labellum fleshy, in general outline narrowly ovate, obtuse, rounded to truncate, basal margins extended, making the labellum subtrilobate, 2–2.6 cm long, 1.8–2 cm wide between the spread basal lobes, margins ciliate and glandular papillose or coarsely verrucose, the ventral face glandular verrucose, especially toward the margins, leaving an almost longitudinally smooth central zone, basally with a transverse, truncate low callus having a verrucose surface; the labellum excavate in front of the callus, forming a shallow, conical rounded sack; the apex of the labellum callus thickened. Column green or maroon or maculated with green and maroon, straight, apically thickened, conspicuously rostrate, 16–22 mm long; clinandrium apiculate and slightly incurved apically; antennae bilaterally symmetrical, subparallel or somewhat divergent, smooth or finely glandular verrucose, 6–8 mm long. Anther yellowish green, maroon at the base and apex. Pollinia 2, cleft, waxy, yellow, compressed, more than twice as long as wide, attached to a light yellow-green stipe with a white, adhesive viscidium.

Paratypes. VENEZUELA. BOLÍVAR: Distrito Roscio, 60 km al oeste de Santa Elena de Uairén, por la vía de Icabarú, *G. Carnevali 2614* (VEN); Distrito Piar, on tributary to Río Carrao, ca. 10 mi. above Canaima and Río Churún, *G. C. K. Dunsterville 259* (line drawing, AMES).

Etymology. Named after the Río Parguaza, where the type of the species was collected.

This species has been collected several times in the Venezuelan Guayana and in Brazil (see color photograph in Miranda, 1987). In the past it had been assigned incorrectly to *C. bicallosum* Cogn. (Dunsterville & Garay, 1979: 78; Foldats, 1970: 58; Miranda, 1987), a species from the upper Río Orinoco closely related to *C. barbatum* Lindley. The type specimen of *C. bicallosum* Cogn. in the Cogniaux Herbarium (BR, photo) and the original description clearly show this affinity. *Catasetum*

parguazense belongs in the *C. callosum* Lindley alliance (Pabst & Dungs, 1975: 172). It differs from *C. callosum* by having a subcordate labellum and truncated basal callus, and it differs from *C. poriferum* Lindley (see color photo in Fergusson, 1967) by having long, fully developed antennae and a labellum with erect-patent lateral lobes. It is further distinguished by flowering almost invariably from the developing leaf shoot.

Catasetum ×dunstervillei G. Romero et Carnevali, hybr. nat. nov. inter *Catasetum pileatum* Reichb. f. et *C. discolor* Lindley. TYPE: Venezuela. Territorio Federal Amazonas: Departamento Atures, Los Oripopos, 7 km al norte de Puerto Ayacucho, 23 Nov. 1982, *G. A. Romero & A. Cortez 914* (holotype, VEN; isotype, TFAV). Figure 2H.

Planta inter parentes ad *C. discolorem* Lindley vergens, sed inflorescencia arcuata vel pendula, floribus resupinatis majoribus, labello leviter saccato, callo V-formi praedito, antennis longioribus, columnae clinandrio apiculo brevi recedit.

Plant epiphytic, indistinguishable vegetatively from other members of the genus. Staminate inflorescence lightly arcuate to pendent, racemose, to 7-flowered, originating from the base of the fully grown pseudobulb, to 16 cm long. Staminate flowers resupinate. Tepals white, maroon, light green or greenish yellow with maroon dots. Dorsal sepal concave, lanceolate, acuminate, erect, 23–25 mm long, 9–10 mm wide; lateral sepals concave, obovate, slightly oblique, apiculate, recurved, 22–25 mm long, 9–10 mm wide. Petals convex, obovate, slightly oblique, apiculate, 25–27 mm long, 11–13 mm wide. Labellum pearl white, green, light green or waxy yellow, saccate, the sack 15–18 mm deep, simple or with 2 shallow indentations alongside the apex, thus slightly trilobulate, and with a V-shaped callus near the inner apical margin; margins patent or reflexed, finely denticulate to fimbriate. Column light greenish white or yellow, semiterete, straight, apically thickened, shortly rostrate; clinandrium shortly apiculate, incurved apically; antennae bilaterally symmetrical, parallel to slightly convergent, 6–8 mm long. Anther greenish white. Pollinia 2, cleft, waxy, yellow, compressed, shorter than twice as long as wide, attached to a light yellowish white stipe with a white, adhesive viscidium.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: upper Orinoco, (P. Anduze) *G. C. K. Dunsterville 748* (line drawing, AMES); Departamento Atures, Río Pavoni, cerca de su confluencia con el Orinoco, 3 Nov. 1983, *G. A. Romero & J. Moreno 1153* (VEN, TFAV); same locality, 10 Aug. 1987, *G. A. Romero, P. L. Beer-Romero & J. Moreno 1336* (VEN, TFAV); Caño Rueda, 6 Dec. 1983, *G. A. Romero & L. Rojas 1158* (VEN).

Etymology. Named in honor of G. C. K. Dunsterville, who first illustrated this hybrid in his series coauthored by L. A. Garay, *Venezuelan Orchids Illustrated.*

This natural hybrid has been previously assigned to *Catasetum fimbriatum* (Morren) Lindley (Dunsterville & Garay, 1966: 42; 1979: 85; Foldats, 1970: 80). However, three lines of evidence reveal *C. ×dunstervillei* as distinct. First, northern South America lies outside the known geographical range of *Catasetum fimbriatum*: southeastern Brazil, southwestern Bolivia, Paraguay, and northern Argentina (Bicalho, 1965; Dodson, 1978). Second, typical *C. fimbriatum* from southern Brazil differs considerably from *Catasetum ×dunstervillei* in having a column with long antennae; a long, apiculate, acuminate clinandrium; an apiculate, fleshy anther; and a labellum with the fleshy mid-lobe projected forward (see Vasquez & Dodson, 1982). Third, based on fragrance and pollinator data, *Catasetum ×dunstervillei* cannot be assigned to *C. fimbriatum.* Hills et al. (1972) showed that *C. fimbriatum* is a poor fragrance producer with a fragrance spectrum unlike any other species in the genus. Moreover, the only known *C. fimbriatum* pollinator is *Eufriesea auriceps* (Friese) (Pijl & Dodson, 1966: 182). *Catasetum ×dunstervillei,* in contrast, produces a fragrance that attracts *Eulaema cingulata,* one of the pollinators of *Catasetum discolor* Lindley, *C. longifolium* Lindley, and in general the *C. maculatum* Kunth complex (Williams & Whitten, 1983). *Catasetum ×dunstervillei* was also compared with *C. fimbriatum* var. *cogniauxii* L. Linden, described from material presumably collected in Venezuela (Linden, 1895a). A plate in *Lindenia* (Linden, 1895b) and Cogniaux's sketches in the type sheet (BR, photo) reveal *Catasetum fimbriatum* differing from *C. ×dunstervillei* in the characters presented above.

Dressler (1976) pointed out that *Dunsterville 748,* assigned here to *Catasetum ×dunstervillei* (illustrated in Dunsterville & Garay, 1966: 42; 1979: 85), was a hybrid between *Catasetum pileatum* and *C. discolor,* but he never proposed a binomial. Dressler's hypothesis is supported by two lines of evidence. The flowers of *C. ×dunstervillei* are intermediate between *Catastum pileatum* and *C. discolor,* and these two species are by far more abundant than any other possible parent species

found in the general area where *C.* ×*dunstervillei* has been collected, as indicated by plant sampling and by the frequency of their pollinaria on euglossine bees (G. A. Romero, unpubl. data). Furthermore, *Catasetum pileatum* and *C. discolor* share euglossine bee pollinator and have overlapping flowering seasons.

Dodson suggested that *Dunsterville 748* was a hybrid between *Catasetum longifolium* Lindley and *C. macrocarpum* Rich. ex Kunth. (Dodson, 1978), based on plants collected in Dawa, Guyana (also pictured in Tan, 1971, fig. 8). However, the plant illustrated in Dodson (1978) differs from *C.* ×*dunstervillei* in the pendent habit, the long and narrow leaves, and the labellum morphology.

Catasetum ×*dunstervillei* is similar to *Catasetum* ×*issanensis* Pabst (a natural hybrid between *C. pileatum* and *C. longifolium*, Pabst, 1975) but is distinguished by the shorter and wider leaves and the labellum with a V-shaped callus.

Catasetum ×*dunstervillei* flowers from the mature pseudobulb from August to December. The pollen donor in *C.* ×*dunstervillei* is most likely *C. discolor*: the large pollinia of *C. pileatum* could not fit in the narrow stigmatic cleft of *C. discolor*.

Catasetum ×roseo-album (Hook.) Lindley (pro. sp.), hybr. nat. nov. inter *Catasetum discolor* Lindley et *C. longifolium* Lindley. *Monachanthus roseo-albus* Hook., Bot. Mag. 66: t. 3736. 1839. *Catasetum discolor* var. *roseo-album* (Hook.) Mansf., Repert. Spec. Nov. Regni Veg. 30: 264. 1932. TYPE: Brazil. Para: sent by Mr. Campbell to Mr. Murray at the Glasgow Botanical Garden, collector unknown (holotype, K, photo).

Selected specimens examined. VENEZUELA. BOLÍVAR: Distrito Cedeño, Agua Mena, epífita sobre *Mauritia flexuosa*, Dec. 1983 (male fl), *G. A. Romero & J. Moreno 1166* (TFAV). TERRITORIO FEDERAL AMAZONAS: Departamento Atabapo, Laja Cabezón, Río Cabezón, cerca de su confluencia con el Río Atabapo, 11 Sept. 1960 (male fl), *E. Foldats 3884* (VEN); Departamento Atures, Río Pavoni, epífita sobre árbol seco, 10 Nov. 1987 (male fl), *G. A. Romero & J. Moreno 1421* (TFAV); Río Autana, Caño Cabeza de Manteco, epífita sobre *Bactris* sp., 8 Oct. 1987 (male & female fl), *G. A. Romero & J. Moreno 1405* (TFAV); same locality and habitat, 12 Nov. 1987 (male fl), *G. A. Romero & J. Moreno 1423* (TFAV); Departamento Río Negro, Cerro Arauicaua, Río Yatua, 19 Apr. 1970 (male fl), *J. A. Steyermark & G. Bunting 102571* (VEN); same locality and date (female fl), *J. A. Steyermark & G. Bunting 102649* (VEN).

Etymology. The specific epithet probably refers to the rose and white flowers in the original description.

Natural hybrids between *Catasetum discolor* and *C. longifolium* were expected in the Venezuelan Guayana: the two species are separated by less than the flying range of euglossine bees (1–5 km), they share male euglossine bee pollinators, *Eulaema meriana* (Olivier), *E. bombiformes* (Packard), and *E. cingulata* (Fabricius), and they have overlapping flowering seasons. Around Puerto Ayacucho, Venezuela, the same species of *Eulaema* bees have been caught carrying the very distinct *C. discolor* and *C. longifolium* pollinaria in late February through May. The pollinaria of both species are placed on the ventrum of the bees' thorax, but *C. discolor* pollinaria have a dark brown stipe and a very small viscidium (narrower than the involute stipe), whereas *C. longifolium* pollinaria have a light brown stipe and a large viscidium (wider than the involute stipe). Plants bearing flowers intermediate between the two presumed parents had been collected in the Venezuelan Guayana, Guyana (Dodson, 1978), and Brazil (Mansfeld, 1932) and were assigned previously to *Catasetum discolor* var. *roseo-album* (Hook.) Mansf. Dodson (1978) suggested that this taxon may have resulted from a natural cross between *Catasetum discolor* and *C. longifolium*, but he never changed its nomenclatural status to that of nothotaxon.

Catasetum ×*roseo-album* is widespread in lowland "morichales" (gallery forest communities dominated by *Mauritia flexuosa* L.f.) in the northwestern Venezuelan Guayana, where it occupies typical *C. longifolium* habitat, growing near the crown on the stems of *Mauritia flexuosa*. It is also found on *Bactris* sp., and on dead trees in seasonally flooded forest.

The hybrid differs from *C. longifolium* by having generally erect (vs. pendulous) habit; leaves 6–20 cm long, 4–7 cm wide and generally 5-nerved (vs. 15–150 cm long, 1–3 cm wide, and 3-nerved), shortly apiculate, apically incurved (vs. obtuse and flat) clinandrium of the staminate flower, and the *C. discolor*-like pollinarium.

The hybrid differs from *C. discolor* in the epiphytic habit, generally arcuate to pendent staminate inflorescence (always erect in *C. discolor*), and deeply galeate, dorsally compressed labellum of the staminate flower (shallowly concave and globose in *C. discolor*). Pistillate flowers of the hybrid are often distinguished by the deeply galeate labellum (globose in *C. discolor*) but can vary between *C. discolor*-like to *C. longifolium*-like (deeply saccate), ranging in color from light green (yellow-green in old flowers) to deep maroon. The hybrid staminate flowers vary in color between pinkish white to green, purple, orange, or maroon.

Catasetum ×*roseo-album* flowers from the mature pseudobulb from June to January. Pollen flow between either parent is likely, as the pollinia of both species are of similar size.

Catasetum ×wendlingeri Foldats (pro sp.), hybr. nat. nov. inter *Catasetum pileatum* Reichb. f. et *C. planiceps* Lindley. TYPE: Venezuela. Territorio Federal Amazonas: Departamento Atabapo, alrededores de San Fernando de Atabapo, July 1957, *E. Foldats 2890* (holotype, VEN). Figure 2E.

Selected specimens examined. VENEZUELA. BOLÍVAR: Distrito Cedeño, Caripo, June 1980, (I. Sucre) *G. C. K. Dunsterville 1413* (line drawing, AMES); same locality, (I. Sucre) *G. Carnevali 2633* (VEN, TFAV). TERRITORIO FEDERAL AMAZONAS: Departamento Atures, Caño Rueda, 17 July 1984, *G. A. Romero & L. Rojas 1201* (VEN); carretera a Gavilán, ca. del Fundo Doña Juana, 23 June 1985, *G. A. Romero & J. Taine 1263* (TFAV); same locality, 17 May 1987, *G. A. Romero 1310* (TFAV).

Etymology. Named after K. Wendlinger, who cultivated the plant featured in the original description.

C. H. Dodson first proposed this natural hybrid between *Catasetum pileatum* and *C. planiceps* (quoted in Dunsterville & Uzcategui, 1981) based on the floral morphology of the *G. C. K. Dunsterville 1413* specimen cited above. Dodson, however, never proposed a binomial. Since then, plants resulting from the artificial cross between the presumed parents flowered in the collection of A. Pardo in Venezuela, and three more specimens of the presumed natural hybrid were collected around Puerto Ayacucho. Comparison of the staminate flower of the artificial hybrid with the holotype of *Catasetum wendlingeri* and *C. planiceps* (K, photo) showed it to be more similar to *C. wendlingeri*; in fact, some of the hybrids were identical to *C. wendlingeri*. *Catasetum wendlingeri* had been treated previously as a synonym of *C. planiceps* (Foldats, 1959; 1970: 97; Schweinfurth, 1967).

Catasetum ×*wendlingeri* differs from *C. planiceps* in the epiphytic habit and in the generally larger staminate flower with the labellum apex broadly patent or reflexed and the column with a long, apicular clinandrium. Further, the staminate flowers of the hybrid are sometimes resupinate (as in *G. C. K. Dunsterville 1413* and *G. A. Romero & L. Rojas 1201*), or the margins of the labellum are fimbriate (as in *G. C. K. Dunsterville 1413*, illustrated in Dunsterville & Uzcategui, 1981), whereas the staminate flowers of *C. planiceps* are never resupinate and the margins crenate or undulate-dentate. The hybrid differs from *C. pileatum* in the hooded labellum and the bilaterally symmetrical antennae of the staminate flowers.

Catasetum ×*wendlingeri* flowers from the developing leaf shoot from April to July. This hybrid, as is its proposed parent species, is pollinated by *Eulaema cingulata*. The pollen donor of the hybrid is most likely *Catasetum planiceps*; *C. pileatum* pollinia could not be inserted in the narrow stigmatic cleft of *C. planiceps*.

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NOVELTIES IN THE LAURACEAE FROM VENEZUELAN GUAYANA[1]

Henk van der Werff[2]

ABSTRACT

Eleven new species (*Licaria tomentosa*, *Ocotea flavantha*, *O. liesneri*, *O. glabra*, *O. huberi*, *O. megacarpa*, *O. roseopedunculata*, *O. tomentosa*, *Persea croatii*, *P. croizatii*, and *P. fluviatilis*) are described. *Ocotea julianii* is published as a new name for *Phoebe steyermarkiana*, *Phoebe areolatocostae* is transferred to *Persea*, and *Ocotea steyermarkiana* is transferred to *Rhodostemonodaphne*.

During the preparation of the treatment of the Lauraceae for the *Flora of the Venezuelan Guayana*, a number of collections were found that appeared to represent undescribed taxa. Most of these collections were gathered during recent expeditions and are of high quality. As can be expected, there are, after completion of the family treatment, still several sterile or fruiting collections that do not match any of the known species from Guayana and that represent additional or even undescribed species. These species could not be included in the treatment for lack of adequate collections.

In general, the Lauraceae in Venezuelan Guayana are still undercollected. Of the 128 species (*Nectandra* excluded; this genus will be contributed by Dr. J. Rohwer), 55 are known only from one or two collections, while an additional 13 are known from three or four collections. This large number of rarely collected species suggests that there are still several additional species to be collected and that our knowledge about Lauraceae in Venezuelan Guayana is far from complete.

The available data show that about one-third of the species (41 out of 128) are endemic to Guayana. Of these 41, 31 species occur on the slopes and summits of the tepuis, while 10 are lowland species. The number of endemic lowland species will likely diminish when adjoining Colombia and Brazil are better explored, because I expect that lowland species such as *Ocotea tomentosa*, *Persea fluviatilis*, and *Phoebe semecarpifolia*, which occur near the borders with Colombia and Brazil, are not restricted to the Venezuelan side of the borders.

The new species, combinations, and the new name are arranged in alphabetical sequence.

Licaria tomentosa van der Werff, sp. nov. TYPE: Venezuela. Bolívar: Chimantá Massif, along trail from Base Camp to Bluff Camp, western slopes of Chimantá-tepui, 1,100–1,700 m, *Steyermark 75607* (holotype, NY; isotypes, COL, F). Figure 1.

Arbor, ad 10 m. Ramuli teretes, ferrugineo-tomentosi, vetustiores glabrescentes. Folia chartacea, elliptica, 8–11 × 3–4.5 cm, opposita, basi acuta, apice acuminata; supra secus costam nervosque aliquantum tomentosa; subtus ferrugineo-tomentosa. Nervi utroque costae latere 3–5, versus marginem arcuati et conjuncti. Petioli 0.5–1 cm longi, tomentosi, supra plani. Inflorescentiae floresque ignoti. Fructus ellipsoideus, 1.2 × 0.6 cm. Cupula 1.2 cm alta, 1.4 cm lata, extus laevis, margine leviter duplicata, 3 staminibus bilocellatis et 3 staminodiis praedita. Stamina vetera triangularia, locellis extrorso-apicalibus versus apicem aperientibus.

Tree, 10 m tall. Twigs terete, ferruginous tomentose, becoming glabrous with age. Leaves firmly membranaceous, elliptic, 8–11 × 3–4.5 cm, opposite, the base acute, apex acuminate, upper surface with some tomentose pubescence along the midvein and lateral veins, otherwise glabrous, the lower surface ferruginous tomentose, the tomentum wearing off with age; lateral veins 3–5 pairs, immersed above, raised on lower surface, the lateral veins arching upwards and loop-connected. Petioles 0.5–1 cm long, tomentose, not canaliculate. Inflorescence and flowers unknown. Infructescence unknown. Fruit ellipsoid, 1.2 × 0.6 cm when dry. Cupule deeply cup-shaped, 1.2 cm high and 1.4 cm broad, the outside smooth, without lenticels; the margin weakly double-margined, with traces of tomentum and bearing on the inner margin 3 2-celled stamens and 3 staminodia. Old, dried

[1] I thank the curators of F, G, MERF, MY, MYF, NY, and VEN for making their specimens available. Dr. J. Dwyer kindly checked the Latin descriptions, and John Myers drew the fine illustrations.

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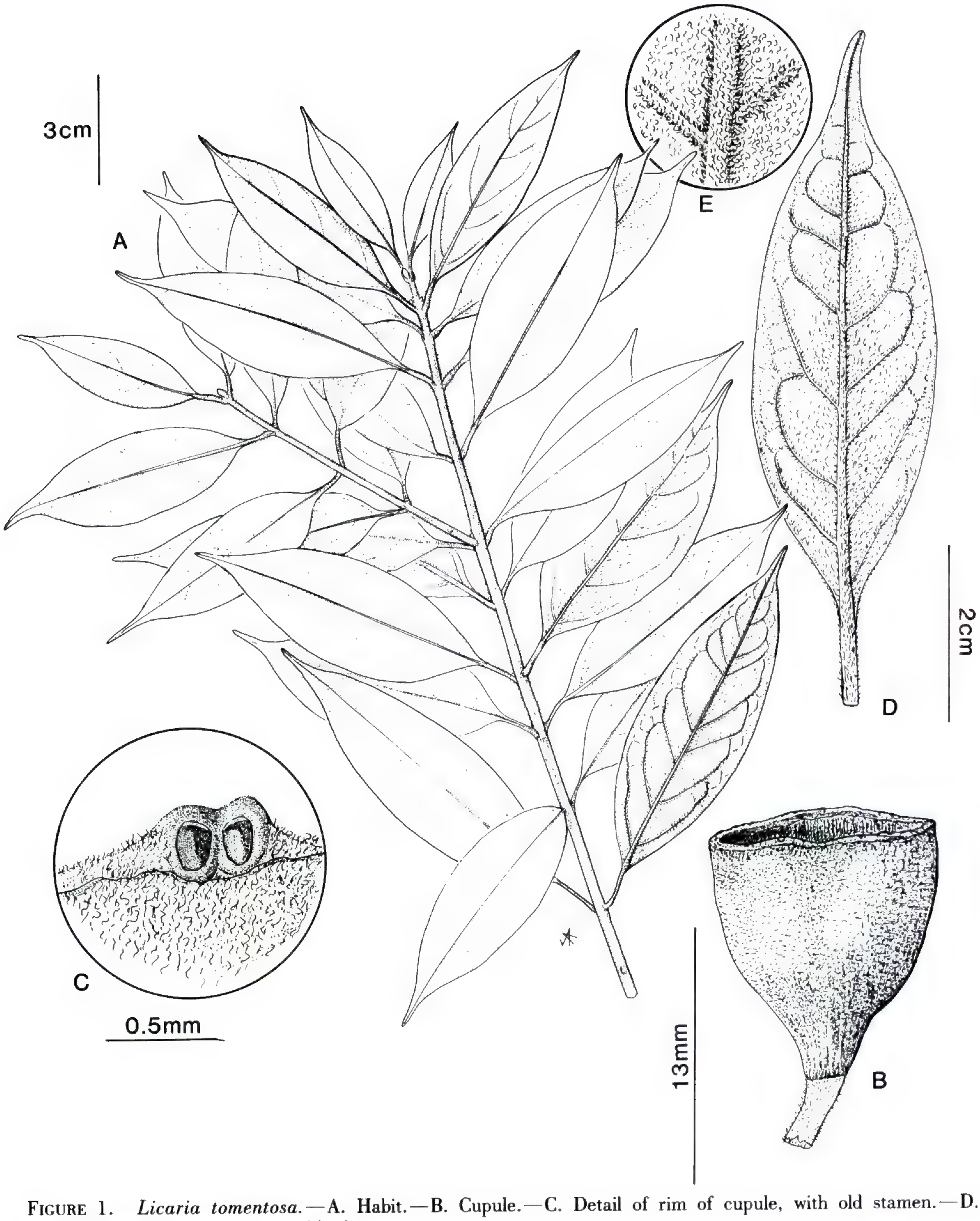

FIGURE 1. *Licaria tomentosa*.—A. Habit.—B. Cupule.—C. Detail of rim of cupule, with old stamen.—D. Leaf.—E. Detail of lower surface of leaf.

stamens triangular, the locelli extrorse-apical and opening towards the tips of the anthers. Staminodia similar in size and shape to stamens but without locelli.

Although the type collection of *Licaria tomentosa* is in fruit, the combination of characters found on the holotype leaves no doubt about the generic identity. Indicative for *Licaria* are the three 2-celled stamens, the double-rimmed margin of the cupule and the opposite leaves with few, loop-connected lateral veins which stay well away from the margin. The ferruginous-tomentose pubescence of this species readily separates it from the other *Licaria* species with opposite leaves, because these all have appressed pubescence (if any at all), usually with a lighter color.

I am not certain if *Licaria tomentosa* has only three staminodia; the staminodia present on the cupule represent whorl II and are only present when the tepals facing them have not fallen off. The tepals in front of the stamens (whorl III) are absent, and it is likely that staminodia representing whorl I would have fallen off as well.

At present, *Licaria tomentosa* is known only from the holotype in NY (with detached cupules) and sterile isotypes in COL and F. Allen (1964) identified and cited these specimens as *Ocotea roraimae* Mez, a species with alternate leaves, four-celled anthers, a canaliculate petiole, without tomentose pubescence, and lacking loop-connected lateral veins. I consider *O. roraimae* now part of *O. aciphylla* (Nees) Mez sensu lato.

Ocotea flaventha van der Werff, sp. nov. TYPE: Venezuela. T. F. Amazonas: Dept. Atures, valley of Río Coro-Coro, W of Serranía de Yutaje. Tree, 28 m, flowers dull golden-yellow, *Holst & Liesner 3443* (holotype, MO; isotypes, HBG, NY, VEN). Figure 2.

Arbor, ad 30 m alta. Ramuli hornotini angulati dense brunneo-tomentulosi, vetustiores teretes, indumento adpresso praediti, denique glabrescentes; partes floriferae cicatricibus conspicuis praeditae. Gemma terminalis brunneo-tomentella vel adpresse pubescens. Folia elliptica, 8 12 × 3–5 cm, coriacea, alterna, supra nitida, subtus pallide viridia, apice acuta vel breviter acuminata, basi acuta margine paulo revoluta, supra glabra, subtus paucis pilis adpressis, praesertim prope basim et secus costam, praedita. Venatio pinnata, nervis utroque costae latere 6–9, costa nervisque supra impressis, subtus paulo elevatis. Petioli adpresse brunneo-pubescentes, glabrescentes, nigricantes. Inflorescentiae brunneo-tomentellae vel adpresse pubescentes, ad 10 cm longae, paniculatae, ramulis ad apicem pluri-cymosis; inflorescentiae in axillis bractearum ad ramulorum apices foliis carentes et cicatricibus praeditas ortae. Flores unisexuales, (sub)sessiles, flavi. Tepala 6, aequalia, utrinque adpresse pubescentia, late ovata, 2.5 × 2.2 mm, sub anthesi erecta. Flos masculinus: stamina 9, 4-locellata, locellis in 2 seriebus dispositis; 6 exteriora ca. 1.6 mm longa, filamentis antheris paulo angustioribus ca. 0.8 mm longis, locellis introrsis; 3 interiora ca. 2 mm longa, filamentis ca. 1 mm longis, fere latitudine antheram aequantibus; glandulis liberis, globosis; staminodia non visa. Pistillodium ca. 2.4 mm longum, praesertim basi pubescens. Tubus floralis pubescens. Flos femineus: (partes florales super fructu juvenali praesentes): staminodia ca. 0.8 mm longa, filamento anthera perangustiore ca. 0.4 mm longo; locellis obscuris. Stylus triangularis, pubescens. Infructescentiae ad 8 cm longae. Cupula immatura profunda, lenticellata, ad 1.5 cm lata, in pedicellum attenuata.

Tree, to 30 m tall. Twigs (especially when young) angled, becoming terete with age; young twigs with a dense, short, brown tomentum, this soon becoming appressed and finally disappearing on older twigs; inflorescence-bearing parts of twigs with conspicuous scars from fallen inflorescences. Terminal bud brown-tomentellous to appressed pubescent. Leaves elliptic, 8–12 × 3–5 cm, coriaceous, alternate, smooth and lustrous above, pale green below, apex acute to shortly acuminate, the base acute with slightly revolute margin; glabrous above, with some appressed hairs below (especially near the base of the leaves and along the costa). Venation pinnate, lateral veins 6–9 pairs, costa and lateral veins impressed above, slightly raised below, a fine reticulation rarely apparent (mostly on young leaves). Petioles appressed-brown-pubescent when young, becoming glabrous and black. Inflorescences brown-tomentellous to appressed pubescent, to 10 cm long, paniculate, the branchlets usually with several cymes near their tips; inflorescences frequently arranged on leafless apical parts of twigs, these to 15 cm long and with large scars of old, fallen inflorescences, the entire complex appearing as one terminal inflorescence. Flowers unisexual, sessile or nearly so, yellow. Tepals 6, equal, appressed-brown-pubescent, broadly ovate, 2.5 × 2.2 mm, the inner surface pubescent, erect at anthesis. Male flower: stamens 9, all 4-celled, the cells arranged in 2 rows. Outer 6 stamens ca. 1.6 mm long, the filaments ca. 0.8 mm long, slightly narrower than the anthers, the cells introrse; inner 3 stamens ca. 2 mm long, the filament ca. 1 mm long and about as wide as the anther; glands free, globose, basally attached; staminodia not seen. Pistillode ca. 2.4 mm long, pubescent, especially near the base; ovary and style poorly differentiated. Floral tube pubescent inside. Pistillate flower (based on remnants found on young fruits): staminodia ca. 0.8 mm long, filament and anther ca. 0.4 mm long, filament much narrower than anther, anther cells difficult to see and not opening. Filament dorsally pubescent near the base. Style deciduous, triangular, pubescent; stigma platelike. Top of young fruit pubescent. Infructescences to 8 cm long. Floral parts persisting on young fruits, tepals slightly fused near the base and falling as a unit. Cupule deeply cup-shaped, enclosing ca. ¾ of the young fruit, lenticellate, to 1.5 cm wide, narrowed into the swollen pedicel at the base.

Paratypes. VENEZUELA. T. F. AMAZONAS: Dept. Atures, valley of Río Coro-Coro, fr, *Holst & Liesner 3402, 3421* (MO, VEN).

Ocotea flavantha is known only from the three type collections in T. F. Amazonas, Venezuela. The nearly sessile flowers, angled twigs, deep cupules, and erect tepals that tend to persist on young fruits place it in the group of *O. glomerata*. Three species

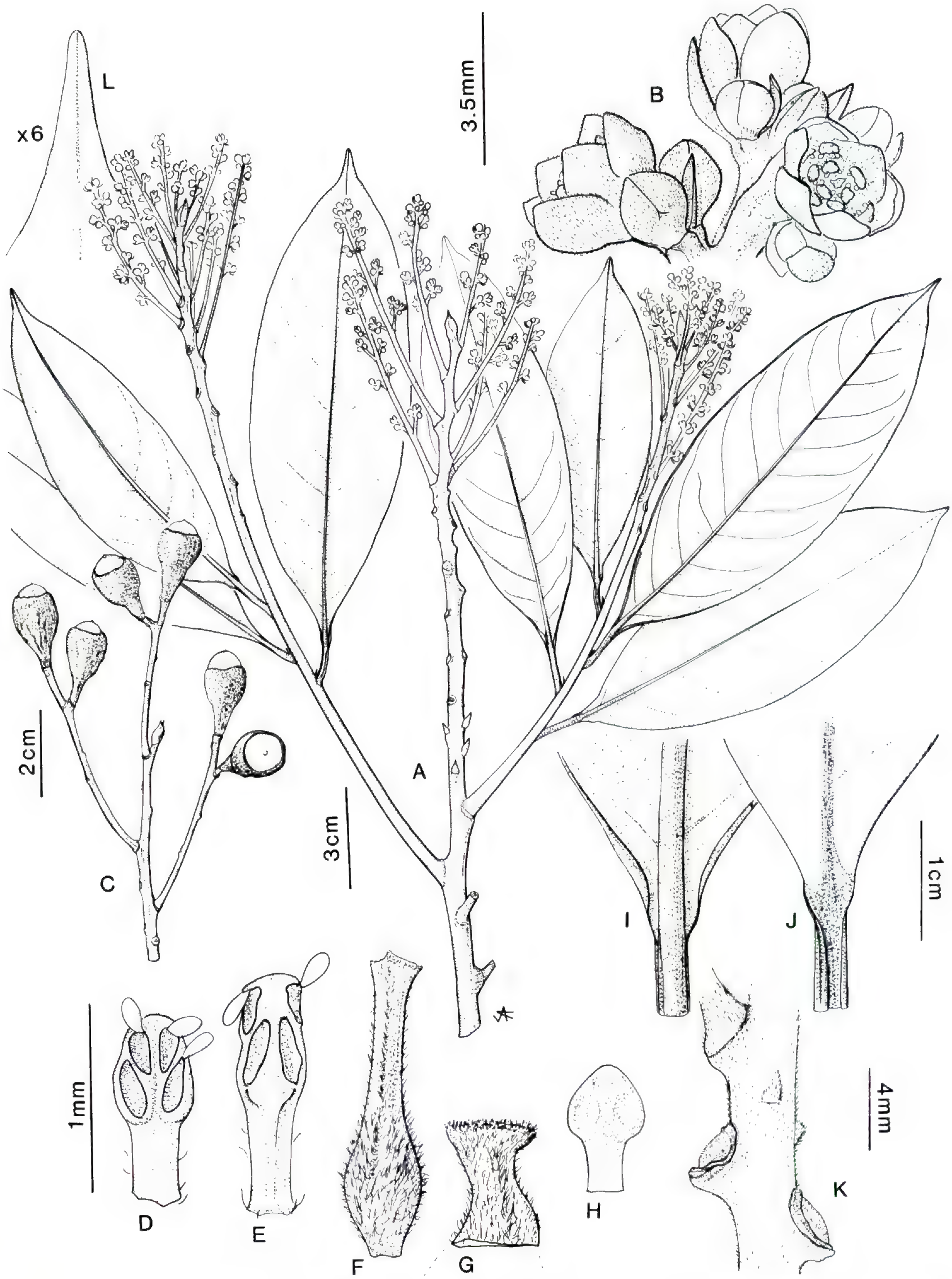

FIGURE 2. *Ocotea flavantha*.—A. Habit.—B. Flowers.—C. Young fruits.—D. Outer stamen.—E. Inner stamen.—F. Pistillode.—G. Style and stigma from young fruit.—H. Staminode.—I, J. Leaf base, seen from below and above.—K. Stem showing scars from fallen inflorescences.—L. Leaf apex.

of this group in the Venezuelan Guayana have a wide distribution (*O. glomerata* (Meissner) Mez, *O. guianensis* Aublet, and *O. longifolia* HBK), but these species have light-colored or very dense pubescence. The color of the indument and the smooth upper leaf surfaces suggest a relationship with the more restricted *O. bracteosa* (Meissner) Mez, *O. cujumary* Martius, and *O. canaliculata* (Rich.) Mez. These three species in Venezuela are known only from the eastern parts of T. F. Delta Amacuro and Estado Bolívar. *Ocotea cujumary* can be readily identified by its double-rimmed cupules; the other two species differ from *O. flavantha* in their glabrous ovary and style and in the absence of leafless, but inflorescences-carrying terminal parts of the twigs. The swollen pedicel supporting the cupule and the rather large (and still immature) cupules are additional distinctive characteristics. Differences in leaf shape are rather subtle. *Ocotea canaliculata* has the petiole poorly differentiated and lacks the weakly recurved leaf base, while *O. flavantha* has an obvious petiole and a slightly recurved leaf base. *Ocotea bracteosa* has larger and wider (to 15 × 6 cm) and more glaucous leaves than *O. flavantha*.

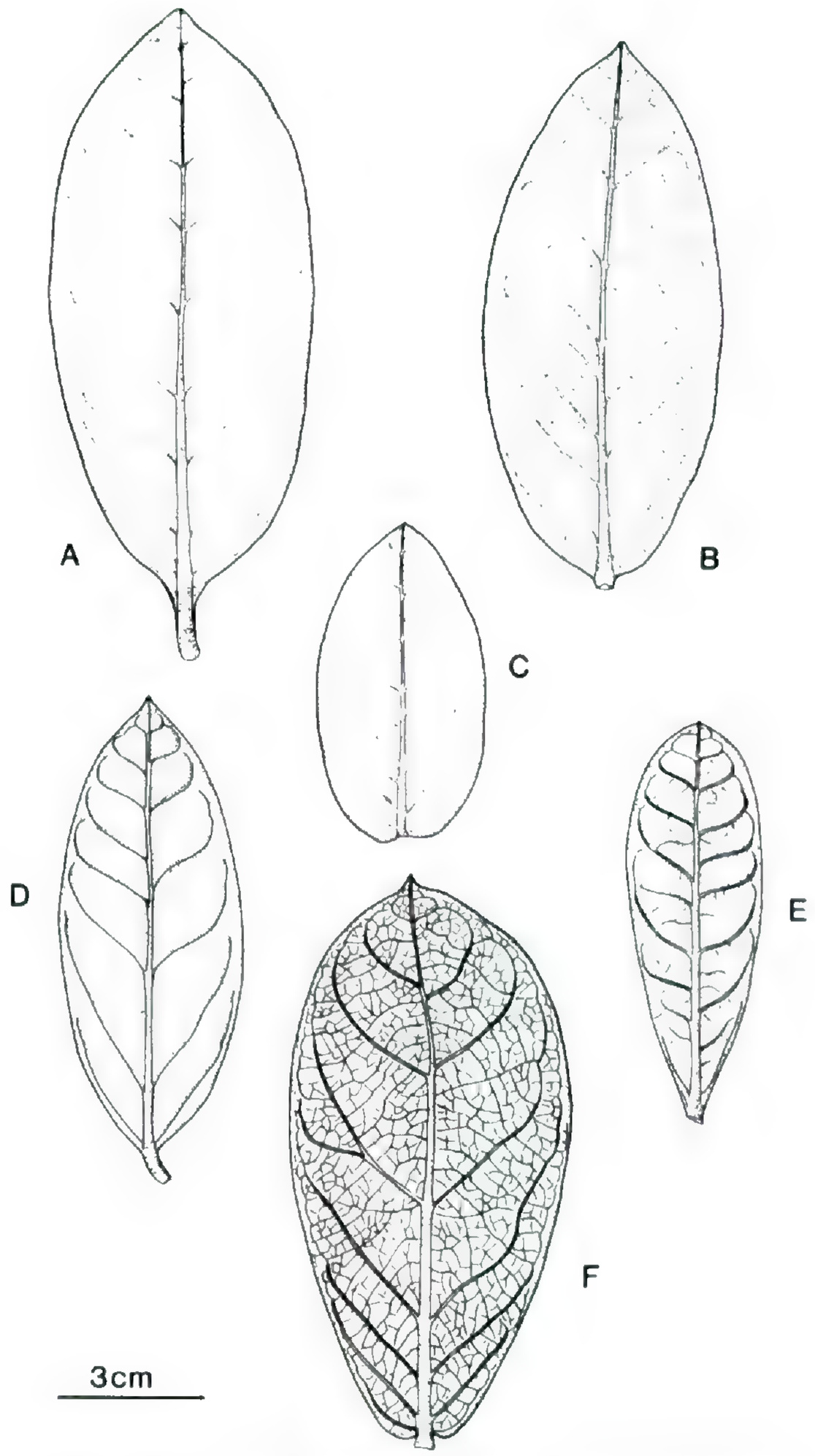

FIGURE 3. Leaf shapes of *Ocotea* species with glabrous twigs, leaves, terminal buds, inflorescences, and flowers.—A. *Ocotea cowaniana* (*Cowan 31106*).—B. *Ocotea venosa* (*Tate 676*).—C. *Ocotea erectifolia* (*Steyermark 97926*).—D. *Ocotea roseopedunculata* (*Huber 10127*).—E. *Ocotea glabra* (*Huber 12003*).—F. *Ocotea huberi* (*Huber 11008*).

Ocotea glabra van der Werff, sp. nov. TYPE: Venezuela. Bolívar: summit of Carrao-tepui, 2,470–2,500 m, shrub 4–8 ft. tall, *Steyermark 60897* (fl) (holotype, VEN; isotype, F). Figure 3E.

Frutex ad 2.5 m altus. Ramuli crassi, glabri, teretes. Gemma terminalis glabra. Folia obovata vel anguste obovata, 5–8 × 1.5–3 cm, alterna, saepe aggregata, coriacea, basi acuta, apice subacuta vel rotundata, glabra, supra polita. Venatio pinnata; nervi laterales utroque costae latere 6–9, sub angulo 70–80° prodeuntes, supra elevati, subtus quasi immersi. Petioli glabri, crassi, in sicco obscuri, ad 2 mm longi. Inflorescentiae glabrae, spicatae vel anguste paniculatae, pauciflorae, ex axillis bractearum persistentium vel infrequenter foliorum ortae. Flores unisexuales, glabri; tepala 6, aequalia, late elliptica, ca. 2 mm longa, 1.7 mm lata; flos masculinus: stamina 9, 4-locellata, glabra, 6 exteriora locellis introrsis, filamento ca. 0.6 mm longa; 3 interiora locellis inferioribus extrorsis, locellis superioribus lateralibus, filamenti base glandulis duabus connatis praedita; staminodia non visa; pistillodium lineare, ca. 0.8 mm longum; in flore femineo: staminodia ca. 0.7 mm longa, ovarium glabrum, ellipsoideum, ca. 2 mm longum, stigmate capitata. Fructus ignotus.

Shrub, to 2.5 m tall. Twigs thick, glabrous, terete, with conspicuous leaf scars. Terminal bud glabrous, usually hidden by the leaves. Leaves obovate to narrowly obovate, widest above the middle, 5–8 × 1.5–3 cm, alternate, somewhat clustered along twigs, coriaceous, the base acute, the apex very shortly acute to rounded, glabrous, the upper surface shiny, especially on young leaves, the lower surface less shiny. Venation pinnate, lateral veins 6–9 pairs, departing from the midvein under an angle of 70–80°, raised on the upper surface and immersed or nearly so on the lower surface; margin often slightly revolute. Petiole glabrous, to 2 mm long, drying dark. Inflorescences glabrous, ca. 6 cm long, few-flowered, mostly in the axils of persistent bracts, these 5–7 mm long, narrowly elliptic, glabrous. Flowers unisexual, glabrous; staminate flowers with tepals erect at anthesis; tepals 6, equal, broadly elliptic, ca. 2 mm long, 1.7 mm wide; stamens 9, 4-celled, glabrous, the outer 6 stamens with introrse cells arranged in 2 rows, filament and anther both ca. 0.6 mm long; inner

stamens with lower cells extrorse, the upper ones lateral, the base of the filament with 2 large, fused glands; staminodia not seen; pistillode present, linear, ca. 0.8 mm long; pistillate flowers with staminodia ca. 0.7 mm long, the ovary ellipsoid, ca. 2 mm long, glabrous, style lacking, stigma capitate. Fruit unknown.

Paratype. VENEZUELA. BOLÍVAR: Municipio Gran Sabana, Caraurén-tepui, ca. 1,950 m, fl, *Huber & Picon 12003* (MYF).

Ocotea glabra is known only from two collections from the summits of Carrao- and Caraurén-tepuis. It is characterized by being completely glabrous, its (narrowly) obovate leaves, and its venation with lateral veins departing at almost 90° from the midvein. This last-mentioned character occurs also in *O. wurdackiana* Allen, a species restricted to the tepuis of Estado Bolívar. Allen (1964) cited the type collection of *O. glabra* as a paratype of *O. wurdackiana* and described *O. wurdackiana* as having hermaphrodite flowers. Recent collections have shown that *O. wurdackiana* has unisexual flowers, like *O. glabra*. The two species, although superficially similar, can be separated as follows: *O. glabra* is entirely glabrous and has the lower leaf surfaces smooth, while *O. wurdackiana* always has a pubescent terminal bud, the inner surface of the tepals densely pubescent, and the lower leaf surface microscopically papillate.

Ocotea glabra has its closest relatives among the ten unisexual *Ocotea* species in the Venezuelan Guayana that share glabrous twigs, leaves, and terminal buds. Two of these have pubescent flowers or inflorescences (*O. myriantha* (Meissner) Mez and *O. perrobusta* (Allen) Rohwer) and are not very closely related. *Ocotea myriantha* is a lowland species, rather common in southern T. F. Amazonas, whereas *O. perrobusta* is restricted to Auyan-tepui, Estado Bolívar. The remaining species in this group have a restricted distribution and are known only from the upper slopes or summits of one or two sandstone mountains. Three have rather large, many-flowered inflorescences: *O. crassifolia* (Sarven-tepui, Roraima), *O. neblinae* (Neblina), and *O. basirecurva* (Serranía de Yutaje, Cerro Coro-Coro). Short, almost spicate, and few-flowered inflorescences, also strongly coriaceous leaves, characterize the last large group of species. Several but not all species in this group have glaucous, clustered, almost sessile leaves, shiny upper leaf surfaces, and lobed or toothed cupules. This group can be subdivided into (1) species from Estado Bolívar, characterized by immersed or elevated costa and lateral veins but without a raised reticulation (*O. erectifolia* (Allen) van der Werff, Cerro Jaua; *O. glabra* van der Werff, Carrao-tepui and Caraurén-tepui; *O. roseopedunculata* van der Werff, Acopán-tepui), and (2) species from T. F. Amazonas with weakly developed lateral veins and raised reticulation on upper and/or lower leaf surface (*O. venosa* Gleason, Cerro Duida, Marahuaca; *O. cowaniana* Allen, Serranía Paru; *O. huberi* van der Werff, Cerro Coro-Coro, Serranía Guanay). *Ocotea glaucophylla* Moldenke, based on material from Cerro Duida, is not well understood; to this small-leaved species also belong collections from Chimantá, revealing an unusual distribution pattern. With the exception of *O. glaucophylla*, these species are well defined by their inflorescence and leaf characters (Fig. 3); they are also geographically separated, and the paucity of collections is probably due to occurrence in inaccessible places. The collection *Maguire 33026* (NY) from Cerro Guaiquinima belongs in this species group (it has glabrous leaves, twigs, and terminal bud, and clustered, glaucous, coriaceous, subsessile leaves) and differs from the other species in its smooth upper leaf surface; it is almost certainly undescribed, but because it is sterile, I do not wish to describe it.

Ocotea huberi van der Werff, sp. nov. TYPE: Venezuela. Bolívar: Distr. Cedeño, Serranía Guanay, ca. 1,700 m, *Huber 11008* (holotype, MO; isotype, MYF n.v.). Figure 3F.

Frutex, ad 3 m altus. Ramuli glabri, juniores subangulares, vetustiores teretes. Gemma terminalis non visa, foliis obtecta. Folia elliptico-oblonga vel leviter obovata, 8–13 × 5–8 cm, coriacea, alterna, basi rotunda vel cordata, apice rotunda vel apiculata, supra polita, praesertim in foliis novellis, subtus subpolita, glauca. Venatio pinnata, nervis lateralibus utroque costae latere 6–8, prope marginem versus apicem curvatis coalitisque; costa utrinque immersa; nervis lateralibus et reticulatione elevata, sed foliis veteribus paulo elevatis. Petioli glabri, crassi, ad 3 mm longi. Inflorescentiae glabrae, flores 5–6 mm diametro; tepalis 6, aequalibus, ovatis, 2–2.2 mm longis, 1.4 mm latis, 3 interioribus pagina interiore paucis pilis praeditis, ceterum glabris; staminibus 9, 4-locellatis, eis seriei primae ca. 1.6 mm longis, antheris ca. 0.9 mm longis, locellis introrsis, filamentis ca. 0.5 mm latis, eis seriei secundae ca. 1.0 mm longis, locellis introrsis, filamentis ca. 0.2 mm latis, eis seriei tertiae ca. 1.4 mm longis, antheris rectangularibus, ca. 0.8 × 0.6 mm, locellis lateralibus, filamentis basi 2 glandulis magnis praeditis; staminodiis 3, ca. 0.5 mm longis, linearibus, basi pubescentibus; ovario ellipsoideo, ca. 1.3 mm longo, sensim in stylum brevem attenuato; stigmate capitato. Cupula non profunda, ca. 1 cm lata, margine 6-lobato vel 6-dentato, sensim in pedicellum attenuata. Fructus ovaloideus, 1.5 × 1 cm.

Shrub, 1–3 m tall. Twigs glabrous, subangular when young, becoming terete. Leaves elliptic-ob-

long to slightly obovate, 8–13 × 5–8 cm, alternate, ± evenly distributed along twigs, coriaceous, the base rounded to cordate, the apex rounded to apiculate, the upper surface shiny, especially the young leaves, the lower surface less so, glaucous. Venation pinnate, the lateral veins 6–8 pairs, curving upward towards the margin and becoming connected; midrib immersed on upper and lower surfaces, lateral veins and tertiary venation raised and forming a coarse reticulum, this less visible on older leaves. Petioles glabrous, thick, to 3 mm long, blackish when dry. Inflorescences glabrous, in the axils of persistent leaves, 12–16 cm long, exceeding the leaves, narrowly paniculate. Flowers glabrous, 5–6 mm diam.; tepals 6, equal, ovate, 2–2.2 mm long, 1.4 mm wide, the inner 3 with a few hairs on the inner surface, otherwise glabrous, reflexed in old flowers; stamens 9, the anthers 4-celled; outer 3 (whorl I) ca. 1.6 mm long, the anther ca. 0.9 mm long, cells introrse, the filament ca. 0.5 mm wide; stamens of whorl II ca. 1.0 mm long, cells introrse, the filaments ca. 0.2 mm wide; stamens of whorl III ca. 1.4 mm long, the anther rectangular, ca. 0.8 mm long, 0.6 mm wide, cells lateral; glands at base of filaments free, ca. 0.5 mm long; staminodes 3, linear, ca. 0.5 mm long, pubescent near base; ovary ellipsoid, ca. 1.3 mm long, gradually narrowed into short style, 0.3 mm long; stigma large, capitate. Cupule a shallow cup, ca. 1 cm wide, with 6 teeth or lobes at the margin and gradually narrowed into the pedicel. Fruit ovaloid, 1.5 × 1 cm fide collector.

Paratypes. VENEZUELA. T. F. AMAZONAS: Depto. Atures, cumbre del Cerro Coro-Coro, 2,200 m, *Huber 12298* (MO, MYF).

Ocotea huberi is restricted to the Departamento Atures and Distrito Cedeño, along the border of Estado Bolívar and T. F. Amazonas. Its closest relative is *O. venosa* Gleason, a species only known from the type collection from Cerro Duida and a fruiting specimen from Cerro Marahuaca, both in T. F. Amazonas. The two species have similarly raised reticulation, toothed or lobed cupules, and swollen fruiting pedicels. They differ in their leaf bases, which are obtuse in *O. venosa* vs. rounded to cordate in *O. huberi*, and in the much shorter inflorescences of *O. venosa*. The types of *O. venosa* (NY, US) do not have open flowers, and I have not compared their floral details; I accept *O. huberi* as a distinct species based on its striking leaf shape and long inflorescences.

The group of species to which *Ocotea huberi* belongs is characterized by unisexual flowers. The MO sheet of *Huber 11008* has two twigs, one in young fruit, the other in flower. Dissection showed the flowers to be staminate (anthers with well-developed locelli; pistil hollow). Thus, the flowering and fruiting twigs on the type sheet probably came from different plants, and I select the flowering twig as the holotype. Relationships of *O. huberi* are further discussed under *O. glabra*.

Ocotea julianii van der Werff, nom. nov. Based on *Phoebe steyermarkiana* Allen, Mem. New York. Bot Gard. 10(5): 74. 1964. TYPE: *Steyermark & Wurdack 921* (holotype, NY; isotypes, F, MO).

Ocotea julianii was erroneously described as belonging to the genus *Phoebe* by Allen. The large, cup-shaped cupule excludes this species at once from *Phoebe*, a genus in which the fruit is subtended by a small cupule with the tepals usually persisting. Leaf venation, the large cupule, and the deep floral tube in old flowers all point to the *Ocotea aciphylla* group (I have not seen good flowering material). Because Allen already described *Ocotea steyermarkiana*, a new epithet is needed when *Phoebe steyermarkiana* is transferred to *Ocotea*.

The similarity between *Ocotea julianii* and *Phoebe tetragona* (Meissner) Mez pointed out by Allen (1964) is superficial. Fruiting specimens of the latter species have a cupule typical of *Phoebe*, and the leaves and flowers are glabrous. Distribution also argues against a close relationship, since *P. tetragona* is a cerrado species from Minas Gerais, Brazil. I regard *O. julianii* as closely related to *O. revoluta* Moldenke, a poorly known species from Cerro Duida. This species differs in its narrower, generally smaller leaves with revolute margins and in its smaller, funnel-shaped cupules; both species belong to the *O. aciphylla* group.

Ocotea liesneri van der Werff, sp. nov. TYPE: Venezuela. T. F. Amazonas: Dept. Río Negro, Cerro Neblina Camp IV, 780 m, *Liesner 16687* (holotype, MO; isotypes, HBG, NY, VEN).

Arbuscula, ad 5 m altus. Ramuli teretes (novelli paulo angulati), glabri. Gemma terminalis glabra. Folia late elliptica vel late ovata, 10–17 × 7–11 cm, coriacea, alterna, apice acuta vel rotundata, basi obtusa vel rotundata, margine paulo revoluta, utrinque opaca. Venatio pinnata, nervis utroque costae latere 5–7, prope marginem versus apicem arcutis et evanescentibus; costa nervisque lateralibus supra immersis, subtus elevatis, subtus reticulatione minuta paullo elevata. Petioli glabri, 1.5–2 cm longi, parum canaliculati. Inflorescentiae glabrae, ad 10 cm longae, foliis breviores, paniculatae, ramulis basalibus 2–5-floris, apicalibus unifloris. Pedicelli glabri vel paucis pilis

praediti, 3–4 mm longi. Flores albidi, ad 4 mm diametro, tubo florale infundibuliforme, conspicuo. Tepala 6, aequalia, elliptico-ovata, ca. 1.7 mm longa, intus parte inferiore pubescentia. Stamina 9, 4-locellata, locellis 2 seriebus dispositis; 6 exteriora ca. 1.4 mm longa, filamento 0.7 mm longo, locellis introrsis, filamento pubescente; 3 interiora 1.3 mm longa, filamento 0.7 mm longo, pubescente; glandulis breviter stipitatis, 0.3 mm diametro, locellis inferioribus extrorsis, superioribus lateralibus. Staminodia 3, linearia, pubescentia, apice incrassata et glabra. Ovarium globosum, 1.1–1.2 mm in diametro, in tubo florale intus pubescente inclusum; style 0.8 mm longo, stigmate non incrassato. Fructus ignotus.

Small tree, to 5 m tall. Twigs terete or slightly angled when young, glabrous. Terminal bud glabrous. Leaves broadly elliptic to broadly ovate, 10–17 × 7–11 cm, coriaceous, glabrous, alternate, evenly distributed along twigs, the tip rounded or acute, the base obtuse or rounded, the margin slightly revolute, both surfaces dull. Venation pinnate, lateral veins 5–7 pairs, arching upwards and disappearing near the margin, midvein and lateral veins immersed on upper surface, raised on lower surface, the lower surface with a slightly raised, fine reticulation, this less visible on the upper surface. Petioles glabrous, 1.5–2 cm long, somewhat canaliculate. Inflorescences glabrous, ca. 10 cm long, shorter than the leaves, paniculate, the lower branchlets with 2–5 flowers, otherwise flowers single, the inflorescences few-flowered. Pedicels glabrous or with very few hairs, 3–4 mm long. Flowers whitish, with a few appressed hairs on the outside, 4 mm diam., floral tube funnel-shaped, conspicuous. Tepals 6, equal, elliptic-ovate, ca. 1.7 mm long, the inner surface pubescent in the lower half. Stamens 9, all 4-celled, the cells arranged in 2 rows; outer 6 ca. 1.4 mm long, both filament and anther 0.7 mm long, the cells introrse, filament rather densely pubescent; inner 3 stamens 1.3 mm long, the filament 0.7 mm long, pubescent; glands shortly stipitate, 0.3 mm diam.; lower pair of cells extrorse, the upper pair lateral. Staminodia 3, linear, ca. 0.6 mm long, pubescent, but the tip glabrous and slightly swollen. Ovary globose, 1.1–1.2 mm diam., enclosed in the well-developed floral tube, this with pubescent walls; style distinct, ca. 0.8 mm long, not widened into a distinct stigma. Fruits unknown.

Although *Ocotea liesneri*, known only from the type collection, is in all vegetative parts glabrous like *Ocotea erectifolia* and allies, these species are probably not closely related. *Ocotea liesneri* differs from the *O. erectifolia* group, for instance, by having well-developed petioles, a rather lax inflorescence (comparable to but smaller than that of *O. basirecurva*), relatively long and pubescent filaments, and flowers apparently hermaphroditic. The last-mentioned character, difficult to ascertain, needs verification from additional collections. *Ocotea liesneri* seems quite isolated. In the Venezuelan Guayana, the number of hermaphroditic *Ocotea* species is not great; most belong to the *O. aciphylla* group, which always has pubescent flowers and a quite different venation, and the *O. oblonga* group, which has entirely different leaves. The remaining species are also isolated and possess some striking characters; they include *O. rubra* Mez, *O. cymbarum* HBK, *O. esmeraldana* Moldenke, and *O. fasciculata* (Nees) Mez.

Ocotea megacarpa van der Werff, sp. nov. TYPE: Venezuela. T. F. Amazonas: Depto. Atabapo, Cerro Marahuaca, 1,220–1,350 m, tree, 15 m tall, *Steyermark & Holst 130610* (holotype, MO; isotype, VEN).

Arbor, ad 15 m alta. Ramuli juniores cinnamomeo-tomentosi, parum angulosi, vetustiores glabrescentes teretesque. Folia coriacea, 15–22 × 5–9 cm, alterna, elliptica, saepe conduplicata, basi obtusa vel acuta, apice acuminata; supra glabra, venatione immersa; subtus juniora cinnamomeo-tomentosa, vetustiora glabra, costa prominenti, nervis paulo elevatis. Nervi utroque costa latere 5–8, arcuati, prope marginem evanescentes. Inflorescentiae floresque ignoti. Fructus ellipsoideus, 5–6 × 3.5–4 cm. Cupula ad 4 cm lata, 1.5 cm profunda, verrucosa.

Tree, 10–15 m tall. Twigs brown-tomentose and weakly angled when young, becoming glabrous and terete with age. Leaves stiff, leathery, 15–22 × 5–9 cm, alternate, elliptic, frequently conduplicate, the base obtuse or acute, the apex acuminate, the upper surface glabrous and with the venation immersed, the lower surface brown-tomentose when young, glabrous with age, the midvein prominent, lateral veins slightly raised, in 5–8 pairs, arching upwards and fading away close to the margin. Petioles 1.5–2 cm long, canaliculate, brown-tomentose when young, glabrescent with age. Inflorescences and flowers unknown. Infructescences with few fruits, glabrous, to ca. 7 cm long. Fruit ellipsoid, 5–6 cm long, 3.5–4 cm wide. Cupule (immature) a cup ca. 3 cm wide and 1.5 cm deep, the outside ridged and warty, the inside glabrous or with a few appressed hairs; mature cupules shallower, 3.5–4 cm wide and to 1.5 cm deep, the outside ridged and warty.

Paratypes. VENEZUELA. T. F. AMAZONAS: Depto. Atabapo, Cerro Marahuaca, 1,140 m, *Steyermark & Holst 130555* (MO, VEN); same locality, 1,225 m, *Liesner 17732, 17733* (MO, VEN).

Ocotea megacarpa is known only from three fruiting collections from Cerro Marahuaca. Leaf

shape, venation, canaliculate petioles, and the initially deep cups all point to the *Ocotea aciphylla* group. Within this group (and within the genus *Ocotea*), the large fruits and large, shallow cupules are unmatched, and *O. megacarpa* is solely described on the distinctiveness of its fruits and cupules. In the *Ocotea aciphylla* group, *O. julianii* also has large fruits (3.5 × 3 cm) and cupules (ca. 3 cm wide). However, in addition to its smaller fruits and cupules, *O. julianii* differs in its rounded to subcordate leaf bases, short, thick petioles, and blunt to rounded leaf apices. *Ocotea megacarpa* is in leaf shape (but not in indumentum) very similar to *O. aciphylla* (Nees) Mez s.l., especially to the lowland populations in T. F. Amazonas, which have been identified as *O. costulata* (Nees) Mez in the past, but this species has appressed pubescence, cupules to 2 cm wide, and fruits to 2.5 cm long.

Ocotea roseopedunculata van der Werff, sp. nov. TYPE: Venezuela. Bolívar: Distr. Piar, summit area of Acopán-tepui, ca. 1,950 m, fl, *Huber, Ahti & Pipoly 10127* (holotype, MO; isotype, MYF n.v.). Figure 3D.

Frutex ad 2.5 m altus. Ramuli glabri, cristati petiolis decurrentibus, foliorum cicatricibus conspicuis praediti. Gemma terminalis glabra. Folia elliptica vel anguste elliptica, raro subovata vel subobovata, 7–11 × 2.5–4.0 cm, coriacea, glabra, basi apiceque acuta, alterna sed plerumque conferta, foliis paucis et minoribus inter folios confertos, supra polita, subtus opaca, glauca. Venatio pinnata, nervis utroque costae latere 6–10, basalibus adscendentibus sed distalibus angulo obtuso prodeuntibus, prope marginem versus apicem curvatis et coalitis; costa nervisque lateralibus supra elevatis sed reticulatione (fere) immersa; subtus venatione quasi immersa. Petioli crassi, glabri, ad 5 mm longi, in sicco nigri. Inflorescentiae glabrae, roseae, folios aequantes vel eis paulo longiores, ex axillis foliorum vel bractearum ortae. Pedicelli glabri, ad 5 mm longi, basi bractea lineare ad 0.5 mm longa praediti. Flores glabri, flavi. Tepala 6, aequalia, ovata, 2.5 × 1.8 mm. Stamina 9, 4-locellata, locellis in 2 seriebus dispositis; 6 exteriora subsessilia, filamentis ad 0.3 mm longis, anthera 1.3 × 1.1 mm, locellis introrsis; 3 interiora ca. 1.5 mm longa, anthera ca. 1 mm longa, locellis lateralibus vel laterali-extrorsis, glandulis magnis, liberis, ca. 0.6 mm in diametro; staminodia non visa; pistillodium parvulum, lineare, ad 0.3 mm longum. Flores feminei et fructus ignoti.

Shrub, to 2.5 m tall. Twigs ridged due to decurrent leaf bases and with conspicuous scars from fallen leaves. Terminal bud glabrous. Leaves elliptic to narrowly elliptic, or rarely somewhat ovate or obovate, 7–11 × 2.5–4.0 cm, coriaceous, glabrous, base and tip acute, alternate, mostly clustered, the few leaves between the leaf clusters usually smaller, the upper surface shiny, the lower surface dull, glaucous. Venation pinnate, lateral veins 6–10 pairs, the basal ones ascending, the middle and distal ones leaving the midvein under blunter angles, near the margin curving upwards and becoming loop-connected, midvein and lateral veins raised on the upper surface but not on lower, tertiary venation immersed or nearly so on both sides. Petioles thick, glabrous, to 5 mm long, black when dry. Inflorescences glabrous, pink, about as long as the leaves or slightly longer, spicate or the lower branches with 2 or 3 flowers, in the axils of leaves or bracts. Pedicels glabrous, to 5 mm long, with a linear bract ca. 0.5 mm long at the base. Flowers yellow, glabrous. Tepals 6, equal, ovate, 2.5 × 1.8 mm. Stamens 9, all 4-celled and the cells arranged in 2 rows; outer 6 stamens sessile or nearly so, the filament to 0.3 mm long, the anther 1.3 × 1.1 mm, cells introrse; inner 3 stamens ca. 1.5 mm long, anther ca. 1 mm long, the cells lateral or lateral-extrorse, glands large, free, ca. 0.6 mm diam.; staminodia not seen; pistillode very small, linear, ca. 0.3 mm long, completely hidden by stamens and glands, stigma not developed. Pistillate flowers and fruits not known.

Paratype. VENEZUELA. BOLÍVAR: Distr. Piar, summit area of Acopán-Tepui, ca. 1,950 m, fl, *Huber, Ahti & Pipoly 10120* (MO).

Ocotea roseopedunculata is restricted to Acopán-tepui and is currently known from only two collections. Its nearest relative is *Ocotea glabra*, known from Carrao and Caraurén-tepuis in Estado Bolívar. These two species are best separated by their leaf characters: *O. roseopedunculata* has elliptic leaves with mostly ascending lateral veins, while *O. glabra* has (narrowly) obovate leaves with the lateral veins leaving the midrib under a blunter angle and more rounded leaftips. In addition, there are some small floral differences: in *O. glabra* the filaments and anthers of the outer stamens are about equally long and the pistillode is ca. 0.8 mm long; in *O. roseopedunculata* the anthers are subsessile and the pistillode is smaller, 0.3 mm long. The two species share ridged stems, conspicuous leaf scars, almost spicate, few-flowered inflorescences, and a tendency toward clustered leaves. See also discussion under *O. glabra*.

Ocotea tomentosa van der Werff, sp. nov. TYPE: Venezuela. T. F. Amazonas: San Carlos de Río Negro, IVIC main study site, km 4.3 on Solano Road, small tree 3 m high, flowers white, *Clark & Maquirino 6802* (holotype, MO; isotypes, HBG, NY).

Frutex vel arbor parva, ad 3 m alta. Ramuli angulati, hornotini brunneo-tomentosi, vetustiores tomentelli, de-

nique glabrescentes. Gemma terminalis brunneo-tomentosa. Folia elliptica, 15–25 × 6–8 cm, alterna, coriacea, supra praeter pubescentiam basi costae glabra, subtus secus costam nervisque pilis curvatis brunneis praedita et lamina albo-tomentosa vel cinereo-tomentosa; basi apiceque acuta, nervis utroque costae latere 6–8, sursum curvatis et nervo superiore consociatis; venatione supra immersa, costa et nervis subtus elevatis, indumento brunneo venationis tomento albido laminae discrepante. Petioli ca. 1.5 cm longi, brunneo-tomentelli vel subglabri. Inflorescentiae axillares, brunneo-tomentosae, ad 10 cm longae, paniculatae. Pedicelli ca. 1 mm longi, tomentosi. Flores (tantum feminini visi) albi. Tepala 6, aequalia, ovata, ca. 1 mm longa, extus pilis paucis cinereis praedita et minus pubescentia quam inflorescentia, intus subglabra; staminodia 9, ca. 0.3 mm longa, glabra; ovarium ca. 1 mm diametro, stylum inconspicuum, stigma capitatum. Fructus globosus, ca. 1 cm diametro, cupula non profunda, pedicello incrassato, petalis persistentibus.

Shrub or small tree, to 3 m tall. Twigs angular, brown-tomentose when young, becoming tomentellous and finally glabrous. Terminal bud brown-tomentose. Leaves elliptic, 15–25 × 6–8 cm, alternate, coriaceous, glabrous above except some pubescence on midrib, the lower surface with brown curled hairs along midrib and main veins, the leaf tissue white-tomentose, turning grayish with age, base and apex acute, lateral veins 6–8 pairs, these arching upwards and becoming loop-connected with the distal vein; venation immersed on the upper surface, costa and lateral veins raised on lower surface, the venation with brown indumentum contrasting with the white tomentum on the laminar tissue. Petioles ca. 1.5 cm long, brown-tomentellous to glabrous. Inflorescences axillary, brown-tomentose, to 10 cm long, paniculate. Pedicels ca. 1 mm long, tomentose. Flowers white (only pistillate seen). Tepals 6, equal, ca. 1 mm long, ovate, with some gray hairs on the outside and pubescence on tepals much less than on inflorescence or pedicels; inside of tepals with a few hairs or glabrous; staminodia 9, ca. 0.3 mm long, glabrous; ovary ca. 1 mm diam., style not evident, stigma capitate. Fruit a globose berry, ca. 1 cm diam., the cupule shallow, pedicel swollen and the petals persisting as lobes on the margin of the cupule.

Paratypes. VENEZUELA. T. F. AMAZONAS: San Carlos de Río Negro, IVIC main study site, fl, *Clark & Maquirino 8216* (MO); Río Guainía, ca. 7 km N of Maroa, frequent in shrub savanna, fr, *Maguire et al. 41755* (NY).

Ocotea tomentosa is known only from the upper drainage of the Río Negro between Maroa and San Carlos de Río Negro. Although the area around San Carlos de Río Negro has been reasonably well explored, *O. tomentosa* has only been collected there twice (both collections from the same marked tree) and is apparently rare. It is very likely present in Colombia and can be expected in Brazil.

The angled twigs, somewhat clustered flowers and, above all, scarce pubescence on the tepals in comparison with that on the inflorescence point to the *Ocotea leucoxylon* group as the closest relatives. None of the species in that group has leaves with dense abaxial tomentum or such persistent tepals in the fruiting stage; moreover, *O. tomentosa* lacks the white lenticels on the cupule that so readily identify the *O. leucoxylon* group.

Persea areolatocostae (Allen) van der Werff, comb. nov. BASIONYM: *Phoebe areolatocostae* C. K. Allen, Mem. N.Y. Bot. Gard. 10: 75. 1964.

The type collection of *Phoebe areolatocostae* has buds and immature fruits. However, the fruits are diseased; the relatively long petioles, leaf shape, and leaf reticulation all point to the genus *Persea*. The equal tepals are a character infrequently found in *Persea*; *P. americana* and a few related species share this character, but *P. areolatocostae* is probably not related to those species. In my opinion, the relationship is with a small group of species characterized by equal tepals, a small, round fruit, and persistent tepals in the fruiting stage. This group includes the neotropical *P. steyermarkii*, *P. rigens*, *P. silvestris*, and a few additional, as yet undescribed, species. It is not yet clear to which degree this group is related to the Asian *Persea* subg. *Machilus*.

Persea croatii van der Werff, sp. nov. TYPE: Venezuela. T. F. Amazonas: Cerro Neblina, near Cañon Grande at Camp No. 7, ca. 1,800 m, *Croat 59519* (holotype, MO).

Arbor, ad 4 m. Ramuli teretes, sparse adpresse pubescentes, vetustiores glabri. Folia alterna, subcoriacea, elliptica, 7–10 × 2–3 cm, basi acuta, apice obtusa; supra glabra, subtus adpresse pubescentia, sed superficie foliorum pubescentia non occulta, costa nervisque supra immersis, subtus costa elevata sed nervis immersis vel perpaulo elevatis. Petioli canaliculati, 1–2 cm longi, glabri vel leviter adpresse pubescentes. Inflorescentia axillaris, subterminalis, paniculata, ca. 12 cm longa, adpresse cinereo-pubescens. Pedicelli ca. 4 mm longi. Tepala 6, inaequalia, 3 exteriora ca. 4 mm longa, (anguste) ovata, extus pubescentia, intus glabra; 3 interiora ca. 6 mm longa, anguste ovata, utrinque adpresse pubescentia. Stamina 9, 4-locellata; 6 exteriora 4.5–5 mm longa, locellis introrsis, filamentis pubescentibus, antheris glabris, ca. 1.6 mm longis; 3 interiora locellis lateralibus vel laterali-extrorsis, filamentis pubescentibus, ca. 3 mm longis, basi 2 glandulis praeditis, antheris glabris, ca. 1.5 mm longis; staminodia 3, ca. 1 mm longa, sagittata, pubescentia. Ovarium glabrum vel apice paucis pilis praeditum,

globosum, ca. 1.5 mm diametro; stylo ca. 3 mm longo, pubescente. Fructus ignotus.

Tree, 4 m tall. Twigs terete, sparsely appressed pubescent, becoming glabrous with age. Leaves alternate, subcoriaceous, elliptic, 7–10 × 2–3 cm, evenly distributed along twigs, the base acute, apex obtuse; glabrous on the upper surface, appressed pubescent below, but pubescence not obscuring the leaf surface; costa and lateral veins (6–9 pairs) immersed on upper surface; costa raised on lower surface, lateral veins immersed or very slightly raised on lower surface. Petioles canaliculate, 1–2 cm long, glabrous or with some appressed hairs. Inflorescence axillary, pseudoterminal, paniculate, ca. 12 cm long, appressed gray-pubescent. Pedicels ca. 4 mm long. Tepals 6, unequal; outer 3 ca. 4 mm long, ovate to narrowly ovate, appressed pubescent outside, glabrous inside; inner 3 ca. 6 mm long, narrowly ovate, appressed pubescent on both surfaces. Fertile stamens 9, 4-locellate, the outer 6 with introrse cells, 4.5–5 mm long, filaments densely pubescent, anthers glabrous, ca. 1.6 mm long; inner 3 stamens with lateral or lateral-extrorse cells, 4.5–5 mm long, the filaments ca. 3 mm long, densely pubescent, each with 2 glands attached near the base, anthers glabrous, ca. 1.5 mm long. Filaments of all stamens about as wide as anthers or slightly narrower. Staminodia 3, ca. 1 mm long, sagittate, pubescent. Ovary globose, ca. 1.5 mm diam., glabrous except for some hairs near the tip; style ca. 3 mm long, pubescent.

Persea croatii is known from only one collection from the upper slope of Cerro Neblina. The pubescent style and the few apical hairs on the ovary place it in Kopp's (1966) section *Aurataea*, which includes two other species from the Venezuelan Guayana. *Persea grandiflora*, known from the lower slopes of Cerro Neblina, differs in having larger flowers, prominently raised lateral veins on the lower leaf surface, ovate (vs. elliptic) leaves, and much denser pubescence. *Persea maguirei* differs in having smaller leaves, denser pubescence which covers the lower leaf surface, shorter, more slender inflorescences with smaller flowers, and smaller floral parts. In general appearance *P. croatii* is quite similar to *P. perseiphylla*, but *P. croatii* differs in its sparser, noncupreous pubescence on the lower leaf surface and its noncupreous pubescence on flowers and inflorescence.

Persea croizatii van der Werff, sp. nov. TYPE: Venezuela. T. F. Amazonas: upper Río Orinoco, *Croizat 918* (holotype, F). Figure 4.

Arbor vel frutex. Ramuli teretes, juvenales sparse adpresse pubescentes, glabrescentes. Folia alterna, elliptica, 9–14 × 4–6 cm, firme chartacea, margine paulo reflexa, base apiceque acuta, supra glabra, subtus pilis adpressis praedita, praecipue secus costam nervosque; nervis lateralibus utroque latere 5–6; costa et nervis lateralibus supra immersis, subtus elevatis. Petioli plus minusve glabri, 2–3 cm longi. Inflorescentiae anguste paniculatae, 10–15 cm longae, adpresse pubescentes. Pedicelli ca. 2 mm longi, adpresse pubescentes. Tepala 6, inaequalia; 3 exteriora late ovata, intus glabra, ca. 3 mm longa; 3 interiora ovata, intus adpresse pubescentia, 5–6 mm longa. Stamina 9, 4-locellata; 6 exteriora locellis introrsis, ca. 2 mm longa, filamentis pubescentibus, ca. 1.1 mm longis, antheris glabris, ca. 0.9 mm longis, filamentis quam antheris angustioribus; 3 interiora locellis lateralibus vel extrorsis, ca. 2.5 mm longa, filamentis pubescentibus, basi 2 glandulis praeditis, ca. 1.9 mm longis, antheris glabris, ca. 0.6 mm longis, paulo latioribus quam filamentis; staminodia 3, pubescentia, sagittata, ca. 1.1 mm longa. Ovarium glabrum, globosum; stylo gracile, ca. 1.6 mm longo. Fructus globosus, ca. 8 mm diametro; tepala persistentia, patentia.

Woody plant of unknown size. Twigs terete, with some appressed pubescence when young, soon becoming glabrous. Leaves alternate, elliptic, 9–14 × 4–6 cm, firmly chartaceous, the margin slightly reflexed, base and apex acute, glabrous above, with some appressed hairs below, especially along midvein and lateral veins, or almost glabrous, lateral veins 5–6 pairs; midvein and lateral veins immersed above, raised on lower surface; final reticulation not or very slightly raised. Petioles glabrous or with a few appressed hairs especially near the base, 2–3 cm long. Inflorescences narrowly paniculate, 10–15 cm long, about as long as the subtending leaves, appressed pubescent. Pedicels ca. 2 mm long, pubescent. Tepals 6, unequal; outer 3 broadly ovate, appressed pubescent outside, glabrous inside, ca. 3 mm long, inner 3 appressed pubescent on both surfaces, ovate, 5–6 mm long; tips of inner tepals often breaking off in old flowers or in fruiting stage. Fertile stamens 9, all 4-celled; those of the outer 2 whorls with introrse cells, ca. 2 mm long, the filaments pubescent, 1.1 mm long, the anther glabrous, ca. 0.9 mm long, the filaments distinctly narrower than the anthers; inner 3 stamens linear, ca. 2.5 mm long, the filaments pubescent, ca. 1.9 mm long, with 2 globose glands attached slightly above the base, the anther glabrous, ca. 0.6 mm long, slightly wider than the filament; staminodia 3, pubescent, ca. 1.1 mm long, sagittate. Ovary glabrous, style slender, ca. 1.6 mm long, stigma platelike. Fruit globose, ca. 8 mm diam., with glaucous bloom; tepals persistent, spreading.

Persea croizatii is known only from the type collection, made in July–October 1951, along the

FIGURE 4. *Persea croizatii.*—A. Habit.—B. Old flowers.—C. Fruit.—D. Inner stamen.—E. Arrangement of anther cells of inner stamen.—F. Outer stamen.—G. Staminode.—H. Pistil.

upper Río Orinoco, probably at low elevation. There are no label data indicating habit, size, habitat, or other information. In Kopp's (1966) revision of the neotropical *Persea* species, *P. croizatii* keys to her section *Eriodaphne* because of its glabrous ovary. It does not seem closely related to any of the species of that section with appressed pubescence, consisting mostly of *P. caerulea* and its relatives, but instead resembles more closely species of section *Aurataea*, especially *P. nivea* Mez and

P. benthamiana Meissner. These species both have, however, whitish and more pubescent lower leaf surfaces and smaller flowers. The inflorescences of *P. benthamiana* are also only half as long as the leaves. In all three species, the inner stamens are longer than the outer ones, which is an unusual feature in *Persea*. Unfortunately, all three species are rarely collected, and I have only seen one collection of each. More collections are needed to elucidate the relationships between these three species, whose distributions are not widely separated from each other.

Persea fluviatilis van der Werff, sp. nov. TYPE: Venezuela. T. F. Amazonas: Depto. Río Negro, inundated forest along lower Río Baria, *G. Davidse 27717* (holotype, MO).

Arbor, ad 10 m. Ramuli crassi, fistulosi, hornotini pubescentes annotini glabri. Folia firme chartacea vel coriacea, elliptica vel anguste elliptica, 15–20 × 3.5–7.5 cm, basi acuta vel obtusa, apice acuta; plus minusve aggregata; nervis lateralibus 8–10, supra immersis, subtus elevatis; margine paulo recurvata. Petioli 2–3 cm longi, juvenales pubescentes, vetustiores glabri. Inflorescentiae axillares, foliis perbreviores, dense pubescentes. Flores viridi-lutei, fere sessiles. Tepala 6, subaequalia, extus dense pubescentia; tepala exteriora late ovata, intus glabra, ad 2.5 mm longa; tepala interiora late ovata, intus pubescentia, ca. 3.2 mm longa. Stamina 6 (series I et II), quadrilocellata, ca. 2.2 mm longa; filamentis pubescentibus, sensim in antheris glabris dilatatis; staminodia serei III ca. 1.9 mm longa, dense pubescentia, ad basim 2 glandulis praedita; staminodia serei IV sagittata, ca. 1 mm longa, dense pubescentia. Ovarium paucis pilis praeditum, ca. 0.8 mm diametro; stylo glabro, gracili, ca. 1.5 mm longo. Fructus globosus; tepala persistentia, patentia; pedicellum at maturitatem fructus incrassatum.

Tree, to 10 m. Twigs stout, terete, hollow, the leaf scars clustered, not evenly distributed along the twigs, older twigs glabrous, recent growth with rather dense, spreading pubescence. Leaves firmly chartaceous or coriaceous, elliptic or narrowly elliptic, 15–20 × 3.5–7.5 cm, apex acute, base acute or obtuse, ± clustered along the twigs; lateral veins 8–10 pairs, immersed on the upper surface, prominently raised on the lower surface, arching towards the tip of the leaf, not connected to the upper lateral vein; margin slightly recurved; upper leaf surface glabrous, lower leaf surface with some erect, gray hairs, these denser along midvein and lateral veins. Petioles 2–3 cm long, gray pubescent when young, glabrous in age. Inflorescences axillary, much shorter than the leaves, to 6 cm long, densely gray pubescent. Flowers greenish yellow or tawny, nearly sessile. Tepals 6, their outside surfaces completely covered by dense, gray pubescence, outer 3 tepals broadly ovate, ca. 2.5 mm long, glabrous inside, inner 3 broadly ovate, ca. 3.2 mm long, pubescent inside. Fertile stamens 6, representing the outer 2 whorls, ca. 2.2 mm long, the filament densely pubescent, ca. 1.2 mm long, gradually widened into and poorly differentiated from the glabrous anther; staminodia of whorl III ca. 1.9 mm long, densely pubescent and with 2 large, globose glands near the base, the tip not cordate or sagittate; staminodia of whorl IV ca. 1 mm long, densely pubescent, sagittate. Ovary with a few hairs, 0.8 mm diam., style glabrous, slender, ca. 1.5 mm long. Fruit globose, ca. 1.3 cm diam., with a glaucous bloom; tepals persisting in fruiting stage, spreading; pedicel in fruit strongly swollen, to 7 mm thick.

Paratypes. VENEZUELA. T. F. AMAZONAS: along Río Temi near Yavita, *Ll. Williams 14122* (F); same locality, *Bunting et al. 4041, 4050* (MY).

Persea fluviatilis is known only from periodically inundated forest in Territorio Federal Amazonas, Venezuela, at elevations of about 100 m. In Kopp's (1966) revision of the neotropical species of *Persea*, it keys to section *Heteranthera* because the stamens of whorl III are sterile. Within that section, it is closest to *P. meridensis*, a poorly known Andean species, which differs in its ferruginous pubescence, pedicelled flowers, and solid twigs. Unusual characters of *P. fluviatilis* are the subequal tepals, hollow twigs, clustered leaves, difference in pubescence between the young and old twigs, and swollen pedicels in fruit. Because many of the neotropical *Persea* species are infrequently collected and are poorly known, close relatives of this distinctive species have not been pinpointed. The swollen pedicels in fruit are a very unusual feature, but because there are only two fruiting collections known, it is possible that this condition is caused by a disease and is not typical for the species. At the time of her revision Kopp had only a fruiting collection of this species at hand, which she cited as *P. nivea* Mez, a species that does not occur in Venezuela.

Rhodostemonodaphne steyermarkiana (Allen) van der Werff, comb. nov. BASIONYM: *Ocotea steyermarkiana* C. K. Allen, Acta Bot. Venez. 2: 216. 1967.

Rhodostemonodaphne, as defined by Rohwer & Kubitzki (1985), includes a small number of species previously included in *Nectandra* or *Ocotea* and differing from *Nectandra* in being dioecious and in a general lack of papillose pubescence on the floral parts; they differ from *Ocotea* in having almost sessile anthers and the locelli ar-

ranged in an arc, not in two superposed rows. A study of the available collections of *O. steyermarkiana* shows that this species has all the characters of *Rhodostemonodaphne*, and therefore a new combination is made. I did not find that the outer stamens have distinct filaments and that the anther cells are arranged in two rows, as Allen described and illustrated. Pubescence and inflorescence type suggest that *R. steyermarkiana* is closely related to *R. celiana* (Allen) Rohwer and *Endlicheria vinotincta* Allen, both endemic to the Venezuelan Guayana. I include two collections from Cerro Sarisariñama, cited by Bernardi in Steyermark (1976) as *O. celiana* Allen and *O. ferruginea* (Meissner) Mez, in *R. steyermarkiana*.

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TAXONOMIC STUDIES IN THE MICONIEAE (MELASTOMATACEAE). III. CLADISTIC ANALYSIS OF AXILLARY-FLOWERED TAXA[1]

Walter S. Judd[2]

ABSTRACT

The axillary-flowered members of the Miconieae are hypothesized to be a monophyletic group, and the generic relationships within this group have been investigated by means of a preliminary cladistic analysis, which resulted in the following taxonomic conclusions. *Henriettea* is circumscribed broadly, including *Henriettella* and *Llewelynia*, as is *Loreya*, which is considered to include *Bellucia* and *Myriaspora*. The small genus *Kirkbridea* is likely the sister group of *Henriettea* sensu lato. *Clidemia* sect. *Calophysoides* and *Maieta* form a single clade and are considered congeneric. *Mecranium* (including *Ekmaniocharis*), *Killipia*, *Huilaea*, and the axillary-flowered 5- or 6-merous species of *Ossaea* all are considered generically distinct due to their isolated cladistic positions. Species of *Clidemia* sect. *Sagraea* along with *Necramium* and the axillary-flowered and 4-merous species of *Ossaea* are considered a distinct genus, *Sagraea*; an autapomorphy for this group was not consistently present in the generated cladograms, and the genus is considered metaphyletic. *Clidemia* sect. *Miconiopsis*, although usually considered axillary-flowered, actually has both terminal and axillary inflorescences and may be congeneric with *Miconia* (and likely is related closely to sect. *Tamonea*). Thus, axillary-flowered groups recognized at the generic level include: *Henriettea*, *Huilaea*, *Killipia*, *Kirkbridea*, *Loreya*, *Maieta*, *Mecranium*, *Pentossaea*, and *Sagraea*. Axillary-flowered Miconieae appear to form two major clades based primarily on the crystal type present in the leaf mesophyll and stem. Megastyloids (sometimes along with druses) occur in *Loreya*, *Kirkbridea*, and *Henriettea*, while only druses are found in the remaining genera. Cladistic relationships among the genera possessing only druse crystals are obscure, although *Huilaea* is probably basal within this complex, as reflected by its large flowers with well-developed pedicels, and *Sagraea* is likely most closely related to *Mecranium*, the two being linked by the synapomorphy of 4-merous flowers. Relationships of axillary-flowered taxa to those with terminal infloresences are discussed briefly.

The Miconieae Triana (Melastomataceae) are a diverse tribe of ca. 30 neotropical genera, including ca. 1,800 species. As discussed previously (Judd, 1986a), the genera within the tribe are poorly characterized, often difficult to discern, and defined quite arbitrarily (Cogniaux, 1891; Macbride, 1941; Gleason, 1932, 1958; Wurdack, 1972). In order to clarify relationships within this large and complex group, a preliminary cladistic analysis of the axillary-flowered taxa of Miconieae was conducted as reported here.

Within the Miconieae, the inflorescence may be either terminal or lateral. Plants with terminal inflorescences have hapaxanthic shoots in which the apical meristem of the shoot becomes wholly transformed into a flowering axis after a period of vegetative growth, while plants with axillary inflorescences have pleonanthic shoots in which the apical meristem continues its vegetative activity while producing lateral flowers or inflorescence axes (see Judd, 1986a; Weberling, 1988). Inflorescence position, along with the correlated characters of growth architecture, has been shown to be a valuable taxonomic character in the tribe and is usually uniform within sections or genera (Judd, 1986a).

The axillary-flowered condition is likely a derived state within the Miconieae because nearly all members of the Merianieae show terminal flowers. The latter tribe is a reasonable outgroup taxon considering possible tribal relationships suggested

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by J. Wurdack (Welle & Koek-Noorman, 1981). The same conclusion would be reached through the use of a generalized melastomataceous outgroup and the tree counting algorithm of Frolich (1987), since terminal cymose inflorescences are the strongly predominant condition within non-Miconieae melastomes. Terminal inflorescences occur in over 80% of non-Miconieae genera, and strongly predominate in all tribes except the Blakeeae Benth. & Hook. f. In addition, Weberling (1988) noted that all melastomes show monotelic inflorescences, with the basic form being a pleiothyrsoid terminating a leafy shoot. In this study the monophyly of the axillary-flowered Miconieae was accepted as a useful preliminary hypothesis and a cladistic analysis of these taxa was conducted. The results of this analysis are then used to suggest generic realignments and to reevaluate the preliminary hypothesis of monophyly of the axillary-flowered taxa.

Cladistic Analyses

METHODS

The cladistic analyses were conducted using the Wagner parsimony algorithm (with global branch-swapping and multiple parsimony options) of the PAUP (i.e., Phylogenetic Analysis Using Parsimony, Version 2.4; Swofford, 1985) package of computer software.

Fifteen Evolutionary Units (EUs) were used in most of the analyses (Table 1), based on a survey of ca. 370 herbarium specimens representing 150 species (and supplemented, where possible, by the addition of information from recent taxonomic studies). Several taxa also were studied during the course of fieldwork in Haiti, the Dominican Republic, Puerto Rico, and Jamaica. In some analyses, an additional EU representing either a generalized terminal-flowered taxon or *Clidemia* sect. *Miconiopsis* Cogn. was used. Although terminal-flowered, *Clidemia* sect. *Miconiopsis* has been considered to be related to the other sections of *Clidemia* included in this study, and its inclusion in a few analyses was designed to test this hypothesis. The inclusion of a generalized terminal-flowered taxon in some analyses was designed, in a very preliminary way, to evaluate the hypothesis that the axillary-flowered Miconieae are monophyletic. Placement of this generalized terminal-flowered taxon is considered very tentative because this EU is extremely heterogeneous, making the determination of its ancestral character states problematic (see Table 1).

Forty-two characters were used and assigned plesiomorphic (ancestral: scored as 0) and apomorphic (derived: scored as 1) states (Table 1). Apomorphic features used in the computer analyses are listed below. Nearly all characters were polarized using the Merianieae as an outgroup, with character states uniformly found (or, for a few characters, those states most commonly represented) in the out-group considered plesiomorphic (Stevens, 1980; Wheeler, 1981; Wiley, 1981; Maddison et al., 1984; Frolich, 1987). When EUs are polymorphic for a given character, an estimate of the ancestral condition was made. The states of a few characters were unknown for certain taxa, and these are scored as "missing data," indicated by a "?" in the data matrix (Table 1). Trees were rooted by using a hypothetical ancestor with all characters scored as plesiomorphic.

APOMORPHIC CHARACTERS

1. Stems quandrangular and 4-winged/ridged; plesiomorphic condition: stems ± terete. Quadrangular stems are considered an autapomorphy of *Killipia* Gleason and occur in *K. quadrangularis* Gleason (the type species). However, two other species have terete stems, and the ancestral condition within *Killipia* is not known. A coding of "0" for this EU would not affect the analyses because the feature is autapomorphic.

2. Growth pleonanthic (indeterminate); plesiomorphic condition: growth hapaxanthic (determinate). (See character 12.)

3. Megastyloid crystals present; plesiomorphic condition: only small styloids and/or druse crystals present. (See character 4.)

4. Crystals exclusively druses; plesiomorphic condition: small or large styloids and druse crystals present. The polarity of characters 3 and 4 was determined by using the Crypteroniaceae (Dahlgren & Thorne, 1984) as an outgroup (see discussion in Johnson & Briggs, 1984; Vliet et al., 1981). This family, which is closely related to the Melastomataceae, contains genera with druses and with small styloids (Baas, 1981), and this crystal complement is taken as the ancestral condition in melastomes. It is likely that megastyloids have evolved in a few lineages (sometimes with the loss of druses), while styloids have been lost in other lineages, resulting in druses being the only crystal type in those groups. That styloids and druses are known from more distantly related families of Myrtales, such as Myrtaceae and Combretaceae (Vliet & Baas, 1984) supports this polarity. Variation in crystal complement within the Merianieae is poorly known.

5. Elongate multicellular hairs absent; plesio-

TABLE 1. Character divergence values for taxa used in cladistic analyses. Taxon names abbreviated by first four letters of genus name, except *Henriettea* (HENT), *Henriettella* (HENL), *Clidemia juruensis* (CJUR), generalized terminal-flowered taxon (TERM). An asterisk indicates that the opposite state occurs in some species of that taxon; a question mark indicates that the character state is in doubt or unknown.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
MECR	0	1	0	1	1	0	1	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0*	0	0	1	0	0	0	0	0	0	0	1	0	0
SAGR	0	1	0	1	0	0	0	0	0*	0	0	1	0*	1	1	0	1	0	1	0	0	0	0	0	0*	0	0	0	0*	0*	0	0	0	0	0	0	0	0	0	1	0	0
KILL	1*	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	?	?
PENT	0	1	0	1	0	0	0	0	0	0	0	1	0*	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0*	0	0	0	0	0	0	0	0	0	1	?	?
HUIL	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	?
MAIE	0	1	0	1	0	0	0	0	1	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0?	0?
CALO	0	1	0	1	0	0	0	0	1	1	0	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	?	?
CJUR	0	1	0	1	0	0	0	0	0	1	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	?	?
HENT	0	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0*	0	0	0	0	0	0	0	0	0	0	0*	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0
HENL	0	1	1	0	0	1	0	0	0	0	0	1	1	0	0*	0	1	0	0	0*	0	0	0	0	0*	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0
LLEW	0	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	0	0	1	?	?
KIRK	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0*	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	?	?
LORE	0	1	1	0	0*	0	0	0	0	0	0	1	0*	0	0	0*	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1*	0	0	1	0	0	0	1	0	1	0	1
BELL	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1*	0	0	1	0	0	0	1	0	1	0	1
MYRI	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	1	1	0	1
MICO	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	?	?
TERM	0	0	0	1	0*	0	0	0	0*	0*	0	0	0	1	0*	0*	0*	0*	0*	0	0*	0	0*	0	0	0*	0	0	0*	0	0*	0	0	0	0	0	0	0	0	1	0	0

morphic condition: elongate multicellular hairs present, often strigose. *Mecranium* Hook. f. and *Killipia* are unique in lacking a well-developed indumentum. A few species of *Loreya* DC., e.g., *L. ovata* Berg ex Triana, *L. arborescens* (Aublet) DC., and *L. nigricans* Triana, lack such hairs as well. Renner (in press) hypothesized the loss of strigose hairs to be a synapomorphy of a species group within *Loreya*. Thus, the presence of such hairs is considered the ancestral condition within the genus.

6. Multicellular hairs elongate with radiate to stellate-globular basal portion (or clearly derived types); plesiomorphic condition: multicellular hairs various, but not as above. This distinctive hair morphology is much modified (see discussion, and Judd, 1986b) in a few species, but such extremes are connected by intermediate types, sometimes even on the same plant.

7. Multicellular hairs minute, globular, and unbranched to irregularly branched and matted (not strigose); plesiomorphic condition: multicellular hairs various but not as above. This character is limited to *Mecranium* (including *Ekmaniocharis* Urban) and *Ossaea acuminata* DC. The feature is important in determining that *Mecranium* spp., *Ossaea acuminata*, and *Ekmaniocharis crassinervis* Urban form a monophyletic group but does not help in inferring relationships among the EUs.

8. Multicellular hairs conspicuously stellate (with stalk and elongated arms); plesiomorphic condition: multicellular hairs various but not as above. In these analyses this feature is considered an autapomorphy of *Clidemia* sect. *Miconiopsis*. Very similar hairs occur in many terminal-flowered species, e.g., *Miconia* sects. *Jucunda* (Cham.) Naudin and *Tamonea* (Aublet) Cogn.

9. Leaves clearly anisophyllous; plesiomorphic condition: leaves isophyllous or nearly so. A few specialized species of *Clidemia* sect. *Sagraea* (DC.) Cogn. have anisophyllous leaves. The isophyllous condition is considered ancestral within *Clidemia* sect. *Sagraea*, following a preliminary analysis of variation within the group.

10. Leaves with pair of pouchlike formicaria at base of blade; plesiomorphic condition: leaves lacking formicaria. Similar ant-domatia that occur in terminal-flowered taxa, e.g., *Tococa* Aublet, *Clidemia* D. Don, *Myrmidone* Mart., probably evolved independently (see discussion). *Ossaea bullata* (Pilger) Gleason, possibly a member of the *Sagraea* group, has been reported to possess similar formicaria (Whiffin, 1972).

11. Cuticle of abaxial leaf epidermis papillose; plesiomorphic condition: epidermis nonpapillose. Renner (in press) pointed out that this feature correlates well with cuticle thickness and suggested that the character has important ecological consequences.

12. Inflorescences axillary (in leaf axils or at nodes on old wood); plesiomorphic condition: inflorescences terminal. Terminal cymose inflorescences (as discussed above) occur in over 80% of genera within non-Miconieae melastomes. Thus, proliferating inflorescences (in which the terminal axis returns to vegetative growth, producing axillary buds that develop vegetative branches instead of flower-bearing paracladia—see Weberling, 1988) are considered derived. The process of proliferation results in a vegetative shoot in which the flowers are borne in axillary cymose paracladia. Delayed anthesis of the paracladia can even result in cauliflory.

13. Inflorescences fasciculate; plesiomorphic condition: inflorescences cymose. Although fascicles occur in a few species of *Loreya*, *Clidemia* sect. *Sagraea* (including axillary, 4-merous species of *Ossaea* DC.), and the 5-(6-)merous species of *Ossaea*, cymose inflorescences are considered to be the ancestral condition in these groups. Renner (in press) also considered fasciculate inflorescences to be derived within *Loreya*.

14. Flowers more or less sessile; plesiomorphic condition: flowers pedicellate.

15. Flowers 4-merous; plesiomorphic condition: flowers other than 4-merous. (See character 16.)

16. Flower parts frequently more than 5; plesiomorphic condition: flowers 4- or 5-merous. Generally, 5-merous flowers are considered primitive, with higher and lower floral numbers treated as derived. *Henriettea* DC. and *Loreya* contain a few species with numerical plans greater than five, while *Henriettella* Naudin and *Kirkbridea* Wurdack contain a few species with 4-merous flowers. Within each of these genera, 5-merous flowers are considered ancestral. Renner (in press) considered floral numbers greater than five to be derived and used this feature to link some species of *Loreya* with *Bellucia* Raf. The ancestral condition in *Kirkbridea* is in doubt; however, recoding the state of this EU as "1" for this character does not change the topology of the discovered cladograms.

17. Flowers small; plesiomorphic condition: flowers moderate to large.

18. Hypanthium strongly ribbed; plesiomorphic condition: hypanthium nonribbed. This character is an autapomorphy of *Clidemia* sect. *Calophysoides* Cogn.

19. External calyx lobes more or less conspicuous and well developed; plesiomorphic condition: external calyx lobes absent or inconspicuous.

20. External calyx lobes absent; plesiomorphic

condition: external calyx lobes present. Some species of *Henriettella* have lost external calyx lobes independently of the loss in *Loreya*, *Bellucia*, and *Myriaspora* DC. This was determined because it is evident that *Henriettella* evolved out of a group within *Henriettea*, which has external calyx lobes.

21. Internal calyx lobes very elongate and closely associated with external lobes; plesiomorphic condition: internal calyx lobes not elongate, variously developed but not closely appressed to internal lobes. This feature is an autapomorphy of *Killipia*.

22. Internal calyx lobes connate into a membranous, dome-shaped, apiculate cap that ruptures irregularly at anthesis; plesiomorphic condition: internal calyx lobes free. This character is an autapomorphy of *Mecranium* (including *Ekmaniocharis*). Although *Ossaea acuminata* has somewhat caplike calyx lobes, they are only partially connate. The internal calyx lobes are free and imbricate at their extreme apices. This species is included within the *Mecranium* EU since it has the other apomorphies of this clade (characters 7, 19, and 32; see discussion).

23. Internal calyx lobes circumscissilly dehiscent (and noncalyptrate); plesiomorphic condition: internal calyx lobes more or less persistent, or if circumscissile, then calyptrate. This character is considered an autapomorphy of *Clidemia* sect. *Miconiopsis*, although a similar condition is seen in *Miconia* sects. *Tamonea* and *Jucunda* (a group included within the generalized terminal-flowered taxon).

24. Buds closed, with thick triangular calyx lobes that cover bud up to the final stage prior to anthesis (and sometimes fused into a cap); plesiomorphic condition: buds open, calyx lobes of variable shape and thin, the petals exposed much before anthesis. This feature is an autapomorphy of *Bellucia*.

25. Internal calyx lobes reduced to a more or less smooth rim; plesiomorphic condition: internal calyx lobes clearly evident. This is a noninformative character (see Table 1) because it is found only in a few derived species within *Henriettella* and *Clidemia* sect. *Sagraea*.

26. Internal calyx lobes fused into a conical, apically closed calyptra and conspicuously strigose; plesiomorphic condition: internal calyx lobes noncalyptrate (or if so, then not as above). This is an autapomorphy of *Myriaspora*.

27. Internal calyx lobes fused into an apically open cap (opening into sepal-like segments or circumscissilly); plesiomorphic condition: internal calyx lobes noncalyptrate (or if so, then not as above). This feature is limited to *Llewelynia* Pittier and a few (probably related) species of *Henriettea* (see discussion).

28. Calyx a cap open at apex and falling off by circumscissile slit; plesiomorphic condition: calyx not open-calyptrate, or if so, then opening by longitudinal slits into triangular sepal-like segments. This character is an autapomorphy of *Llewelynia* and is a further specialization of character 27.

29. Petals narrowly triangular and more or less acute at apex; plesiomorphic condition: petals ovate to elliptic (or obovate) with blunt to more or less acuminate apices. Preliminary analyses of variation within *Mecranium* (including *Ekmaniocharis*) and *Clidemia* sect. *Sagraea* (including axillary, 4-merous species of *Ossaea*) have led to the conclusion that ovate to elliptic petals with more or less acuminate to blunt apices constitute the ancestral condition within these groups. Obovate petals have evolved within a group of *Mecranium* species. It is noteworthy that *Ossaea acuminata*, a narrow-petaled species, is a sister species to *Mecranium amygdalinum* (Desr.) C. Wright in Sauv., a fairly blunt-petaled species (Skean, in prep.).

30. Petals with a dorso-apical tooth; plesiomorphic condition: petals lacking a dorso-apical tooth. This feature occurs in a few species of *Clidemia* sect. *Sagraea* (including the species of *Ossaea* with axillary, 4-merous flowers) and in the 5- or 6-merous species of *Ossaea*. A scoring of "1" for this character in these two EUs does not alter their placement in relation to the very different *Henriettea* group.

31. Petals usually pubescent, sometimes only with very few hairs near apex; plesiomorphic condition: petals glabrous (or with a single apical hair). Hairs on the petals have been lost in a few species of *Loreya* and *Bellucia*.

32. Androecial fringe present; plesiomorphic condition: androecial fringe absent. This feature is a strong and consistent synapomorphy of *Mecranium* species, including *Ekmaniocharis crassinervis* and *Ossaea acuminata*.

33. Anthers with two well-developed dorso-basal projections; plesiomorphic condition: anthers various but lacking two well-developed dorso-basal projections.

34. Anthers usually robust and fleshy, opening by one or two minute pores; plesiomorphic condition: anthers not robust and fleshy, various.

35. Anther sacs basally bifurcate, i.e., sagittate; plesiomorphic condition: anther sacs not bifurcate at base.

36. Anther sacs more or less wrinkled; plesiomorphic condition: anther sacs smooth. The best expression of this feature is in *Maieta* Aublet.

37. Stamens numerous, i.e., more than twice

the number of petals; plesiomorphic condition: stamens twice the number of petals. This is an autapomorphic character of *Llewelynia*.

38. Stigma very conspicuously and radiately ridged; plesiomorphic condition: stigma not radiately ridged.

39. Placenta highly divided; plesiomorphic condition: placenta undivided or nearly so. This is an autapomorphy of *Myriaspora*.

40. Fruit a berry; plesiomorphic condition: fruit a capsule.

41. Chromosome number of $n = 28$; plesiomorphic condition: $n = 17$ (or 15, 20). (See character 42.)

42. Chromosome number of $n = 15, 20$; plesiomorphic condition: $n = 17$ (or 28). The terminal-flowered Miconieae were used as a generalized outgroup for the determination of polarity of the incompletely known characters 41 and 42.

RESULTS

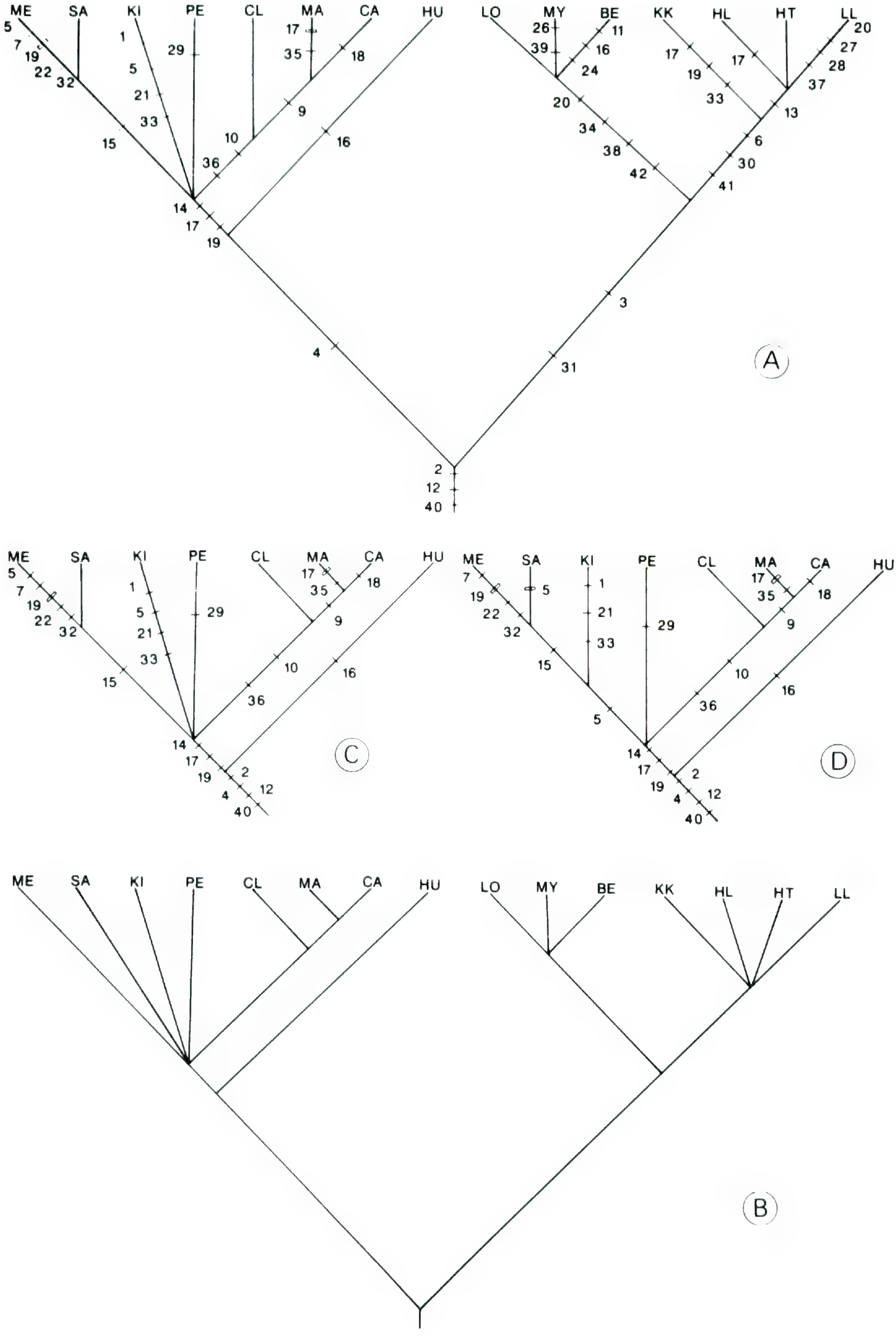
Initial computer runs using the entire data set for the 15 axillary-flowered EUs resulted in the discovery of 100+ equally parsimonious trees (but only 15 different topologies when multi-furcations are taken into account), all with a length of 28 steps and a consistency index of 0.714 (or 48 steps and consistency index of 0.813 when autapomorphies and uniform characters were included). The strict consensus tree resulting from this analysis is presented in Figure 1B. In addition a tree indicating character state changes is presented (Fig. 1A). This tree is preferred due to its pattern of character variation, especially the linking of *Mecranium* and *Clidemia* sect. *Sagraea* on the basis of 4-merous flowers (15), and the linking of *Henriettea*, *Henriettella*, and *Llewelynia* on the basis of fasciculate inflorescences (13). The relationships of the EUs representing *Loreya*, *Bellucia*, *Myriaspora*, *Henriettea*, *Henriettella*, and *Llewelynia* did not vary in any of the trees generated by PAUP. In addition, *Kirkbridea* consistently linked with *Henriettea*, *Henriettella*, and *Llewelynia*, in some trees as the cladistically basal member of this clade, in others as the sister group of *Henriettella*. In all trees, the EUs representing *Maieta*, *Clidemia* sect. *Calophysoides*, and *Clidemia juruensis* (Pilger) Gleason were always joined, and *Huilaea* Wurdack was always the basal member of the clade representing taxa with only druse crystals. Thus the large number of generated trees is due to the numerous possible topologies among the remaining EUs in the analyses, i.e., *Mecranium* (including *Ekmaniocharis* and *Ossaea acuminata*), *Clidemia* sect. *Sagraea* (including *Necramium* Britton and axillary 4-merous species of *Ossaea*), *Killipia*, and *Pentossaea*, here described to include the axillary-flowered, 5-merous (or less commonly 6-merous) species of *Ossaea*.

Thus, several analyses were conducted using just those EUs possessing only druse crystals (i.e., top eight EUs listed in Table 1) with characters not pertaining to this complex deleted. These analyses generated 45 equally parsimonious trees (but comprising only seven different tree topologies) of 11 steps and with a consistency index of 0.727 when all characters were weighted equally (or of 25 steps and a consistency index of 0.880 when autapomorphies and uniform characters were included). However, when the apomorphy of 4-merous flowers was stressed (weighted by 2, as seems reasonable, since this character is quite uniform within EUs under investigation), only 15 trees (representing only two topologies) were produced, all with 12 steps and a consistency index of 0.750 (or of 26 steps and a consistency index of 0.889 when autapomorphies and uniform characters were included). The consensus tree resulting from the analysis in which all characters are weighted equally is identical to that produced in the analysis of all axillary-flowered taxa (Fig. 1B). Both cladograms resulting from the weighted-character analysis are given in Figure 1C and D.

When an EU representing a generalized terminal-flowered taxon is included in the analysis, over 100 equally parsimonious trees were found, all with a length of 32 steps and a consistency index of 0.688 (or of 50 steps and a consistency index of 0.780 when autapomorphies and uniform characters were included). These trees are very similar to those generated in the analyses involving only axillary-flowered taxa (Fig. 1), and the four different topologies involving their basal branches are presented in Figure 2, illustrating the various positions of the genus *Huilaea* and a generalized terminal-flowered taxon. When *Clidemia* sect. *Miconiopsis* (another taxon producing terminal inflorescences) is included in the analysis, many trees are again generated (of 55 steps and a consistency index of 0.745, including autapomorphies), all linking this entity with either *Killipia* or a clade containing *Killipia*, *Clidemia* sect. *Sagraea*, and *Mecranium*.

DISCUSSION

The cladograms presented in Figures 1 and 2 indicate that the axillary-flowered Miconieae are divided into two major clades. The first is composed of those taxa containing megastyloids (3) in their leaf and stem tissues (often with druse crystals as well) and usually possessing slightly pubescent petals (31). The group also generally has distinctly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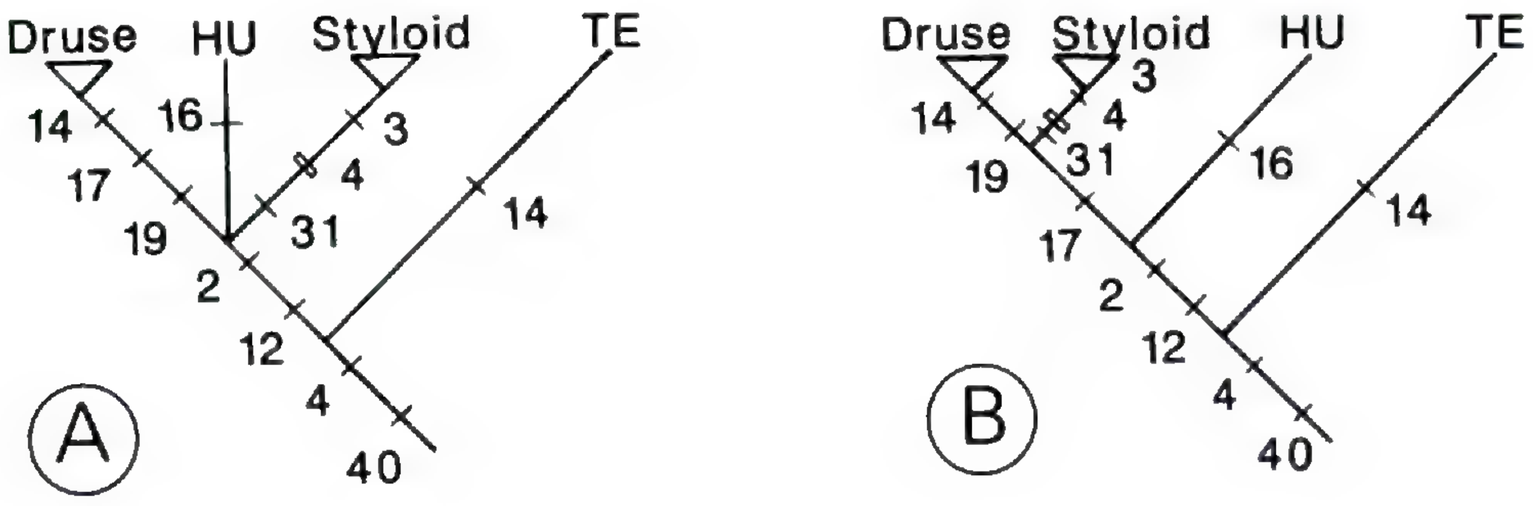

FIGURE 2. Basal portion of cladograms resulting from analysis of axillary-flowered taxa and generalized terminal-flowered taxon, all of 50 steps, consistency index = 0.78. Reversals indicated by open bars. Taxon abbreviations: *Huilaea* (HU), exclusively druse-containing group (Druse), megastyloid-containing group (Styloid), and generalized terminal-flowered taxon (TE). *These characters could also have evolved independently in basal members of megastyloid- and druse-containing lineages (see text).

pedicellate flowers. This clade may be divided into two clearly marked subgroups based on vegetative and reproductive characters. *Loreya*, *Bellucia*, and *Myriaspora* are united by the synapomorphies of flowers lacking external calyx lobes (20), possessing robust fleshy anthers (34), an expanded and radiately ridged stigma (38), and a chromosome number of $n = 15$ or 20 (42). In contrast, *Henriettea*, *Henriettella*, *Llewelynia*, and *Kirkbridea* form a clade based upon the presence of multicellular strigose hairs with a stellate, radiate, irregularly branched, or suprabasally expanded base, or hair types clearly modified from these conditions (6), petals with an apical apiculum on the abaxial surface (30), and a chromosome number of $n = 28$ (where known, 41). *Kirkbridea* likely is cladistically basal in this group, with *Henriettea*, *Henriettella*, and *Llewelynia* being united by the additional synapomorphy of fasciculate inflorescences (13). (It should be noted that parallelism in flower size (17) occurs within these genera, which is not surprising considering the variability of this feature within the tribe. Linking *Kirkbridea* and *Henriettella* on the basis of this character is considered implausible.)

The remaining taxa included in the analysis form a second clade based on the following synapomorphies: presence of only druse crystals in leaf and stem tissues (4), small more or less sessile flowers (17, 14), and usually well-developed external calyx lobes (19). The extremely isolated genus *Huilaea* probably is basal within this clade (Fig. 1A, B) because it shows only the synapomorphy of exclusive presence of druse crystals (4), having large and clearly pedicellate flowers. The relationships among the taxa comprising this clade are not well resolved. However, it is clear that *Maieta*, *Clidemia* sect. *Calophysoides*, and *C. juruensis* form

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FIGURE 1. Cladograms resulting from PAUP analyses.—A. Preferred tree resulting from analysis of all axillary-flowered taxa, 48 steps, consistency index = 0.813.—B. Consensus tree.—C, D. Cladograms resulting from PAUP analyses of taxa containing only druse crystals—two 26-step trees generated in analysis weighting character 15; topology C equals consensus tree of this analysis. Reversals indicated by open bars; taxa abbreviated by first two letters of generic or sectional name, except *Henriettea* (HT), *Henriettella* (HL), and *Kirkbridea* (KK).

a monophyletic group based on the presence of morphologically very similar pouchlike ant-domatia (formicaria) at the base of the leaf blade (10) and wrinkled anthers (36). In addition, *Maieta* and *Clidemia* sect. *Calophysoides* have anisophyllous leaves (9). If the character of 4-merous flowers is stressed, then *Mecranium* is probably most closely related to *Clidemia* sect. *Sagraea*, and the two may be linked by this feature (15). Linking *Killipia* with *Sagraea* and *Mecranium* in some trees on the basis of the shared loss of strigose hairs (5) probably has little phylogenetic significance.

The terminal-flowered taxa of Miconieae may be a paraphyletic or monophyletic group basal to all the axillary-flowered taxa (Fig. 2A–C) or a possible sister taxon to the taxa containing only druses (Fig. 2D). In the first alternative, the axillary-flowered condition evolved just once and serves as a synapomorphy of all axillary-flowered Miconieae; in the second, axillary arrangements are hypothesized to have evolved in the druse and megastyloid clades independently (or, less likely, evolved in the stem lineage of the entire tribe with a reversal to terminal cymes occurring in the ancestor of *Miconia* and relatives). The possible polyphyly of the axillary-flowered Miconieae clade will be investigated more thoroughly in a later paper. It is certainly possible that *Miconia* and relatives are more closely related to the axillary-flowered "druse-containing" genera than initially hypothesized.

When an EU representing a generalized terminal-flowered taxon is included in the analysis, the position of *Huilaea* in the cladograms becomes more variable than in the initial analyses (compare Figs. 1 and 2). This variability may reflect the presumed phylogenetic isolation of this genus. It seems more reasonable to link *Huilaea* with *Mecranium*, *Clidemia* sect. *Sagraea*, *Maieta*, and *Killipia* on the basis of the presence of only druse crystals in its tissues (4) than with *Loreya*, *Henriettea*, and *Kirkbridea* on the basis of a reversal to pedicellate flowers (14) (Fig. 2).

The presence of both terminal and axillary flowers in *Clidemia* sect. *Miconiopsis* (Cogniaux, 1888, 1891) is not surprising (see Judd, 1986a, for discussion of similar variation evident in *Miconia*, especially in sects. *Octomeris* (Naudin) Benth. & Hook. and *Tamonea*; and Troll, 1964, and Weberling, 1965, 1988, for more general discussion of inflorescence structure and position). Wurdack's suggestion (pers. comm.) that this group is closest to *Miconia* is likely correct. Note especially the similarity in stellate indumentum (8; Fig. 4) and circumscissilly dehiscent calyx (23). The section may be quite close to *Miconia* sects. *Tamonea* and *Jucunda*. The linking of *Clidemia* sect. *Miconiopsis* with *Killipia* or a clade containing *Killipia*, *Clidemia* sect. *Sagraea*, and *Miconia* in the cladistic analysis probably is due to homoplasy in several fairly weak characters, e.g., loss of strigose hairs (5), or to several potential synapomorphies between the axillary-flowered taxa containing only druse crystals and *Miconia* (and relatives), e.g., more or less sessile flowers (14) or well-developed external calyx lobes (19).

In spite of the necessarily preliminary nature of these cladistic analyses, their results help determine the previously confused generic limits within this difficult tribe (see also Judd, 1986a, b). In interpreting these results, I have attempted to delimit monophyletic and phylogenetically equivalent genera within the tribe that are recognizable on the basis of several morphological characters. Thus *Huilaea*, *Mecranium* (including *Ekmaniocharis* and *Ossaea acuminata*), *Killipia*, *Maieta* (including *Clidemia* sect. *Calophysoides* and *C. juruensis*), *Loreya* (including *Bellucia* and *Myriaspora*), *Henriettea* (including *Henriettella* and *Llewelynia*), and *Kirkbridea* are considered to be generically distinct. In addition, *Clidemia* sect. *Sagraea* (including *Necramium* and the species of *Ossaea* with axillary 4-merous flowers) is recognized at the generic level. Finally, the species of *Ossaea* with axillary 5- (or 6-)merous flowers are in need of generic recognition and are described herein as *Pentossaea*. The systematics of each of these taxa is discussed briefly below.

Discussion of axillary-flowered genera. *Loreya* is clearly delimited by its distinctive usually robust fleshy anthers (34), expanded and radiately ridged stigma (38), lack of external calyx lobes (20), and range of chromosome numbers (42, see Solt & Wurdack, 1980). The group possesses megastyloids in its leaf and stem tissues (pers. obs.; Baas, 1981) and is clearly monophyletic. However, if *Bellucia* and *Myriaspora* are segregated as separate genera, the result is a paraphyletic *Loreya* (Fig. 1). *Bellucia* is characterized by papillose abaxial leaf cuticle (11), closed buds (24), i.e., the buds have thick calyx lobes that cover the buds up to the final stage prior to anthesis (and are even fused into a cap in a few species, e.g., *Bellucia dichotoma* Cogn. and *B. acutata* Pilger), and tendency for floral merosities greater than five (16) (see Renner, in press). In contrast, *Myriaspora* is characterized by its highly divided placentae (39), calyx lobes fused into an unusual cap (26, which is probably not homologous with the cap of some species of *Bellucia*), and long hairs on the abaxial

surface of its petals. In addition, *Myriaspora* produces inflorescences in the leaf axils (as do several species of *Bellucia*), while the usual condition in *Loreya* is to have the inflorescences lateral on leafless nodes below the leaves; it should be noted, however, that this character is often variable within a genus (Judd, 1986a; Renner, in press).

No autapomorphies are evident for *Loreya* when certain species are segregated as either *Bellucia* or *Myriaspora* (Fig. 1). The paraphyly of *Loreya* is made even more apparent when it is realized that *Loreya subrotundifolia* (Wurdack) S. Renner and *L. riparia* S. Renner link with *Bellucia* on the basis of higher numbers of floral parts and that *L. mespiloides* Miq., *L. spruceana* Benth. ex Triana, and *L. klugii* S. Renner link with *Myriaspora* on the basis of testa characters and one-pored anthers (Renner, in press).

Thus, recognition of *Bellucia* and *Myriaspora* distorts the best estimate of phylogenetic structure currently available for this group of species. Their recognition is also doubtful on purely phenetic grounds, since the patristic distances separating *Bellucia* and *Myriaspora* from the cladistically related taxa within a narrowly delimited *Loreya* are comparable to those separating other clades within *Loreya* (Renner, in press). Thus, as is characteristic of traditional taxonomic procedure (see Stevens, 1984, 1986), recognition of *Bellucia* and *Myriaspora* can only be justified by selective weighting of certain features (in this case the characters of cuticular papillae, bud structure, placental form, and inflorescence position) due to their supposed greater ecological significance. I see no reason to weight these characters more than any others used in these analyses. The decision to recognize a broadly circumscribed *Loreya* is not new; Baillon (1877) also considered *Bellucia* and *Loreya* congeneric (although only few species were known to him), and Macbride (1941: 497) considered this treatment "preferable it seems . . . to 'straining at a gnat' to keep them apart." Gleason (1932) considered the genera only "weakly separated"; however, they were maintained as distinct by Wurdack (1973, 1980) and Renner (in press).

Henriettea is easily recognized by its usually fasciculate inflorescences (13), distinctive indumentum of elongate multicellular hairs with an expanded, radiate to globular-stellate basal portion (or easily derived types, such as stellate-hairs, peltate-scales, elongate hairs with numerous small mainly basal projections, elongate hairs with a suprabasal expanded region and a narrowed basal attachment, or hairs very reduced, e.g., *Henriettella caudata* (DC.) Naudin, *H. glabra* Cogn.; see Wurdack, 1986) (6), petals with a minute dorsoapical apiculum (30), and chromosome number of $n = 28$ (41, Solt & Wurdack, 1980). Fasciculate inflorescences have evolved independently in a few species of *Loreya* (Renner, in press), and the inflorescences of *Henriettea squamulosa* (Cogn.) W. Judd have reverted to a pedunculate condition (Judd, 1986b). *Henriettea* is clearly monophyletic and shows the presence of calcium oxalate megastyloids (similar in structure to those of *Loreya*) in its leaf and stem tissues (pers. obs.; see also Welle & Mennega, 1977; Welle & Koek-Noorman, 1981; Baas, 1981).

As with *Loreya*, problems of paraphyly occur when *Llewelynia* and *Henriettella* are recognized as distinct from *Henriettea* (Fig. 1). *Llewelynia* is phenetically distinctive (Pittier, 1939; Wurdack, 1973) and easily recognized by its loss of external calyx lobes (20), open calyx cap that opens by a circumscissile slit (27, 28), and numerous stamens (37), while *Henriettella* is only marginally separable due to its smaller flowers (17) and tendency to have shorter anthers that open by larger, gaping pores (see Wurdack, 1973, 1980). A nearly obsolete internal calyx has evolved in a few species of *Henriettella*, e.g., *H. sessilifolia* (L.) Triana, and in many species the internal calyx lobes are not well developed. *Henriettea* and *Henriettella* were considered congeneric by Macbride (1941: 500), who stated that "there seems to be no significant concomitance of the characters of petals, anthers or pubescence that have been used to maintain two similar but distinct genera." He added that "the characters moreover often exist in degrees of development." Richard A. Howard also will consider *Henriettea* and *Henriettella* to be congeneric in his Lesser Antilles flora (pers. comm.). Wurdack (1972: 418) maintained these genera but noted that "a generic transition zone exists between *Henriettella ovata* Cogn. and *Henriettea patrisiana* DC., with *Henriettella parviflora* (Griseb.) Triana perhaps not distinct from the latter."

The genera differ in flower size, anther characters, and indumentum, but intermediates exist. Not surprisingly, there are no autapomorphies for *Henriettea* when defined narrowly, and its species certainly intergrade with *Henriettella*.

The floral buds of some other species of *Henriettea* (e.g., *H. spruceana* Cogn., *H. succosa* (Aublet) DC., *H. stellaris* Berg ex Triana, and *H. ramiflora* (Sw.) DC.) possess an expanded and open cap formed by the inner calyx lobes very similar to (and likely homologous with) that of *Llewelynia*, although opening longitudinally rather than cir-

cumscissilly. These species are likely basal members of the clade leading to *Llewelynia*. It is of interest that Wurdack (1973) suggested a similarity in general facies between *Llewelynia* and *Henriettella*, and Welle & Koek-Noorman (1981) reported similarity in wood anatomical characters between *Llewelynia* and *Henriettella*. It thus seems best to recognize a broadly defined, and monophyletic *Henriettea* by including both *Henriettella* and *Llewelynia* within it.

Kirkbridea clearly is related closely to *Henriettea* s.l. (Fig. 1). *Kirkbridea* (Wurdack, 1976) is quite distinctive due to its pedunculate inflorescences and anthers with two well-developed dorsobasal projections (33). *Kirkbridea* and *Henriettea* show variation in number of floral parts.

Huilaea is evidently very isolated, as Wurdack (1957, 1976) suggested at the time of his description of the genus. It clearly is distinct generically and is recognizable due to its pendent, three-flowered cymose inflorescences with very long peduncles and large, clearly pedicellate, 6-merous flowers.

Maieta, defined broadly, is a monophyletic group best recognized by its characteristic pouchlike formicaria at the base of its leaf blades (10) (Fig. 3; see discussion of morphology, development, and ecological functions of these structures in Gleason, 1931; Schnell, 1967; Whiffin, 1972; Neto & Asakawa, 1978; Benson, 1985). It should be noted that ant-domatia of various types undoubtedly have evolved independently in a few to many species of several other genera (e.g., *Sagraea* DC., *Tococa*, *Clidemia*, *Henriettea*, and *Conostegia* D. Don), and additional developmental studies are necessary in order to determine appropriate homologies of such structures within the tribe. The presence of structurally and positionally very similar pouchlike ant-domatia is accepted as a provisional synapomorphy of *Maieta* s. str. and *Clidemia* sect. *Calophysoides* until such developmental investigations are conducted. The group also tends to have slightly wrinkled anthers (36) and clearly anisophyllous leaves (9). Druses are the only crystals known in this group. The species of *Maieta* (defined narrowly—see Aublet, 1775; Wurdack, 1980) have sagittate anthers (35) and show a reversal toward large flowers (17), while those of *Clidemia* sect. *Calophysoides* have a distinctly ribbed hypanthium (18). Both, along with possibly a few other species of *Clidemia*, such as *C. juruensis*, are considered congeneric. The close relationship between these species of *Clidemia* with pouchlike formicaria and the phenetically similar species of *Maieta* has long been recognized. Macbride (1941: 479) remarked that "*Clidemia* remains . . . a concept rather arbitrarily retained but conveniently so on account of *Maieta* (in which Baillon, Hist. Pl. 7: 56. 1880 rightly merged it) being the older name." I agree and here consider *Maieta* to be congeneric with *Clidemia* sect. *Calophysoides* (and *C. juruensis*).

Killipia (Fig. 4) is a distinctive genus not easily confused with any other in the complex of genera possessing only druse crystals. Noteworthy apomorphies are the very long internal calyx lobes with closely associated external calyx lobes (21) and distinctive anthers with two dorso-basal projections (33); see description of genus in Gleason (1925). The stems of *Killipia quadrangularis* are quadrangular and ridged-winged (1); however, two other species have terete stems. The abaxial leaf surface of *K. quadrangularis* is usually red, an apomorphy not included in the analysis, which has also evolved within several genera with terminal inflorescences. The cladistic relationships of *Killipia* are obscure, although it is closest to *Maieta*, *Mecranium*, *Sagraea*, and *Pentossaea* (Fig. 1).

The species formerly of *Ossaea* with axillary 5-merous or occasionally 6-merous flowers warrant generic recognition (Fig. 5). The petals of this group are narrowly triangular with an acute apex (29), and the group is clearly separable from related taxa (see key). It is not surprising that a group of *Ossaea* species was found to be in need of generic recognition, since the genus has long been suspected of being polyphyletic (see Judd, 1986a). Wurdack (1962: 206), for example, stated that "the genus is an artificial assemblage of various species groups." The distinctive clade, with axillary 5-(6-)merous flowers, is here described as the genus *Pentossaea*.

Pentossaea W. Judd, gen. nov.

Genus novum, *Sagraea* DC. affine, a quo floribus 5-meris (vs. 4-meris), petalis semper anguste triangularibus, apicibus acutis differt. TYPE SPECIES: *Pentossaea brachystachya* (DC.) W. Judd.

Evergreen subshrubs or shrubs with pleonanthic shoots; twigs ± terete, nodose, glabrous to densely strigose, with a ridge encircling each node; druse crystals present. Indumentum of conspicuous, unbranched, slender to stout, strigose, multicellular hairs with or without glandular apices and of minute, multicellular, glandular hairs (or sometimes glandular-stellate hairs) occurring on stems, leaves, inflorescence axes, and hypanthia, or in some species ± restricted to reproductive parts. Buds narrowly ovoid, sylleptic, usually densely pubescent. Leaves

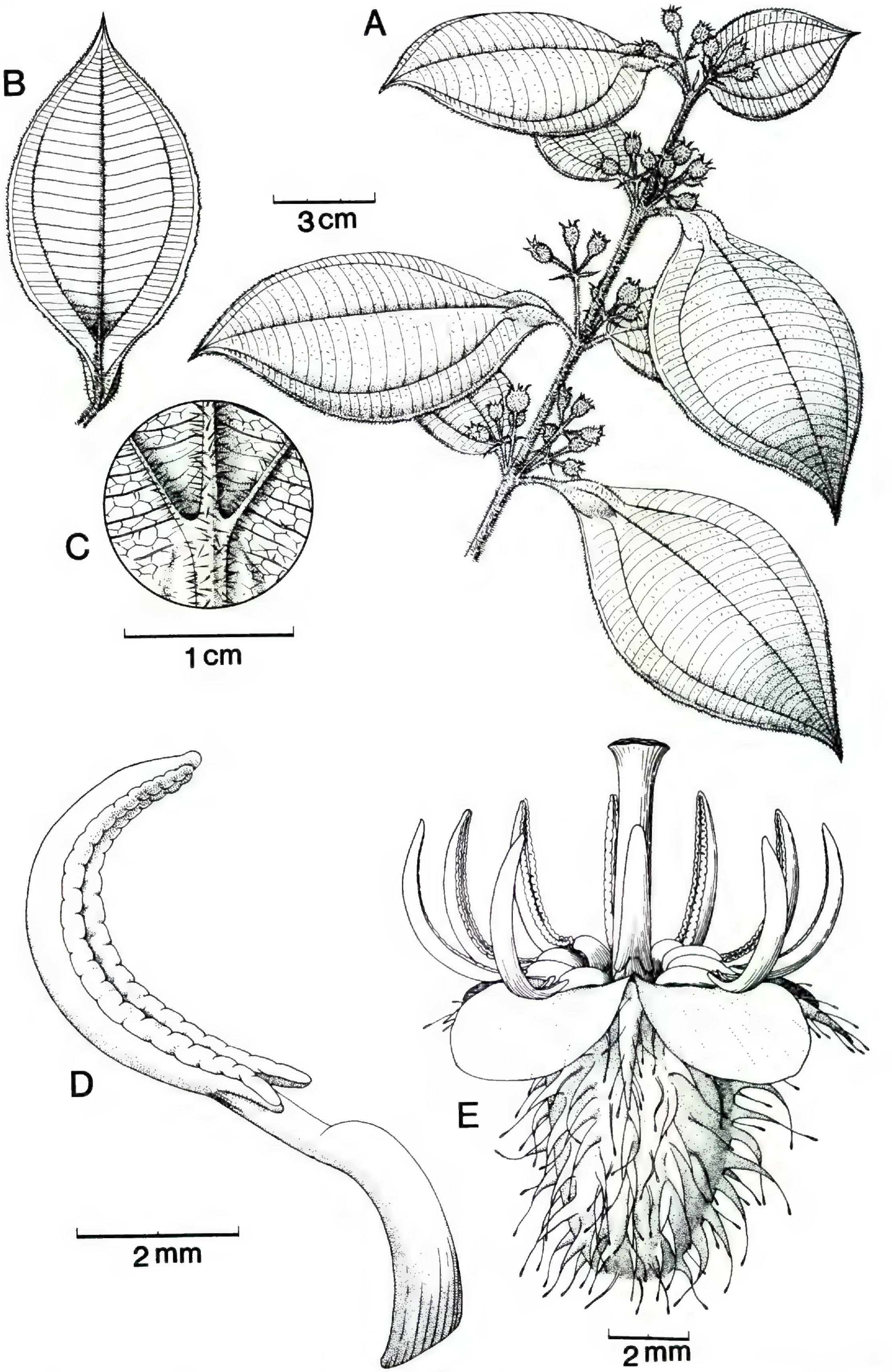

FIGURE 3. *Maieta poeppigii* Mart. ex Cogn.—A. Habit.—B. Leaf, abaxial view showing formicaria.—C. Detail showing entrance to formicaria.—D. Stamen.—E. Flower.

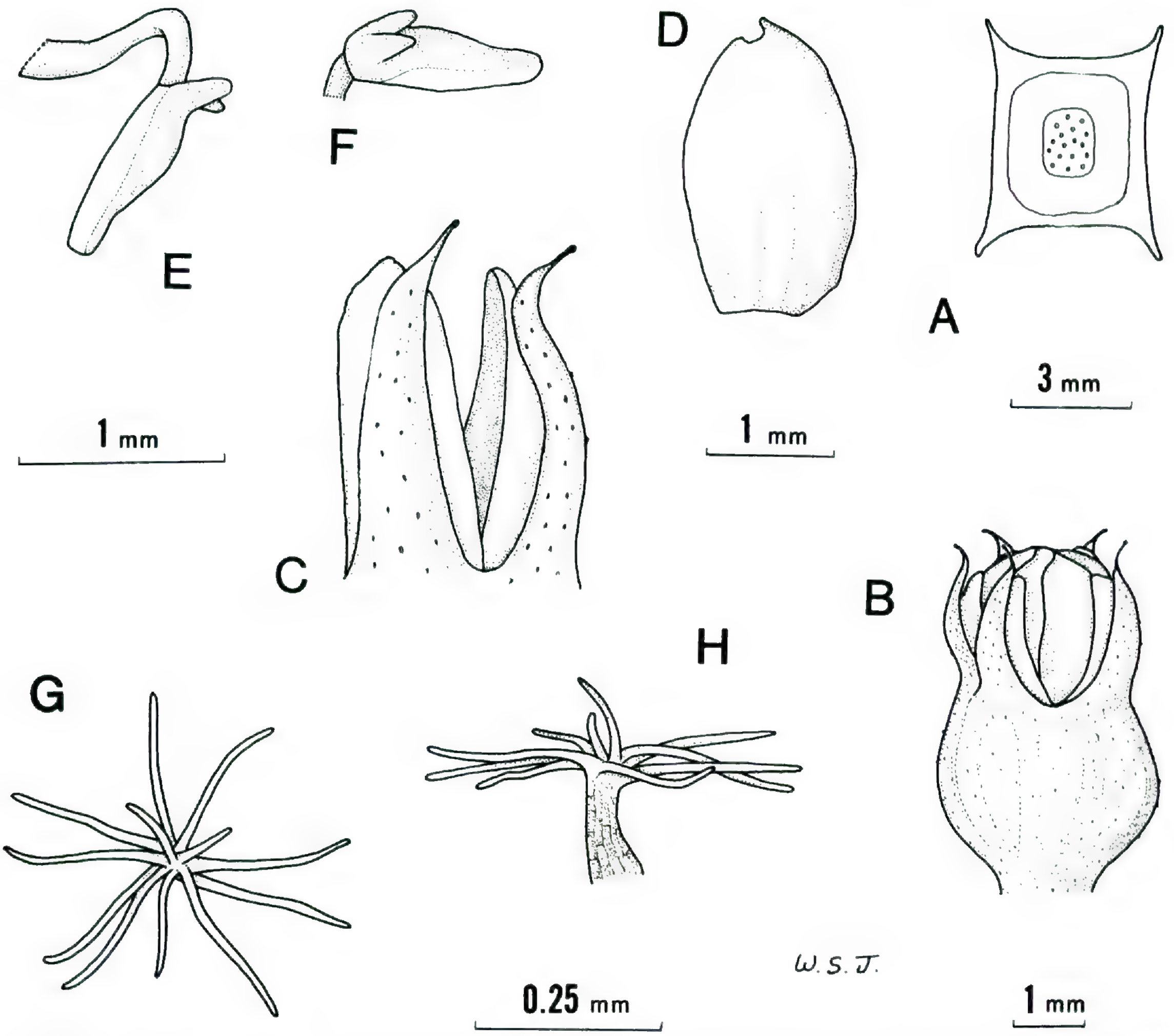

FIGURE 4.—A–F. *Killipia quadrangularis*. A. Stem, section. B. Flower bud. C. Calyx lobes. D. Petal. E, F. Stamens.—G, H. *Clidemia kappleri* Cogn., stellate hairs.

opposite, decussate, petiolate to nearly sessile, estipulate, herbaceous to coriaceous, ± plane; adaxial surface essentially glabrous (at maturity) or sparsely to densely covered with unbranched, elongate, multicellular hairs and sometimes also with minute glandular hairs (especially in vein impressions or at petiole junction); abaxial surface usually sparsely to densely covered with slender to stout, unbranched, elongate, multicellular hairs along with minute glandular to glandular-stellate, multicellular hairs (i.e., glandular hairs unbranched or sparsely branched with one branch glandular and the others nonglandular), sometimes only with glandular hairs and becoming ± glabrous with age; domatia not observed in vein axils; margin serrate in distal ca. ¾ of lamina to entire, plane to slightly revolute near base, the teeth ending in an elongate multicellular hair (and often associated with additional elongate hairs); venation acrodromous, slightly suprabasal, with a prominent midvein, 1–4 pairs of secondary veins (1 of these often intramarginal and inconspicuous), numerous percurrent tertiary veins ± perpendicular to midvein and reticulate to orthogonal quaternary and higher-order veinlets; petiole caniculate, essentially glabrous to densely strigose-pubescent. Inflorescences axillary cymes (occasionally reduced and ± fasciculate) borne in the leaf axils and in a few species on leafless nodes below the leaves, usually borne singly, rarely 2 per axil, bracteate, with opposite, narrowly triangular to ovate or oblong bracts (the 2 lowest protecting the inflorescence in bud and quickly caducous). Flowers perfect, 5- or 6-merous, sessile. Hypanthium ± cylindrical, abaxially with conspicuous, unbranched, elongate hairs with or without glandular apices, intermixed with minute glandular or glandular-stellate hairs, adaxially glabrous or with a few hairs around apex. External calyx lobes 5 or 6, conspicuous, elongate, terete. Internal calyx lobes 5 or 6, distinct (noncalyptrate), ± triangular, with obtuse, acute, to acuminate apices. Petals 5 or 6, ± white, narrowly triangular with acute api-

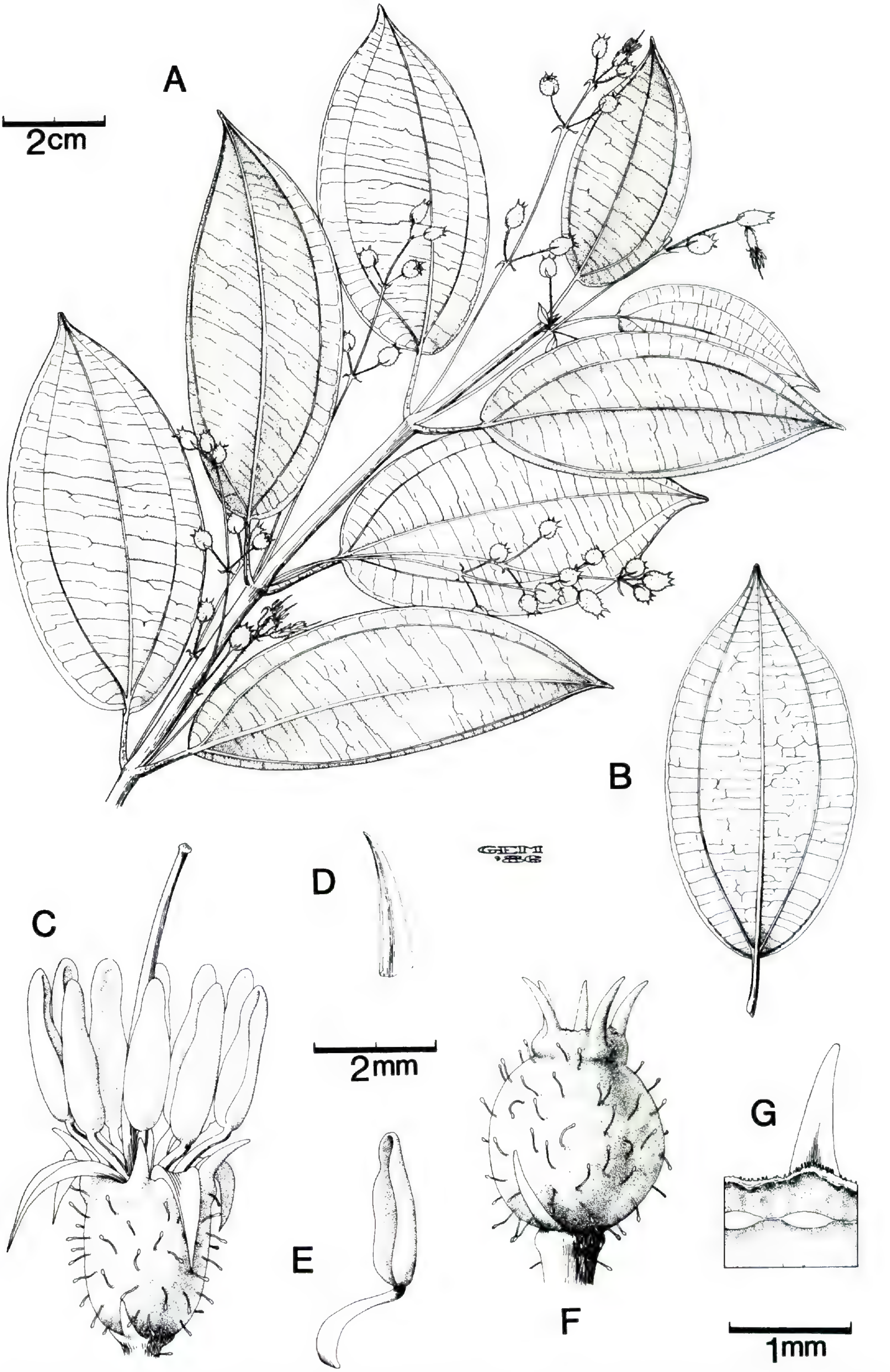

FIGURE 5. *Pentossaea coriacea*.—A. Habit.—B. Leaf.—C. Flower.—D. Petal.—E. Stamen.—F. Berry.—G. Calyx and inner surface of hypanthium; note absence of androecial fringe.

ces, 1-veined, glabrous or occasionally with a single dorso-apical projection (hair), rarely with a few glandular hairs. Stamens 10–12, ± isomorphic, glabrous, geniculate, inserted at apex of hypanthium, androecial fringe lacking; filament narrowly ovate to oblong, flattened dorsally; anther narrowly ovate to oblong, sometimes slightly curved, the 2 anther sacs dehiscing confluently by means of a single small apical pore, the connective sometimes slightly prolonged beyond the bases of the anther sacs. Ovary inferior or nearly so, 3–5-locular, with axile placentation and numerous ovules, the apex occasionally prolonged into several blunt appendages surrounding the style. Style cylindrical, ± straight; stigma capitate, papillose. Berries red to blue, with indumentum similar to hypanthium. Seeds small, rounded- to angular-obovate, the testa smooth to slightly roughened.

Pentossaea angustifolia (DC.) W. Judd, comb. nov. *Leandra angustifolia* DC., Prodr. 3: 154. 1828.

Pentossaea brachystachya (DC.) W. Judd, comb. nov. *Clidemia brachystachya* DC., Prodr. 3: 156. 1828.

Pentossaea confertiflora (DC.) W. Judd, comb. nov. *Clidemia confertiflora* DC., Prodr. 3: 156. 1828.

Pentossaea congestiflora (Naudin) W. Judd, comb. nov. *Clidemia congestiflora* Naudin, Ann. Sci. Nat. Bot., Ser. 3, 17: 344. 1852.

Pentossaea coriacea (Naudin) W. Judd, comb. nov. *Clidemia confertiflora* DC., Prodr. 3: 156. 1828.

Pentossaea heteronervis (Naudin) W. Judd, comb. nov. *Sagraea heteronervis* Naudin, Ann. Soc. Nat. Bot., Ser. 3, 18: 98. 1852.

Pentossaea marginata (Desr.) W. Judd, comb. nov. *Melastoma marginata* Desr. in Lam., Encycl. 4: 32. 1797.

Additional new combinations will certainly become necessary following a detailed revision of the genus.

The axillary-flowered 4-merous species of *Ossaea* and the very similar species traditionally placed in *Clidemia* sect. *Sagraea* (also axillary-flowered and 4-merous; see Cogniaux, 1891) are typically separated by the technical character of apically acute vs. blunt petals. However, I found this character to vary continuously within the group, and several species placed in *Clidemia* sect. *Sagraea* actually have acuminate or acute petals (e.g., *C. oligantha* Urban, *C. fuertesii* Cogn., *C. domingensis* (DC.) Cogn., *C. crossosepala* Griseb.), while others treated in *Ossaea* may have blunt-tipped petals (e.g., *O. barahonensis* Urban & E. Ekman or *O. setulosa* Urban). Some taxa have been considered members of both groups by various authors. In addition, phenetically very similar species have sometimes been placed in the two "genera," e.g., *Clidemia crossosepala* and *Ossaea hirtella* (Sw.) Triana (see Adams, 1972), and petal shape and apex occasionally vary infraspecifically, as in *Clidemia fuertesii*. Thus, all 4-merous, axillary-flowered members of the "druse-containing group" (Fig. 2) with free internal calyx lobes, no androecial fringe, and a usually well-developed strigose indumentum are placed together in *Sagraea* (Fig. 6; also see key).

Necramium (Britton, 1924), a genus with 4-merous axillary flowers having ovate, sharply acuminate petals and with an indumentum of long strigose hairs and irregularly branched-stellate hairs, clearly also belongs to this clade. A close association between *Necramium* and some species of *Ossaea* was recognized by Wurdack (1973: 721–722), who stated that *Necramium* was "realmente bien acomodado dentro de *Ossaea* DC. sensu Cogniaux pero la necesidad por una transferencia posterior cuando ese conjunto artificial se disperse se opone a la sinonimización inmediata." Wurdack (pers. comm.) suggested affinity of *Necramium* to *Ossaea* sect. *Octopleura* (Griseb.) Cogn. This is judged unlikely, however, since the latter group has terminal inflorescences (although frequently deflexed to a seemingly lateral position, see Judd, 1986a), a glandular dorso-basal connective appendage, and strongly costate fruits.

Necramium (Britton, 1924) is not the oldest name available for this clade, the names *Ossaea* and *Sagraea* (de Candolle, 1828) both having priority. Because the types of *Sagraea* (*S. capillaris* (Sw.) DC., here designated) and *Ossaea* (*O. scalpta* (Vent.) DC., here designated) fall within the group circumscribed above, and the two genera were described at the same time (de Candolle, 1828), either name is available for this group. The name *Sagraea* is chosen here, since I wish to avoid the use of *Ossaea*, a name that has been used for a great many discordant species-groups (see Wurdack, 1962, 1973, and Judd, 1986a). It is noteworthy that Triana (1871) considered these axillary-flowered species (along with a few discordant elements) to be generically separable (as *Sagraea*) from the terminal-flowered *Clidemia*.

Sagraea may be most closely related to *Mecranium*, a more specialized genus also showing 4-merous flowers, this a potential synapomorphy (15, Figs. 1, 2). *Sagraea* is considered to be metaphyletic (Donoghue, 1985; Mishler, 1985; Mishler & Brandon, 1987) because its ca. 60 species show no autapomorphies in some of the generated clado-

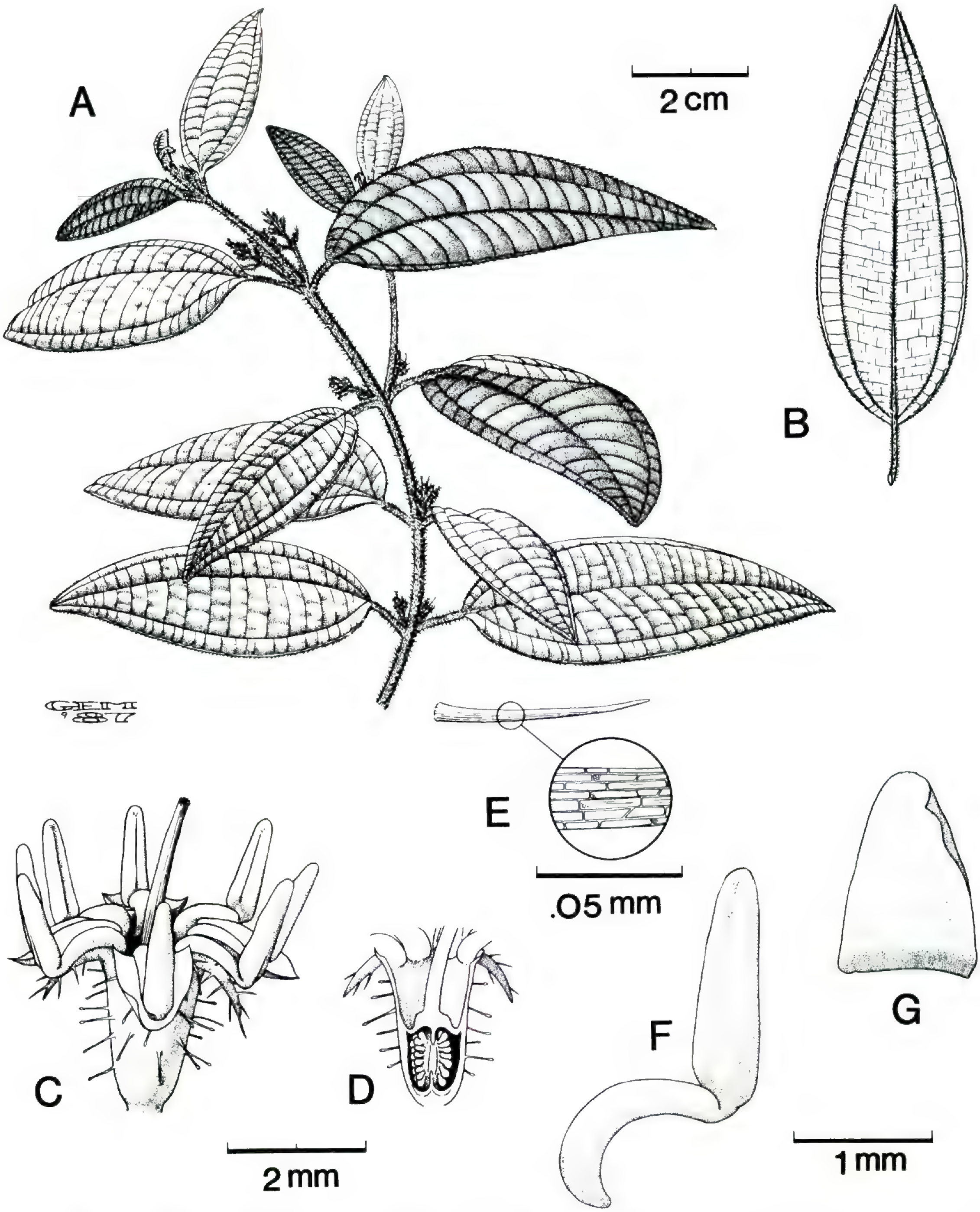

FIGURE 6. *Sagraea* (represented by the species better known as *Ossaea barahonensis*).—A. Habit.—B. Leaf.—C. Flower—D. Longitudinal section of flower showing hypanthium; note lack of androecial fringe.—E. Elongate multicellular hair.—F. Stamen.—G. Petal.

grams. However, in other equally parsimonious trees, the group appears monophyletic, being defined by a reversal to strigose hairs (5) or by a parallel evolution of 4-merous flowers (15). The group is possibly paraphyletic, but no character conclusively demonstrating this has been determined. Generic recognition of this phenetically rather variable group is considered appropriate and preferable to leaving its species in several artificially delimited genera.

Several species of *Sagraea* have evolved formicaria at the base of the petiole, e.g., *Clidemia*

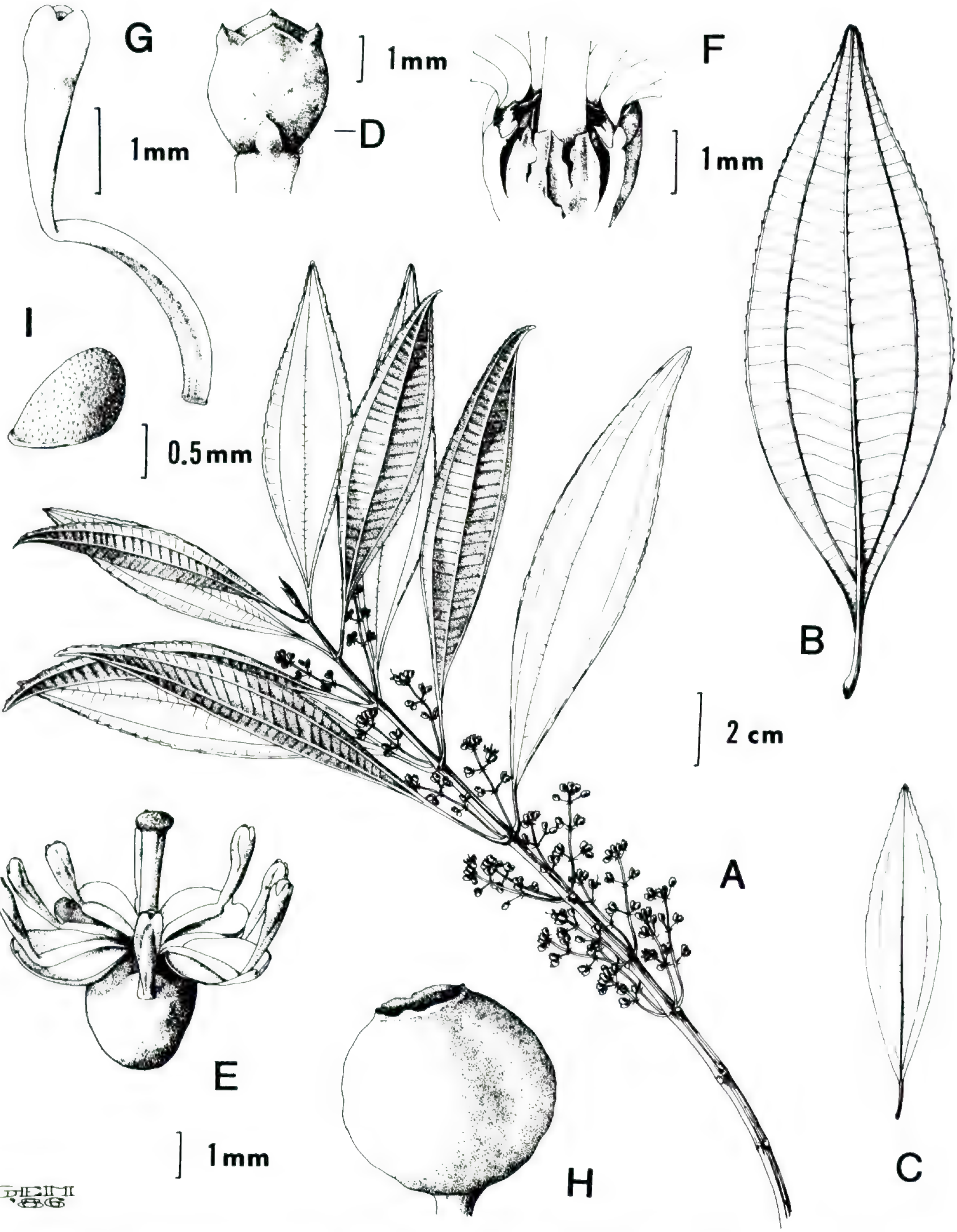

FIGURE 7. *Mecranium multiflorum* (Desr.) Triana.—A. Habit.—B, C. Leaves.—D. Flower bud.—E. Flower.—F. Hypanthium, androecial fringe, and ovary apex.—G. Stamen.—H. Berry.—I. Seed.

tococoidea (DC.) Gleason and *C. crenulata* Gleason; these species have sometimes been confused with *Maieta* (see Gleason, 1931). The structure and position of these formicaria are quite different from those of the *Maieta* and likely due to convergent evolution. Plants with a climbing habit and strongly anisophyllous leaves occur in *Clidemia epiphytica* (Triana) Cogn., a species that is also cytogenetically distinctive (Solt & Wurdack, 1980). As discussed above, anisophyllous leaves are char-

acteristic of *Maieta*, and this feature undoubtedly has evolved in parallel in the two genera.

It is not considered appropriate to make the many necessary new combinations in *Sagraea* until a thorough taxonomic revision of the genus has been completed. The species considered to belong in *Sagraea* and used in this cladistic investigation are: *Clidemia aphanantha* (Naudin) Sagot, *C. capituliflora* Cogn., *C. ciliata* D. Don, *C. crenulata* Gleason, *C. crossosepala* Griseb., *C. cursoris* Wurd., *C. discolor* (Triana) Cogn., *C. divaricata* (C. Wright ex Griseb.) Cogn., *C. domingensis* (DC.) Cogn., *C. epiphytica* (Triana) Cogn., *C. fendleri* Cogn., *C. fuertesii* Cogn., *C. graciliflora* Huber, *C. grisebachii* Cogn., *C. heteroneura* Cogn., *C. insularis* Domin (= *Sagraea capillaris* (Sw.) DC.), *C. involucrata* (Griseb.) C. Wright ex Sauv., *C. minutiflora* (Triana) Cogn., *C. monantha* L. Williams, *C. obliqua* Griseb., *C. oligantha* Urban, *C. plumosa* (Desr.) DC., *C. purpureo-violacea* Cogn., *C. pusilliflora* Cogn., *C. pycnaster* Tutin, *C. quadripetala* Almeda, *C. rubra* (Aublet) Mart., *C. rubrinervis* Cogn., *C. septulinervia* Cogn., *C. sericea* D. Don, *C. sessiliflora* (Naudin) Cogn., *C. silvicola* Gleason, *C. tococoidea* (DC.) Gleason, *C. trichotoma* C. Wright, *C. ulei* Pilger, *C. umbrosa* Cogn., *Ossaea curvipila* Urban & E. Ekman, *O. hirtella* (Sw.) Triana, *O. navasensis* Britton & Wilson, *O. nipensis* Britton & Wilson, *O. petiolaris* (Naudin) Triana, *O. rufescens* (Griseb.) C. Wright, *O. scabrosa* (L.) DC., *O. scalpta* (Vent.) DC., *O. setulosa* Urban, and *O. woodsii* W. Judd & Skean.

Mecranium (Fig. 7) is a distinctive monophyletic species group distinguished from other genera containing druse crystals by its internal calyx lobes fused into a domelike, apiculate, and membranous cap that is ruptured irregularly by elongation of the style and emergence of the petals at anthesis (22), the external calyx lobes reduced in length and often inconspicuous (reversal of 19), androecial fringe (i.e., a ring of erose to ciliate appendages arising from apex of hypanthium [torus] internal to the stamens [32]), and usually sparse and poorly developed indumentum (7); see Judd (1986a) and Skean & Judd (1986). Because these apomorphic characters are found also in the monotypic *Ekmaniocharis* (*E. crassinervis*; Urban, 1921; Judd, 1986a; Skean, in press), it is clear that this genus belongs in *Mecranium*. Likewise, *Ossaea acuminata* (Judd, 1986a) shows all these apomorphies except that of a domelike, apiculate cap. In this species the apices of the internal calyx lobes are distinct and imbricate, although the lobes are connate for most of their length, forming a structure that may be similar to the condition from which an apiculate cap was derived. It is obvious that *O. acuminata* is a basal member of the *Mecranium* clade. The nomenclatural transfers will be made by James D. Skean, Jr. in a monographic study of *Mecranium* currently near completion. A more detailed analysis of the phylogeny of this genus will be presented by Skean (in prep.).

In summary, the phylogenetic relationships (and taxonomic diversity) among the axillary-flowered Miconieae are most clearly represented by a taxonomic system recognizing the following nine genera as delimited above: *Henriettea*, *Huilaea*, *Killipia*, *Kirkbridea*, *Loreya*, *Maieta*, *Mecranium*, *Pentossaea*, and *Sagraea*.

Key to Axillary-Flowered Miconieae

1a. Plants with large elongate crystals (megastyloids) in leaf and stem tissues (easily observable with a hand lense in oblique razor blade sections); flowers usually clearly pedicellate; petals densely to sparsely pubescent abaxially, or with a few obscure hairs near apex, occasionally glabrous.
  2a. Flowers with radiately ridged, conspicuously expanded stigmas and with usually robust, fleshy anthers; indumentum of very slender to stout, elongate, unbranched, multicellular hairs ..... *Loreya*
  2b. Flowers with nonridged, less conspicuous stigmas and with nonfleshy anthers; indumentum of slender to stout, elongate, multicellular hairs with radiate to stellate-globular basal portion (or derived types, e.g., stellate hairs, peltate scales, elongate hairs with minute projections near base, or elongate hairs with a suprabasal expanded region and narrowed basal attachment).
    3a. Anthers with 2 well-developed dorso-basal projections; inflorescences clearly pedunculate ..... *Kirkbridea*
    3b. Anthers without dorso-basal projections; inflorescences usually sessile and fasciculate ..... *Henriettea*
1b. Plants with only ± spherical crystals (druses) in leaf and stem tissues, lacking megastyloids; flowers ± sessile or pedicellate; petals usually glabrous or with a single apical hair.
  4a. Flowers clearly pedicellate, i.e., pedicels ca. 1–1.5 cm long; inflorescences pendulous and 3-flowered with peduncle ca. 10–35 cm long ..... *Huilaea*
  4b. Flowers ± sessile; inflorescences various but the peduncle shorter than ca. 6 cm.
    5a. Flowers 5- or sometimes 6-merous.
      6a. Plants with pouchlike formicaria (ant-domatia) at bases of leaf blades; leaves often clearly anisophyllous ..... *Maieta*
      6b. Plants without formicaria; leaves ± isophyllous.
        7a. Petals narrowly triangular, with acute apices; plants with elongate, multicellular, un-

branched hairs (often strigose), with or without glandular tips; anthers lacking dorso-basal projections ..... *Pentossaea*

7b. Petals ovate to elliptic, with ± blunt apices; plants lacking elongate, multicellular hairs; anthers with 2 dorso-basal projections ..... *Killipia*

5b. Flowers 4-merous.

8a. Inner calyx lobes fused in a usually conspicuous, membranous dome that ruptures irregularly at anthesis; hypanthium with a ring of erose to ciliate appendages arising internally at base of stamens, i.e., an androecial fringe; indumentum usually not well developed, of minute, multicellular, globular, or unbranched to irregularly branched, and matted hairs ..... *Mecranium*

8b. Inner calyx lobes free; hypanthium lacking an androecial fringe, although occasionally with a few hairs on adaxial surface; indumentum often conspicuously strigose, almost always with elongate, branched or unbranched, multicellular hairs, often with glandular apices ..... *Sagraea*

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A SURVEY OF REPRODUCTIVE BIOLOGY IN NEOTROPICAL MELASTOMATACEAE AND MEMECYLACEAE[1]

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Abstract

In the Neotropics, the Melastomataceae and Memecylaceae comprise over 3,000 species in 106 genera. Pollination observations have been reported for 126 species in 35 genera of Melastomataceae and for four species in one genus of Memecylaceae. Genetic self-incompatibility has been found in 22 Melastomataceae species, self-compatibility in 25 species. A single Memecylaceae species tested is self-compatible. Agamospermy is known in 19 New World and some Old World species of Melastomataceae. The incidence of polyploidy in Melastomataceae seems high, but only about 8% of the species have been counted. Most Melastomataceae and Memecylaceae are hermaphroditic; dioecism is known in a few species in one genus of Melastomataceae. The principal mode of promoting outcrossing in both families is spatial separation of pollen and stigma (herkogamy), achieved by the pollen being enclosed in poricidal anthers, which have to be manipulated to release pollen. New World Memecylaceae are pollinated in the same way and by some of the same bee species as most Melastomataceae. All bee species known to visit Melastomataceae and Memecylaceae are listed; they comprise a wide spectrum of the neotropical bee fauna. It is not yet clear whether the stamen dimorphism and the conspicuous connective appendages present in many Melastomataceae have a function in the pollination mechanism beyond that of enhancing the visual attractiveness of the flowers and making the stamens easier to grasp. In most Melastomataceae, flowers offer only pollen; however, some 60 species in 8 genera offer nectar as a reward for pollinators (probably, some species in at least one additional genus do, too). The nectariferous species are pollinated by birds, bats, rodents, and bees. The nectar is rich in sucrose and, as a rule, its production is correlated with floral morphological changes relating to the fact that, except for bees, nectar consumers do not vibrate the stamens to collect pollen actively. I suggest that the capacity for developing nectaries is basic in Melastomataceae but suppressed in most modern members. The staminal glands of Memecylaceae produce minute quantities of a secretion containing lipids which, however, is not collected by the pollinators; the glands may in some way enhance stamen attractiveness. In seed dispersal systems, major diversifications occurred, with 40% of the neotropical Melastomataceae having capsular fruits and wind-dispersed seeds and 60% having soft, juicy berries taken mainly by birds, but also by marsupials, monkeys, bats, other mammals, turtles, and other reptiles. All Memecylaceae have berries, and their seeds are dispersed by birds, monkeys, and fish. I conclude that the east and west Gondwanian lineages of Melastomataceae and Memecylaceae, in parallel, coevolved with the earliest bees in the lower mid-Cretaceous. This may have been the time when the ancestors of these families switched from nectar-reward flowers to pollen-reward flowers. In the further extensive radiation of both families, special adaptations to pollinators were of limited importance; diversification in seed dispersal systems, vegetative characters, and edaphic adaptations were more important.

The neotropical Melastomataceae and Memecylaceae are particularly suitable for a study of reproductive biology in view of the relative ease with which members of these families are found in the field and the availability of several recent treatments in monographs and floras. As Gleason (1932) stated, "a dozen or more species . . . grow naturally on every square mile of tropical America, unless

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TABLE 1. New World Melastomataceae and Memecylaceae. Tribal arrangement following Cogniaux (1891), except for more recently described, transferred, or synonymized genera. Species numbers are those of the most recent treatment, or based on a herbarium survey (Renner, 1986). + indicates a recorded observation, citation in Table 4; − no observation presently known.

	Species Number	Pollination Observation
MELASTOMATACEAE		
BERTOLONIEAE		
Bertolonia	8	−
Boyania	1	−
Diplarpea	1	−
Macrocentrum	21	−
Maguireanthus	1	−
Monolena	15	−
Opisthocentra	1	+
Salpinga	8	+
Tateanthus	1	−
Triolena (incl. *Diolena*)	22	−
Tryssophyton	1	−
MERIANIEAE		
Acanthella	2	−
Adelobotrys	25	+
Axinaea	30	−
Behuria	3	−
Benevidesia	1	−
Bisglaziova	1	−
Centronia	15	+
Dolichoura	1	−
Graffenrieda (incl. *Calyptrella* and *Ptilanthus*)	44	+
Huberia	6	−
Meriania	74	+
Merianthera	3	−
Neblinanthera	1	−
Ochthephilus	1	−
Phainantha	4	−
Tessmannianthus	3	−
MICROLICIEAE		
Bucquetia	3	−
Cambessedesia (incl. *Pyramia*)	21	−
Castratella	1	−
Centradenia	6	+
Centradeniastrum	1	−
Chaetostoma	12	−
Eriocnema	1	−
Lavoisiera	46	+
Lithobium	1	−
Microlicia	100	−
Poteranthera	2	−
Rhynchanthera	15	+
Siphanthera (incl. *Farringtonia*)	16	+
Stenodon	1	−
Trembleya	11	+
TIBOUCHINEAE		
Aciotis	30	+
Acisanthera	17	+
Appendicularia	1	−
Brachyotum	50	+
Chaetolepis	10	−
Comolia	22	−
Comoliopsis	1	−
Desmoscelis	1	+
Ernestia	16	+
Fritzschia	1	−
Heterocentron	6	−
Loricalepis	1	−
Macairea	22	+
Mallophyton	1	−
Marcetia	23	−
Microlepis	4	−
Nepsera	1	+
Pilocosta	3	−
Pseudernestia	1	−
Pterogastra	4	+
Pterolepis	15	−
Sandemania	1	+
Schwackaea	1	−
Svitramia	1	−
Tibouchina (incl. *Itatiaia* and *Purpurella*)	243	+
Tibouchinopsis	2	−
RHEXIEAE		
Monochaetum	45	+
Pachyloma	6	−
Rhexia	13	+
MICONIEAE		
Anaectocalyx	3	−
Bellucia	7	+
Calycogonium	23	−
Catacoryne	1	−
Chalybea	1	+
Charianthus	11	−
Clidemia	117	+
Conostegia	43	−
Ekmaniocharis	1	−
Henriettea	12	+
Henriettella	51	+
Heterotrichum	10	−
Huilaea	4	+
Killipia	4	−
Kirkbridea	1	−
Leandra (incl. *Platycentrum*)	175	+
Llewellynia	1	−
Loreya	13	+
Maieta	2	−
Mecranium	21	−
Miconia	ca. 1,000 (at least 958)	+
Mommsenia	1	−
Myriaspora	1	+
Myrmidone	2	−
Necramium	1	−
Ossaea	91	−
Pachyanthus	16	−
Pleiochiton	7	−
Tetrazygia	21	−
Tococa	54	+

TABLE 1. Continued.

	Species Number	Pollination Observation
CYPHOSTYLEAE		
Allomaieta	1	–
Alloneuron	7	–
Cyphostyla	1	–
BLAKEEAE		
Blakea	100	+
Topobea	62	+
MEMECYLACEAE		
Mouriri	81	+
Votomita	8	–

the land is under intense cultivation, and the various genera extend from the coastal marshes at sea-level to the high páramos above the tree line." The Melastomataceae are a large family (v.i.) and diverse in terms of habit, reproductive and vegetative architecture (Cremers, 1983), and indument (Wurdack, 1986). Memecylaceae comprise about 89 species in the Neotropics and are much less diverse in these characters.

The present survey is based on my observations of the reproductive biology of many Brazilian and some Venezuelan species and on a review of the literature. The survey is presented in five sections. First, an outline of the classification and reproductive morphological features of the Melastomataceae and Memecylaceae is given; second, breeding systems and cytology are discussed; third, the pollination spectra found in the two families are described; fourth, a brief survey is made of seed dispersal in the two families; fifth, the reproductive biological information is related to the fossil record and distributional data to contribute to a better understanding of the historical evolution of the two families.

Flowering and fruiting phenology of neotropical melastomes and Memecylaceae are not dealt with here, but reference may be made to Snow (1965), Croat (1978), Opler et al. (1980), Hilty (1980), Lumer (1982), and Renner (1984 and in prep.). Suffice it to say that synchronous, episodic flowering with the episodes of short duration (a few days) characterizes some of the arborescent species of the largest genus, *Miconia*, whereas extended flowering periods (several weeks or months) are characteristic of many of the shrubs, herbs, epiphytes, and some of the tree species.

CLASSIFICATION AND REPRODUCTIVE MORPHOLOGICAL FEATURES

Worldwide, the Melastomataceae A. L. Juss. (excluding the ca. ten species of *Crypteronia*, *Axinandra*, and *Dactylocladus*, i.e., the Crypteroniaceae; Dahlgren & Thorne, 1984) and the Memecylaceae DC. consist of ca. 190 genera and approximately 4,800 species. In the Neotropics, the Melastomataceae comprise over 3,000 species in 107 genera (Table 1) and the Memecylaceae 89 species in two genera. About half of these genera contain only one to four species, whereas one genus, *Miconia*, has some 1,000 species. Though the Memecylaceae are often included in the Melastomataceae as a subfamily, it has been pointed out (see Morley, 1953; Dahlgren & Thorne, 1984; Johnson & Briggs, 1984) that the differences between these families are such that their union obscures rather than reflects our knowledge of the two groups. The Memecylaceae consist of the Asian genera *Memecylon* (ca. 300 spp.) and *Lijndenia* (4 spp.) (Bremer, 1982, 1983), the African *Spathandra* (6 spp.) and *Warneckea* (31 spp.), and the neotropical *Votomita* (8 spp.; Morley, 1963) and *Mouriri* (81 spp.). There is a consensus that the Melastomataceae and Memecylaceae belong to the core families of the order Myrtales (Dahlgren & Thorne, 1984; Johnson & Briggs, 1984).

The classification of the Melastomataceae sensu stricto is essentially that of Triana (1867), who was closely followed by Cogniaux (1891). Wurdack (1980) has realigned the New World tribes in a sequence generally resembling that of A. P. de Candolle (1828). The main dichotomy in the Melastomataceae is between the capsular-fruited and the berry-fruited genera. The genera are arranged into tribes on the basis of fruit and seed characters and the presence and position of connective appendages (D. Don, 1823; Triana, 1867; Cogniaux, 1891; Gleason, 1929; comp. also Whiffin & Tomb, 1972).

Most Melastomataceae are characterized by poricidal anthers, the connectives of which are frequently prolonged (however, species of *Miconia* sects. *Chaenopleura* and *Chaenanthera* have anthers that open by 1–2 slits). They usually have a pronounced foliar venation consisting of the midvein and one to four pairs of subparallel longitudinal veins. Memecylaceae, on the other hand, mostly have pinnate venation; their anthers open by short slits or pores. In a reproductive biological context, the presence of an elliptic, concave gland on the dorsal side of the connective is a unique feature characterizing most Memecylaceae.

The flowers in both families are actinomorphic or weakly to strongly zygomorphic as a result of movements of the stamens and style immediately after the expansion of the petals (Troll, 1922; Ziegler, 1925; pers. obs.). In Melastomataceae, the flowers are usually borne in well-developed cymose inflorescences, whereas in Memecylaceae the cymes are often condensed or reduced to a few flowers in fasciculate tufts. In both families, the mostly 4- or 5-merous flowers are perigynous or epigynous with a cup-shaped hypanthium that bears on its rim the calyx lobes, petals, and stamens. The antepetalous stamens are usually longer than the antesepalous ones, which may be staminodial; this dimorphism is more or less pronounced and has given occasion to much speculation concerning its role in pollination. In Melastomataceae with poricidal anthers, the anthers are one- or two-pored, a character that is consistent at the species level but varies within genera; there is also considerable variation in the size and position of the pores. Pollen grains are usually free, small, and rather smooth, although polyads and tetrads are known in species of *Tococa* and *Miconia* (Patel et al., 1984).

Breeding Systems

The principal mode of promoting outcrossing in most Melastomataceae and Memecylaceae is the very effective spatial separation of pollen and stigma in the flowers (herkogamy). This is achieved by the pollen being enclosed in tubular anthers with apical or subapical pores or slits, which are generally minute, and positioned well distant from the punctiform or capitate stigmas. Also, the stamens are usually shorter than the styles. In bud, the stamens are always folded over in such a way that the anther pores point downward and are maximally distant from the stigma, which lies at the tip of the bud. Thus, chances for automatic selfing before and during anthesis are very low or nil. If, however, during anthesis, an anther or the style bends in such a way that the pore is brought into contact with the stigma, automatic selfing may occur. This has been reported for *Monolena trichopoda* (Melastomataceae; Warner, 1981) where, late in anthesis, the stamens fold over and the thecae are effectively stuck to the stigmatic exudate.

No pollen escapes from the anthers unless mediated by a vector, which at least potentially may arrive bearing conspecific pollen. Almeda (1977, 1978) suggested that vigorous mechanical movement of the anthers by gusty winds or rains might release pollen in species of *Monochaetum* and *Centradenia* (Melastomataceae). Additionally, he often observed pollen in water droplets connecting anthers and stigma and suggested that this might be another possible route for selfing to occur. However, bees, which regularly collect pollen from Melastomataceae, use vibrations of around 420 Hz or higher (this frequency was found to effect ample pollen emission from the large anthers of *Bellucia*; see below). Therefore, it seems unlikely that the low-frequency vibrations produced by wind could release pollen from melastome anthers. This impression is supported by the lack of fruit set in bagged flowers of nonagamospermic species exposed to strong wind (Renner, 1984). While autogamy may be extremely rare, vector-mediated selfing (i.e., geitonogamy), a function of pollinator behavior and number of conspecific flowers available at a time, may be frequent in self-compatible species.

Temporal separation of male and female function has been suggested for species of *Monochaetum* (Almeda, 1978) in which "the ill-defined stigmatic region . . . appears to be non-receptive during the first day." This may be a rare condition because, as a rule, poricidal flowers that offer only pollen as a reward (subsequently also called "pollen-only flowers") receive foreign pollen at the same time a visitor harvests pollen from them; in female-phase flowers, there is nothing to reward visitors (only mimicry or deception might account for visits to female-phase flowers). Homogamy, i.e., the simultaneous functioning of the male and female parts, is thus to be expected in pollen-only flowers. Temporal separation of the male and female function in single flowers has been reported twice in nectariferous melastomes (Ule, 1896; Vogel, 1957); in both cases, the flowers were protandrous.

The Melastomataceae are not entirely hermaphroditic. Wurdack (1964) was the first to describe dioecism in *Miconia dioica* Wurdack; herbarium specimens of this species had female flowers with abortive stamens and male flowers with poorly developed stigmas. He also suspected dioecism in some other minute-flowered Andean species of *Miconia* (*M. dielsii* Markgraf, *M. clathrantha* Tr. ex Cogn., *M. minuta* Gleason; Wurdack, 1980: 261–262) and in *M. rubens* (Sw.) Naudin from the West Indies and Venezuela (Wurdack, 1964). Field observations on the reproductive biology of these and some other suspected dioecious melastomes are lacking.

At least one species of *Lijndenia* (Memecyla-

ceae) has hermaphrodite-flowered individuals and purely male-flowered ones (Bremen, 1982).

GENETIC COMPATIBILITY

As shown in Table 2, genetic self-incompatibility occurs in at least 22 species in the two families. As Darwin remarked (in a letter to J. D. Hooker on Nov. 28, 1871, in F. Darwin (ed.), 1903), melastomes "are troublesome beasts to fertilise." This is due to the closed anthers and mostly punctiform stigmas. In some large-flowered species, such as *Bellucia* (Melastomataceae), it is possible to collect large amounts of pollen for experimental purposes by holding a tuning fork to the stamens. Self-compatibility is found in 26 species (Table 2). Since no efforts have ever been made to distinguish pseudogamy from self-compatibility, several of the supposedly self-compatible species reported earlier (Darwin, 1876; Ziegler, 1925) may have set fruit as a result of agamospermy rather than of self-fertilization. Related species such as *Tococa guianensis* and *T. bullifera* or *Centradenia grandiflora* and *C. paradoxa* (all Melastomataceae) differ in their compatibility conditions (Table 2). The humid stigmatic surface and the binucleate pollen of the Melastomataceae and Memecylaceae (Tobe & Raven, 1984) indicate that the incompatibility system is gametophytic (Nettancourt, 1977).

AGAMOSPERMY

Experimental proof of agamospermy in melastomes is readily obtained by cutting off the style in freshly opened unvisited flowers. (To ensure that flowers are unvisited before the style is cut off, they must be bagged the evening before.) Apart from the 22 apomictic Melastomataceae listed in Table 3, polyembryony, with additional embryos being formed by nucellus or suspensor cells, has been reported from the Asiatic species *Osbeckia hispidissima* Wight, *Sonerila wallichii* Benn., and *Melastoma malabathricum* L. (Subramanyam, 1942, 1944, 1948). Polyembryony is often correlated with agamospermy (Gustafsson, 1946–47). *Mouriri nervosa* is the only member of the Memecylaceae so far tested for agamospermy, with negative results (Renner, unpubl.). In several of the neotropical species showing apomixis, for instance in *Clidemia novemnervia* and *Macairea theresiae*, the anthers contain very few pollen grains. In cultivated neotropical *Leandra cordifolia* Cogn., Subramanyam (1942) also found that a low percentage of fertile pollen grains was combined with the frequent formation of two embryo sacs. In most neotropical species, agamospermy is correlated with low stainability of fresh pollen in cotton blue with lactophenol. This stain indicates presence of callose, a saccharide found in the intine of pollen. Lack of an intine could make a grain unviable and is usually accompanied by lack of cytoplasm. However, in *Aciotis acuminifolia* and *Miconia argyrophylla*, pollen grains stain heavily, yet these species are capable of producing seeds apomictically. In *Clidemia novemnervia* and *Maieta poeppigii*, the stamens do not unflex completely upon anthesis but remain curved, and are thus not available for legitimate bee pollinators. Both species regularly set seeds apomictically.

Lumer (1982) observed that *Blakea gracilis*, *Blakea* sp. (originally identified as *B. grandiflora*), and *Topobea brenesii* ripened a large number of seedless fruits from emasculated flowers; however, in *T. pittieri*, she found that of the bagged flowers, 35% produced mature fruits containing seeds. Darwin (1876) and Ziegler (1925) observed fruit set in cultivated plants of *Monochaetum*, *Tibouchina*, *Centradenia*, *Calvoa*, and *Dissotis* in the greenhouse. Assuming that there were no bee pollinators in the greenhouses, it is likely that such fruits resulted from agamospermy rather than from autogamy, which, as pointed out above, is mechanically difficult in Melastomataceae.

The number of species investigated is still too small to draw firm conclusions about correlations between habit, habitat, and breeding system. Of the agamospermous species, 13 are shrubs of various types of savannas or of secondary vegetation; five are treelets, two are herbs, and one is a climber. The sample is clearly biased towards shrubby species, however, because of their accessibility.

CYTOLOGY

Some 300 of the over 3,000 species of neotropical Melastomataceae and only one species of Memecylaceae (*Mouriri myrtilloides*) are known cytologically (Solt & Wurdack, 1980). Only a few of these have been examined twice. Melastome chromosomes are very small (0.5–1 micron; Solt & Wurdack, 1980) and stain poorly. The most common base numbers are 9 and 17 (Wurdack & Kral, 1982). Based on Solt & Wurdack's results, the incidence of polyploidy in the Melastomataceae seems high. It cannot yet be answered whether polyploidy is more frequent in species with strong agamospermous reproduction than in those which lack apomixis, nor whether there is a correlation between polyploidy and growth habit.

POLLINATION SYSTEMS

In neotropical Melastomataceae and Memecylaceae, the most widespread pollination system

TABLE 2. Compatibility systems in Melastomataceae.

	System[1]	Reference
MELASTOMATACEAE		
MERIANIEAE		
Adelobotrys rachidotricha Brade	SC	Renner, 1984
Graffenrieda latifolia (Naudin) Triana	SC	Sobrevila & Arroyo, 1982
BERTOLONIEAE		
Bertolonia marmorata Naudin	SC	Ziegler, 1925
MICROLICIEAE		
Centradenia floribunda Planchon	SC	Darwin, 1876
C. grandifolia (Schldl.) Endl. ssp. *grandiflora*	SIC	Almeda, 1977
C. paradoxa (Kraenzlin) Almeda	SC	Almeda, 1977
Rhynchanthera grandiflora (Aubl.) DC.	SC	Renner, 1984
TIBOUCHINEAE		
Nepsera aquatica (Aubl.) Naudin	SIC	Renner, 1984
Monochaetum amabile Almeda	SC	Almeda, 1978
M. calcaratum (DC.) Triana (as *M. ensiferum* Hook.)	SC	Darwin, 1876
M. floribundum (Schldl.) Naudin	SC	Almeda, 1978
M. neglectum Almeda	SC	Almeda, 1978
M. talamancense Almeda	SC	Almeda, 1978
M. vulcanicum Cogn.	SC	Almeda, 1978
RHEXIEAE		
Rhexia alifanus Walter	SIC	Kral & Bostick, 1969
R. aristosa Britton	SIC	Kral & Bostick, 1969
R. cubensis Griseb.	SIC	Kral & Bostick, 1969
R. lutea Walter	SC	Kral & Bostick, 1969
R. mariana var. *interior* (Pennell) Kral & Bostick	SIC	Kral & Bostick, 1969
R. mariana L. var. *mariana*	SIC	Kral & Bostick, 1969
R. mariana var. *ventricosa* (Fern. & Griscom) Kral & Bostick	SIC	Kral & Bostick, 1969
R. nashii Small	SIC	Kral & Bostick, 1969
R. nuttallii James	SIC	Kral & Bostick, 1969
R. parviflora Chapman	SIC	Kral & Bostick, 1969
R. petiolata Walter	SC	Kral & Bostick, 1969
R. salicifolia Kral & Bostick	SIC	Kral & Bostick, 1969
R. virginica L.	SIC	Kral & Bostick, 1969
MICONIEAE		
Bellucia acutata Pilger	SIC	Renner, 1986/1987
B. dichotoma Cogn. (as *B. imperialis* Saldanha & Cogn.)	SIC	Renner, 1984
B. grossularioides (L.) Triana	SIC	Renner, 1986/1987
Conostegia macrantha Triana	SIC	Lumer, 1982
Miconia araguensis Wurdack	SC	Sobrevila & Arroyo, 1982
M. dodecandra (Desr.) Cogn.	SC	Sobrevila & Arroyo, 1982
M. laevigata (L.) DC.	SIC	Sobrevila & Arroyo, 1982
M. macrodon (Naudin) Wurd. (as *Heterotrichum macrodon* (Naudin) Planchon)	SIC	Ziegler, 1925
M. sp. 254	SIC	Renner, 1984
M. sylvatica (Schldl.) Naudin	SC	Sobrevila & Arroyo, 1982
M. tuberculata (Naudin) Triana	SIC	Arroyo & Cabrera, 1977
Tococa bullifera DC.	SC	Renner, 1984
T. longisepala Cogn.	SIC	Renner, 1984
BLAKEEAE		
Blakea anomala J. D. Smith	SC	Lumer, 1982
B. chlorantha Almeda	SC	Lumer, 1980

TABLE 2. Continued.

	System[1]	Reference
B. gracilis Hemsley	SC	Lumer, 1982
B. sp. (as *B. grandiflora* Hemsley)	SC	Lumer, 1982
B. tuberculata J. D. Smith	SC	Lumer, 1982
Topobea brenesii Standley	SC	Lumer, 1982
T. durandiana Cogn.	SC	Lumer, 1982
MEMECYLACEAE		
Mouriri nervosa Pilger	SC	Renner, 1984

[1] SC = self-compatible, SIC = self-incompatible.

involves female bees; it occurs in an estimated 98% of the species. Pollination by hummingbirds, bats, and rodents is found in an estimated 60 species of *Meriania*, *Centronia*, *Brachyotum*, *Tibouchina*, *Miconia*, *Huilaea*, *Chalybea*, and *Blakea* (Table 4), and probably also in *Axinaea* (see below). The mode of pollination is determined by the type of reward offered: Melastomataceae and Memecylaceae with pollen-only flowers are, as a rule, pollinated exclusively by bees because the morphology of the anthers excludes all other pollen-collecting vectors. In contrast, the nectar-offering species attract a wide variety of pollinators.

MELASTOMATACEAE

POLLINATION BY POLLEN-COLLECTING BEES

a) Methods of pollen collection and kinds of bees

Pollination by bees has been reported for some 120 species in 31 genera of Melastomataceae (Table 4). In addition, a few species occurring at Finca La Selva, Costa Rica, and near Kourou, French Guiana, have been observed to be pollinated by small and medium-sized bees (Bawa et al. 1985; Roubik, 1979a). Many unidentified melastomes are indicated as visited by bees in apidological studies (e.g., Sakagami et al., 1965, and Roubik, 1979b).

TABLE 3. Agamospermous Melastomataceae.

	Habit	Habitat	Reference
Aciotis acuminifolia (DC.) Triana	herb	forest understory	Renner, 1984
Clidemia capitellata (Bonpl.) D. Don	shrub	savannas and disturbed vegetation	Renner, 1984
C. epibaterium DC.	climber	forest understory	Renner, 1984
C. fendleri Cogn.	shrub	forest understory	Sobrevila & Arroyo, 1982
C. hirta (L.) D. Don	shrub	disturbed vegetation	Renner, 1984
C. novemnervia (DC.) Triana	shrub	disturbed vegetation	Renner, 1984
C. rubra (Aubl.) Mart.	shrub	savannas and disturbed vegetation	Renner, 1984
Macairea theresiae Cogn.	shrub	Amazonian white sand savannas	Renner, 1984
Maieta guianensis (Aubl.) DC	shrub	forest understory	original
Maieta poeppigii Cogn.	shrub	forest understory	original
Miconia alata (Aubl.) DC.	shrub	disturbed vegetation	Renner, 1984
M. albicans (Sw.) Triana	shrub	savannas (cerrado)	Renner, 1984
M. argyrophylla DC.	treelet	secondary forest	Renner, 1984
M. campestris (Benth.) Tr.	shrub	disturbed vegetation	Renner, 1984
M. egensis Cogn.	treelet	secondary forest	Renner, 1984
M. minutiflora (Bonpl.) DC.	treelet	secondary forest	Renner, 1984
M. prasina (Sw.) DC.	treelet	secondary forest	original
M. regelii Cogn.	treelet	secondary forest	Renner, 1984
M. spinulosa Naudin	shrub	forest understory	Sobrevila & Arroyo, 1982
M. stenostachya DC.	shrub	savannas	Renner, 1984
M. tomentosa (L. C. Rich.) D. Don ex DC.	treelet	disturbed vegetation	Renner, 1984
Rhexia mariana L.	herb	swamps, marshes	Etheridge & Herr, 1968

TABLE 4. Pollinators of Melastomataceae and Memecylaceae.

	Important Pollinators[1]	References
MELASTOMATACEAE		
BERTOLONIEAE		
Opisthocentra clidemioides Hook. f.	*Euglossa intersecta*; *Melipona fulva*	Renner, 1984
Salpinga secunda DC.	*Euglossa* sp., *Eulaema nigrita*; *Melipona* sp.	Renner, 1984
MERIANIEAE		
Adelobotrys rachidotricha Brade	*Pseudaugochloropsis* sp.	Renner, 1984
Centronia phlomoides Triana	bats	Vogel, 1988
Graffenrieda fruticosa Wurdack	*Bombus* spp.; *Xylocopa* sp.; *Melipona lateralis*	Renner, in press
G. polymera Gleason subsp. *neblinensis* Wurd.	*Bombus* spp.; *Melipona lateralis*	Renner, in press
G. reticulata Wurdack	*Bombus* spp.; *Melipona lateralis*; *Dialictus* sp.; *Neocorynura* sp.	Renner, in press
Meriania longifolia Cogn.	*Xylocopa* sp.	Vogel, 1978
M. tomentosa (Cogn.) Wurd. (= *Centronia excelsa* (Bonpl.) DC.)	hummingbirds	van der Werff, pers. comm.; *Neill et al.*, label data
MICROLICIEAE		
Centradenia grandifolia (Schldl.) Endl.	*Bombus* sp.; *Melipona* sp.	Almeda, 1977
Lavoisiera cordata Cogn.	*Bombus* spp.	Renner, 1984
L. glandulifera Naudin	*Bombus* spp.	original
Rhynchanthera grandiflora (Aubl.) DC.	*Xylocopa frontalis*, *X. tegulata*, *X. muscaria*; *Centris nitens*, *C. flavifrons*; *Eulaema nigrita*; *Monoeca* sp.	Renner, 1984, and original
R. hispida Naudin	*Xylocopa transitoria*; *Centris fuscata*; *Ptiloglossa* sp.	Renner, 1984
R. sp.	*Augochloropsis scabrifrons*, *A. sparsilis*, *A. terrestris*, *Augochloropsis* sp.; *Pseudaugochloropsis graminea*	Laroca, 1970
Siphanthera cordifolia (Benth.) Gleason	*Dialictus* sp.	N. Ramirez, pers. comm., 1986
Trembleya phlogiformis DC.	*Thygater analis*; *Bombus* sp.; *Xylocopa* sp.	Renner, 1984; Semir, pers. comm., 1982
TIBOUCHINEAE		
Aciotis acuminifolia (DC.) Triana	*Megommation ogilvei*; *Paratetrapedia duckei*; *Melipona fulva*, *Melipona* sp.; *Exomalopsini* halictids; *Paratetrapedia* sp.	Renner, 1984
A. annua (DC.) Triana		Renner, 1984
A. circaeifolia (Bonpl.) Triana	*Megommation* sp.	Renner, 1984
A. polystachya (Bonpl.) Triana	*Paratetrapedia* sp.; *Augochloropsis callichroa*, *Augochloropsis* sp.; *Euglossa* sp.	Renner, 1984, and original
Acisanthera uniflora (Vahl) Gleason	halictids	original
Brachyotum ledifolium (Desr.) Triana	hummingbirds	Lagerheim, 1899
Brachyotum ca. 40–45 species	hummingbirds	Lagerheim, 1899; Wurdack, 1954; Fitzpatrick et al., 1979; B. Stein, pers. comm., 1985
Desmoscelis villosa (Aubl.) Naudin	*Dialictus* sp.; *Augochloropsis* sp.; *Xylocopa* cf. *tegulata*; *Augochlora* sp.; *Melipona* sp.	Roubik, 1979b; Renner, 1984, and original

TABLE 4. Continued.

	Important Pollinators[1]	References
Ernestia tenella (Bonpl.) DC.	*Augochloropsis* sp.	original
Macairea pachyphylla Benth.	*Melipona* sp.	N. Ramirez, pers. comm. 1986
M. parvifolia Benth.	*Euglossa* sp.	N. Ramirez, pers. comm. 1986
M. rufescens DC.	halictids	original
Monochaetum alpestre Naudin	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. amabile Almeda	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. compactum Almeda	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. cordatum Almeda	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. deppeanum (Schldl. & Cham.) Naudin	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. exaltatum Almeda	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. floribundum (Schldl.) Naudin	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. linearifolium Almeda	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. macrantherum Gleason	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. neglectum Almeda	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. talamancense Almeda	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. tenellum Naudin	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. trichophyllum Almeda	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
M. vulcanicum Cogn.	*Bombus* sp.; *Melipona* sp.; Anthophoridae	Almeda, 1978
Nepsera aquatica (Aubl.) Naudin	*Megaloptidia contradicta*; *Megommation* sp.; *Melipona* sp.	Roubik, 1979b, Renner, 1984
Pterogastra divaricata (Bonpl.) Naud.	halictids	original
Purpurella see *Tibouchina*		
Sandemania hoehnei (Cogn.) Wurd.	*Megommation* sp.; *Augochloropsis callichroa*, *Augochloropsis* sp.; *Melipona fulva*	Renner, 1984, and original
Tibouchina arborea (Gardner) Cogn.	*Bombus morio*	F. Mueller, 1873
T. aspera Aubl.	*Xylocopa transitoria*; *Bombus* sp.; *Augochloropsis* sp.; *Euglossa* sp.; *Melipona* sp.; *Ptiloglossa* sp.	Roubik, 1979b, Renner, 1984
T. benthamiana (Gardner) Cogn.	*Augochloropsis* sp.	original
T. clavata (Pers.) Wurd.	*Bombus morio*; *Pseudaugochloropsis graminea*	Laroca, 1970
T. cleistoflora Ule (= *T. cleistopetala* Ule, 1896, nom. emend. = *Itatiaia cleistopetala* (Ule) Ule, 1909	*Bombus* sp.	Ule, 1896
T. frigidula (DC.) Cogn.	*Bombus* sp.; *Oxaea flavescens*; *Pseudaugochloropsis graminea*	original
T. gardneriana (Triana) Cogn.	*Trigonopedia* sp.	original
T. grandifolia Cogn.	halictids	original

TABLE 4. Continued.

	Important Pollinators[1]	References
T. grossa (L. f.) Cogn.	bats (*Anoura geoffroyi*); hummingbirds	Vogel, 1957
T. hospita (DC.) Cogn.	halictids	original
T. longifolia (Vahl) Baillon	halictids	Renner, 1984
T. moricandiana (DC.) Baillon	*Bombus morio*	original
T. mutabilis (Vell.) Cogn.	*Bombus morio*	original
T. pilosa Cogn.	*Micrommation larocai*	Laroca, 1970
T. spruceana Cogn.	*Augochloropsis callichroa*	Renner, 1984
T. trichopoda (DC.) Baillon	*Bombus morio*	Laroca, 1970
T. ursina (Cham.) Cogn.	*Bombus atratus*; *Xylocopa augusti*; *Exomalopsis* sp.; *Augochloropsis cleopatra, A. euphrosyne, A. iris, A. leucotricha, A. scabrifrons, A. sparsilis, A. terrestris*	Laroca, 1970
RHEXIEAE		
Rhexia virginica L.	"bees"; bumblebees	Leggett, 1881; Eyde & Teeri, 1967
MICONIEAE		
Bellucia acutata Pilger	*Xylocopa frontalis*; *Centris lilacina*	Renner, 1984, 1986/1987
B. aequiloba Pilger	*Xylocopa* spp.; *Epicharis* sp.	Renner, 1986/1987
B. dichotoma Cogn. (= *B. imperialis*)	*Ptilotopus superbus*; *Centris lilacina*, *Centris* sp. nov.; *Oxaea flavescens*; *Epicharis conica, E. rustica, E. affinis*; *Xylocopa frontalis, X. tegulata, X. similis*; *Bombus* spp.; *Euglossa intersecta, E.* cf. *ignita*; *Eulaema meriana, Eulaema nigrita, E. moczaryi*	Renner, 1984, 1986/1987
B. grossularioides (L.) Tr.	*Xylocopa* spp.; *Centris* spp.; *Epicharis conica*; *Bombus* sp.; *Euglossa* sp.	Roubik, 1979b; Renner, 1984, 1986/1987
B. pentamera Naudin (= *B. axinanthera*)	*Xylocopa frontalis*; *Centris* spp.; *Epicharis* sp.	Renner, 1984, 1986/1987
Chalybea corymbifera Naudin (= *Pachyanthus corymbifera* (Naudin) Cogn.)	hummingbirds	B. Stein, pers. comm., 1986
Clidemia bullosa DC.	*Melipona eburnea*; *Augochloropsis* sp.	Renner, 1984, and original
C. capitellata (Bonpl.) D. Don	*Augochloropsis* sp.	Renner, 1984
C. hirta (L.) D. Don	*Augochloropsis hebescens, A. callichroa*, halictids; *Melipona fulva, M. lateralis, Melipona* spp.; *Euglossa* sp.	Renner, 1984, and original
C. japurensis DC.	*Augochloropsis* sp.; *Melipona eburnea, M. compressipes, Melipona* spp.	Renner, 1984
C. rubra (Aubl.) Mart.	halictids; *Melipona* sp.	Renner, 1984
Henriettea horridula Pilger	*Xylocopa tegulata*; *Melipona* sp.	Renner, 1984
Henriettella caudata Gleason	*Euglossa* sp.; *Melipona* sp.	Renner, 1984
Huilea macrocarpa Uribe	hummingbirds	Snow & Snow, 1980
H. penduliflora Wurd.	hummingbirds	Snow & Snow, 1980
Leandra micropetala Cogn.	*Augochloropsis* sp.; Exomalopsini	Renner, 1984
L. secundiflora (DC.) Cogn.	*Augochloropsis* sp.	Renner, 1984
Leandra sp. 884	halictids	Renner, 1984
Loreya riparia Renner	*Xylocopa frontalis*	original
L. spruceana Triana	*Eulaema meriana*; *Xylocopa frontalis*	Vogel, 1966; Renner, 1984, in press

TABLE 4. Continued.

	Important Pollinators[1]	References
Miconia alata (Aubl.) DC.	*Melipona fulva*; *Lophothygater decorata*; *Paratetrapedia* sp.; *Augochloropsis hebescens*, *A. cupreola*, *A. callichora*; *Pseudaugochloropsis graminea*; *Exomalopsis auropilosa*; gen. nov. near *Megommation*	Renner, 1984 and original
M. alborufescens Naudin	*Augochloropsis callichroa*	original
M. affinis DC.	medium-sized bees	Bawa et al., 1985
M. argentea (Sw.) DC.	"numerous spp. of bees"	Frankie, 1976
M. argyrophylla DC.	halictids	Renner, 1984
M. dispar Benth.	*Augochloropsis* sp.; Exomalopsini; *Melipona marginata*; *Xylocopa similis*	Renner, 1984, and original
M. egensis Cogn.	*Xylocopa ornata*; *Exomalopsis auropilosa*; *Paratetrapedia* sp.	original
M. gratissima Benth.	*Xylocopa frontalis*; *Melipona* sp.	Renner, 1984
M. ibaguensis (Bonpl.) Triana	*Augochloropsis* sp.; *Xylocopa tegulata*, *X. muscaria*; *Melipona* sp.; Exomalopsini	Renner, 1984, and original
M. minutiflora (Bonpl.) DC. (824)	*Augochloropsis callichroa*; halictids; *Melipona* sp.	Renner, 1984; Ducke, 1902; Mori & Pipoly, 1984
M. myriantha Benth.	*Melipona* sp.	Renner, 1984
M. nervosa (Smith) Triana	*Paratetrapedia* sp.; *Augochloropsis* sp.	Renner, 1984
M. pileata DC.	*Augochloropsis* spp.	Renner, 1984
M. poeppigii Triana	*Melipona fulva*; *Paratetrapedia* sp.	original
M. radulifolia (Benth.) Naudin	*Paratetrapedia* sp.	Renner, 1984
M. robinsoniana Cogn.	*Xylocopa darwinii*	Linsley et al., 1966; McMullen, 1985
M. rufescens (Aubl.) DC.	*Melipona eburnea*; *Thygater* sp.	Renner, 1984
M. splendens (Sw.) Griseb.	*Melipona* sp.	Renner, 1984
M. tomentosa (L. C. Rich.) D. Don ex DC.	*Xylocopa frontalis*, *X. similis*; *Melipona* spp.	Renner, 1984
Miconia sp. 254	*Augochloropsis* sp.	Renner, 1984
Miconia sp. 626	*Melipona* sp.	original
Miconia sp. 1004	*Xylocopa tegulata*; *Melipona fulva*	original
Miconia sp.	*Eulaema cingulata*	Dodson, 1966
Miconia sp.	*Melipona* sp.	Roubik, pers. comm., 1987
Myriaspora egensis DC.	*Xylocopa* sp.	original
Tococa bullifera DC.	*Euglossa intersecta*, *E. piliventris*, *E. chalybeata*, *E. ignita*; *Eulaema meriana*; *Melipona fulva*; *Paratetrapedia* sp.; *Megaloptidia* sp.	Renner, 1984
T. coronata Benth.	*Euglossa* sp., *E. intersecta*; *Augochloropsis* sp.	Renner, 1984 and original
T. guianensis Aubl.	*Melipona compressipes*, *Melipona* sp.; *Xylocopa* sp.; *Eulaema* sp.; *Augochloropsis* sp.	Roubik, 1979b; Renner, 1984
T. longisepala Cogn.	*Eulaema mocsaryi*, *E. meriana*; *Euglossa intersecta*; *Centris* sp.; *Xylocopa frontalis*; *Melipona fulva*	Renner, 1984 and original
T. pachystachya Wurd.	*Bombus* spp.; *Xylocopa* sp.	Renner, in press
T. subciliata (DC.) Triana	*Euglossa* sp.	Renner, 1984
T. tepuiensis Wurd.	*Bombus* spp.	Renner, in press

TABLE 4. Continued.

	Important Pollinators[1]	References
Tococa sp.	*Melipona quinquefasciata*; *Exomalopsis fulvofasciata*	Laroca, 1970
BLAKEEAE		
Blakea anomala J. D. Smith	*Bombus ephippiatus, B. volucelloides*; *Eulaema seabrai*; *Epicharis* sp.; *Melipona fasciata, M. flavipennis*; *Neocorynura rupa*	Lumer, 1982
B. austin-smithii Standley	rodents (Peromyscini, Oryzomini)	Lumer & Schoer, 1986
B. chlorantha Almeda	rodents (Peromyscini, Oryzomini)	Lumer, 1980, 1982
B. gracilis Hemsley	*Bombus epihippiatus, B. volucelloides*; *Eulaema seabrai, E. cingulata, E. polychroma*; *Epicharis* spp.; *Melipona fasciata*; *Xylocopa frontalis*; halictids	Lumer, 1982
B. penduliflora Almeda	rodents (Peromyscini, Oryzomini)	Lumer & Schoer, 1986
B. sp. (as *B. grandiflora* Hemsley)	*Bombus epihippiatus, B. volucelloides*; *Melipona fasciata*; halictids	Lumer, 1982
B. tuberculata J. D. Smith	*Bombus epihippiatus, B. volucelloides*; *Eulaema seabrai*; *Xylocopa frontalis*	Lumer, 1982
Topobea brenesii Standley	*Bombus epihippiatus, B. volucelloides*; *Eulaema seabrai, E. polychroma*; *Epicharis* sp.; *Melipona fasciata*; *Xylocopa frontalis*; *Crawfordopsis* sp.; *Pseudaugochloropsis nigerrima*	Lumer, 1982
T. durandiana Cogn.	*Euglossa* sp.; *Pseudaugochloropsis nigerrima*	Lumer, 1982
T. praecox Gleason	*Eulaema "mexicana"* (Surely another species, since *E. mexicana* does not occur in Panama; J. Ackerman, pers. comm., 1985)	Croat, 1978
MEMECYLACEAE		
Mouriri guianensis Aubl.	*Ceratina* sp.; *Euglossa* spp.	Renner, 1984, and original
M. brevipes Hook.	*Eulaema nigrita*; *Xylocopa frontalis*	original
M. myrtilloides (Sw.) Poiret	*Euglossa imperialis, E. tridentata, Euglossa* sp.; *Paratetrapedia calcarata*	Buchmann & Buchmann, 1981
M. nervosa Pilger	*Euglossa chalybeata, E. crassipunctata, E. purpurata, E. viridis*; *Eulaema mocsaryi, E. meriana*; *Xylocopa frontalis, X. similis, X. ornata*; *Melipona fulva, M. marginata*	Renner, 1984, and original

[1] "Important pollinators" excludes the numerous *Trigona* species, which are omnipresent pollen scavengers on Melastomataceae. Note that "halictids" stands for many different species, the correct names of which cannot be ascertained at present.

Bees gathering pollen from Melastomataceae flowers must be able to shake it out of the anthers or else pull pollen grains out through the pores with their tongues. This latter mode of exploiting melastome flowers is used by a group of *Trigona* bees and does not usually result in pollination because these bees are too small to contact the stigmas. Another subgroup of *Trigona* bees, characterized by having toothed mandibles, cuts up melastome anthers and robs their pollen (Laroca, 1970; Renner, 1983).

The method of pollen collecting used by all other bees to extract pollen from melastome anthers was first described correctly by van der Pijl (1954). When approaching a flower, in flight, the bees orient themselves with the group of stamens and the style and then straddle the stamens. They usually grasp the filaments or the bases of the anthers, quite often using their mandibles. Therefore, after having been visited, flowers often show necrotic spots on the outside of the stamens where the bees held onto them. When the bees position themselves over the androecium, their potentially pollen-bearing surface contacts the stigma even before they start exploiting the anthers. Also, they strive to establish a firm contact with as many stamens as their body size permits, going to considerable efforts in order to bundle all 8, 10, or 12 stamens. Close contact between the bee and the stamens is necessary for pollen collection by means of thorax vibrations, which are transmitted to the stamens and cause the pollen to stream out of the anther pores. Electrostatic forces due to the net positive charge of the bees and the negative charge of pollen greatly aid pollen-load adhesion (Thorp, 1979). When a pollen load, taken with forceps from a freshly captured bee, is released near this bee, it jumps back onto it (pers. obs.). The very rapid distortions of the thorax-box (with the wings at rest) are made possible by the unique contractile properties of the bees' fibrillar indirect flight muscles. Pollen collecting by this method is always accompanied by a characteristic buzzing sound and has been termed "buzzing method" (van der Pijl, 1954; Michener, 1962).

The rapid vibrations used when harvesting melastome pollen presumably produce a high temperature of the flight muscles, which may mean that this method of pollen collecting is particularly appropriate during the relatively cool early morning hours. Also, there are ecological constraints on the activity of dark-colored bees during the hottest hours. Buzz pollination continues with very high humidity of the air and even during slight rains.

In most melastomes, pollen deposition and reception is on the lower abdomen (sternotribic) or lateral on the bees (pleurotribic); it is on the back (nototribic) in a few species with downwards-curved styles (e.g., species of *Meriania*, *Adelobotrys*, *Salpinga*) and in *Desmoscelis villosa*. In these cases, bees assume quite unexpected positions in order to vibrate the stamens; in *Adelobotrys rachidotricha*, for instance, they buzz with the head pointing outward and downward. Relatively large flowers, such as those of *Blakea*, *Topobea*, and *Bellucia*, are exploited by a wide range of bees (Lumer, 1982; Renner, 1986/1987). For example, stamens of *Bellucia* are vibrated by 33-mm-long *Centris* and 8-mm-long *Augochloropsis* bees. In the case of self-compatible species, visits by bees too small to contact the stigma and deposit foreign pollen may still result in self-pollen landing on the stigma when such small bees vibrate one or a few stamens.

Bees visiting Melastomataceae exhibit considerable steadiness during individual foraging flights: pollen loads often consist of almost pure melastome pollen with very few grains from nectariferous flowers or with grains from *Cassia* mixed in (Renner, 1984). *Cassia* has buzz-pollinated flowers, and bees often visit several such flowers (see below).

In Brazilian Amazonia, I have captured 80 species of bees, including the Africanized honey bee, *Apis mellifera scutellata* Lepeletier, vibrating melastomes. (A list of all bees, including the species of *Trigona*, may be obtained upon request.) Additional species have been captured in extra-Amazonian areas and at higher altitudes. To date, at least 100 species of bees have been found pollinating melastome flowers (Table 4; this does not include the numerous species of pollen-scavenging *Trigona* bees). The relatively few groups of bees that have been successful in tropical forest environments, the euglossines, halictids, *Xylocopa*, and *Melipona* (Michener, 1979) are the most important pollinators of lowland melastomes. In savannas, Centridini, Oxaeidae, Exomalopsini, and *Ptiloglossa* (Colletidae) become important, as do bumblebees in southern Brazil and at higher altitudes. The bee fauna in neotropical forests and savannas is still incompletely known; however, based on bee inventories in Panama, Costa Rica, French Guiana, Surinam, and at the mouth of the Amazon (Heithaus, 1979; Roubik, 1979a, b; and ref. in Michener, 1979), it may be estimated that only about 300 species of bees occur in these forests, a number that includes non-flower-visiting parasitic and leaf-cutter bees. Thus, between 80 and 100 species collecting pollen from Melastomataceae represents a high proportion of the total Amazonian bee fauna.

b) Floral attractants

Melastome pollen is an important pollen source for neotropical bees. This is clear from a survey of literature on bee foraging: it is collected by female euglossines (Moure, 1970; Janzen, 1971; Michener et al., 1978; Roubik, 1979a, b; Dressler, 1982; Renner, 1984), meliponines and halictids (Ducke, 1901, 1902; Laroca, 1970; Roubik, 1979a, b; Michener et al., 1978; Absy & Kerr, 1977; Absy et al., 1980), mixed with Malpighiaceae oil by anthophorine bees (Vogel, 1974; Renner, 1984), and makes up 96–100% of the nest provision of the colletid bee *Crawfordapis* (Roubik & Michener, 1985). A chemical analysis of *Bellucia dichotoma* pollen revealed high nitrogen and total crude protein. (I am indebted to S. Buchmann for analyzing a pollen sample in 1983.) In this species, the pollen has a strong perfume resembling that of the flowers.

Secondary attractants for bees include sweet or perfumelike floral odors produced by the petals, the connective, and the upper section of the style (as determined by neutral red staining; pers. obs.; method, Vogel, 1963), and the presence of a landing platform provided by the androecium. I have never seen bees land on the petals. Frequently, the filaments are adorned with glandular or eglandular hairs, which may make them easier for the bees to grasp. Also, direct alighting on the stamens may make visits to flowers with poricidal anthers particularly rewarding compared with flowers requiring further crawling and searching after landing.

Most Melastomataceae seem to be visited and pollinated early in the morning, sometimes 20 minutes before sunrise (F. Mueller, 1873; Frankie, 1976; Lumer, 1982; Renner, 1984), and many species close their petals by late morning. However, flowers of *Monochaetum* and *Rhynchanthera* open late, two to four hours after sunrise (Almeda, 1978; pers. obs.). Shedding of the flower parts usually starts at the end of the second day. Again, *Monochaetum* differs in having flowers that stay open for three days (Almeda, 1978), and I have seen *Graffenrieda fruticosa* flowers staying attractive for at least seven days. In the latter case, the adverse climatic conditions at 2,200 m altitude, where *Graffenrieda fruticosa* occurs, may place a high selective advantage on longer flowering periods which presumably heighten the flowers' chances of being visited.

The typical bee colors of most Melastomataceae flowers, white, purple, or pink, are due to total reflection and anthocyanins (Lowry, 1976; Bobbio et al., 1985). Yellow and orange flowers evolved repeatedly in isolated species throughout the family. Contrasting marks at the base of the petals and color changes during anthesis are frequent in Melastomataceae (F. Mueller, 1873; Ule, 1896; Wurdack, 1980; Renner, 1984). The colors change from white to red, from yellow to red, from white to purple, or from pink to white. The bright white of the small flowers of many herbaceous understory melastomes, e.g., species of *Aciotis*, *Leandra*, *Clidemia*, *Miconia*, and *Ossaea*, may be of selective advantage under conditions of low light intensity. Some melastome flowers tested (using a Kodak 18A Wratten filter) did not absorb ultraviolet light (Lumer, 1982), as was to be expected from the absence of flavonols from their petals.

The androecia of many species in the capsular-fruited tribes Merianieae, Bertolonieae, Microlicieae, Tibouchineae, and Rhexieae show a strong morphological differentiation into two sets of stamens. In addition, in such flowers the connective appendages may be large and stiff, forming 5, 10, or 15 usually yellow spurs, sometimes positioned like true anthers. Based on his brother's (Fritz Mueller) observations on a southern Brazilian species of "*Heeria*," Hermann Mueller (1881, 1883) was the first to suggest that this dimorphism was the ultimate result of a "division of labor" between the two sets of stamens (his illustration shows that his brother was probably dealing with a species of *Microlicia*; *Heeria* is synonymous with *Heterocentron*, which does not occur in southern Brazil). According to this idea, the conspicuous anthers attract the bees and offer "food pollen" as a reward, whereas the less conspicuous ones contain "functional pollen." The "functional pollen" is supposed to be placed on a part of the bee where it will not be groomed off and used as food for larvae. It will instead function in fertilization. Hermann Mueller's idea caught on immediately (Forbes, 1882; F. Mueller, 1883) and is usually mentioned as typical of the pollination strategy of Melastomataceae (e.g., Cammerloher, 1931; Percival, 1965; Kugler, 1970; Proctor & Yeo, 1972; Baker, 1978; Faegri & van der Pijl, 1979).

A partitioning of the bee surface would be necessary for selection to favor the pollen grains from one set of stamens over those from the other and thus lead to pollen dimorphism. Pollination mechanisms involving vibration of anthers, however, may not allow a sufficiently precise placement of pollen from two sets of stamens on bees. Forbes (1882), working with unnamed species of *Melastoma*, reported that "only the pollen from the long stamens seemed [sic] to be fertile"; yet he found pollen from both types of stamens on the stigmas. To date, with the exception of Forbes's report

(1882), no morphological or physiological differences between pollen grains from dimorphic stamens have been found in any of the Melastomataceae studied (Darwin, 1876; Ziegler, 1925; Whiffin, 1973; Almeda, 1977; Renner, 1984). Further experimental fieldwork is needed to assess whether the staminal dimorphism and the stamen appendages have a function beyond that of enhancing the visual attractiveness of the flowers and making the stamens easier to grasp for bees. In view of the importance of pollen aromas for guiding bee behavior (cf. Dobson, 1987), it is uncertain if the visual cues provided by the yellow connective appendages by themselves elicit pollen-collecting behavior.

POLLINATION OF NECTAR-PRODUCING MELASTOMATACEAE BY BIRDS, BATS, RODENTS, AND BEES

Some 60 species of *Meriania*, *Centronia*, *Brachyotum*, *Tibouchina*, *Miconia*, *Huilaea*, *Chalybea*, and *Blakea*, all of them, except the species of *Miconia*, occurring at higher altitudes (1,600–3,400 m), offer nectar as a reward for their pollinators. On the basis of their character syndrome (see below), *Meriania drakei* (Cogn.) Wurd., *M. furvanthera* Wurd., *Axinaea weberbaueri* Cogn., and several other species of *Meriania*, *Axinaea*, *Centronia*, and Tibouchina are expected to produce nectar, too.

The first reports on nectar production in melastomes are by Ule (1895, 1896). In three species of *Tibouchina* (Table 4) growing on the Brazilian Itatiaia mountain range, he observed that nectar was produced by the staminal vascular bundle and secreted either directly from the filaments or sometimes through a slit in the filaments. He suggested bumblebees as the probable pollinators of these species. At Ule's request, the chemist T. Peckolt analyzed the stamens of another species that did not secrete nectar (Ule gave the name as *T. glareosa* Cogn.; there is no such name, and he probably meant *T. granulosa* Cogn.). Peckolt found that sugar was present "in great quantity," which suggested to Ule (1896) that this was likely true for other species of *Tibouchina* as well. In several other nectariferous melastomes, slits in the upper ventral side of the filaments have been observed, e.g., in *Tibouchina cleistoflora* Ule (Ule, 1896; pers. obs.), *T. grossa*, *Blakea chlorantha* (Tobe et al., in prep.), *Brachyotum ledifolium*, *B. andreanum* Cogn., *B. benthamianum* Triana, and *B. rugosum* Wurd. (Lagerheim, 1899; pers. obs.). They have also been found in non-nectariferous species—such as *Centradenia grandiflora*, *Heterocentrum roseum*, *Triolena pustulata* (as *Bertolonia pubescens*)—and in paleotropical species of *Dissotis* and *Medinilla* (Ziegler, 1925). These slits appear not to be consistently formed sutures, but rather spontaneous ruptures. The anatomy of the nectariferous tissue is being studied by Tobe et al. (in prep.).

Reports of nectar in *Miconia minutiflora* (Mori & Pipoly, 1984) are unclear, since its presence in the minute flowers (2.5 mm in diameter, style 4 mm long) was only presumed. In central Amazonia, where I have observed this species, it did not produce nectar (Renner, 1984). However, in another *Miconia* species in the Belém region at the mouth of the Amazon, Roubik measured floral nectar of ca. 20% sugar concentration and collected *Melipona* and *Apis* (!) bees (Roubik, pers. comm. 1987). Recently, nectar production has also been confirmed in the Antillean endemics *Miconia sintenisii* Cogn. and *Mecranium amygdalinum* (Desr.) Wright (Dent, pers. comm.). *Miconia robinsoniana*, also with minute white flowers, was included under "nectar sources" in a summary of flower records for *Xylocopa darwinii* by Linsley et al. (1966). McMullen, who made further observations on the floral visits of this bee on Galápagos (McMullen, 1985), has never noticed any nectar in *M. robinsoniana* (McMullen, pers. comm., 1987).

Except in *Miconia*, nectar production in Melastomataceae is correlated with floral morphological changes that relate to the fact that the nectar collectors do not vibrate the stamens. Therefore, when nectar instead of pollen is the pollinator reward, the latter must be deposited on a visitor during nectar uptake. This is achieved by the anthers having rather large pores and being stiffened, particularly at the base. Pressure on the base of the anthers exerted by the head of a bee, the bill of a bird, or the front paws of rodents clasping the flowers ejects pollen onto the visitor. Lagerheim (1899) therefore speaks of "bellow" anthers; he found that a match the thickness of a hummingbird bill pushed into the flower of *Brachyotum ledifolium* so that it pressed the anther bases brought forth a pollen cloud 3 cm long. The flowers of the nectariferous species are inclined or pendent and, in the case of the bird-pollinated ones, usually dark red, deep purple, or bluish to almost black. In *Brachyotum ledifolium* the petals are yellow, but the hypanthium is covered with bright red hairs. In nectariferous melastomes, the petals do not spread at anthesis but remain convolute almost like in bud. Vogel (1957) reported a nocturnal cabbage odor in the predominantly bat-pollinated *Tibouchina grossa*. The other nectariferous melastomes are reported as scentless.

The bulk of nectariferous melastomes seem hummingbird-pollinated (Table 4). Most of them belong to the genus *Brachyotum*, which comprises 50 species, the majority ornithophilous (Wurdack, 1965, 1980; Lagerheim, 1899; Vogel, 1957; Fitzpatrick et al., 1979; label data). Other bird-pollinated species are *Meriania tomentosa* (Cogn.) Wurd. (*Centronia excelsa* (Bonpl.) DC.; van der Werff, pers. comm.; D. Neill, pers. comm.). Nectariferous and hummingbird-pollinated species in the Miconieae are *Huilea macrocarpa*, *H. penduliflora* (Snow & Snow, 1980) and probably also *Chalybea corymbifera* (in which Stein observed nectar but no pollination events; pers. comm., 1987). The Colombian *Tibouchina grossa* is pollinated by bats and hummingbirds (Vogel, 1957; Stein, pers. comm., 1987) and certainly the same is true of *T. Stricta* Wurd. and *T. reticulata* Cogn.

New World rats and mice of the tribes Peromycini and Oryzomini pollinate at least three nectariferous species of *Blakea* in Costa Rica (Lumer, 1980, 1982; Lumer & Schoer, 1986). Lumer found that bees and hummingbirds rarely visited the flowers of these species during the day but that nectar secretion was nocturnal. The *Blakea* species involved are hemiepiphytic, and their flowers are positioned close to the stem where the rodents can reach them conveniently.

The nectar of *Blakea chlorantha* contains ca. 11% sucrose (Lumer, 1982, and pers. comm.); that of *Huilea macrocarpa* has 12–16% with a mean of 13.4% (Snow & Snow, 1980); that of *Chalybea corymbifera* 16.5%; and that of *Brachyotum ledifolium* 20–22% (Tobe et al., in prep.). It would thus be classified as relatively rich in sucrose in the nectar class system of Baker & Baker (1983), who found that sucrose-rich or sucrose-dominated nectar prevails in hummingbird flowers. Thus, nectariferous melastomes offer a reward "intended" for pollinators other than bees.

The evolutionary origin of pollination systems involving nectar in Melastomataceae is considered below.

MEMECYLACEAE

In their pollination mechanism, the neotropical Memecylaceae closely resemble the Melastomataceae, and the above description of bees' methods of pollen collecting from melastome flowers also applies to them. In *Mouriri*, the anthers are stiff, with thickened endothecial walls, and are slightly prolonged just above the insertion of the filaments. The prolongations, termed "caudae" (Morley, 1953), are used as footholds by the bees exploiting *Mouriri* anthers. Pollination in four species of *Mouriri* has been observed (Table 4); the main pollinators seem to be euglossines, followed by *Xylocopa* and *Melipona* species. They are legitimate visitors, i.e., large enough to contact the stigma regularly while collecting the reward. Memecylaceae anthers differ from those of Melastomataceae in bearing dorsal concave glands, 0.3–0.8 mm long. (For illustrations of the permutations in size and position of these glands in *Mouriri* and *Votomita*, see Morley, 1953, 1976, and 1985.) None of the legitimate pollinators show any interest in the staminal glands (Buchmann & Buchmann, 1981; Renner, 1984, and unpubl.).

Earlier (1984), I reported that *Melipona marginata* and *M. fulva* sometimes collected the secretion from the glands with the front legs, and that they mixed this substance with their pollen loads between pollen-collecting bouts on the wing. Further field observations, however, have convinced me that *Melipona* does not regularly touch the glandular surface when buzzing. The bees grip the stamens by the anther caudas just below the glands, and it is difficult to see what they do with their feet or their mouth parts when vibrating because they curve tightly over the anthers to allow the pollen stream to settle on their bodies. Between buzzing bouts, *Melipona* bees (and the euglossines) rotate over the androecium so as to drum out the pollen from all ten anthers. Staining of their freshly collected corbicular loads with Fehling solution showed that the pollen had been wetted with sugar. With Sudan III (a lipid stain), *Mouriri* pollen grains stained red, but the secretion holding them together did not; this implies that the pollen contains lipids, whereas the secretion did not.

Mouriri flowers are also visited by several species of *Trigona*. These small bees do not regularly contact the stigma but rob pollen from the anthers, which they are unable to buzz. Their role as pollen scavengers and robbers in Melastomataceae is well known (Renner, 1983). When cutting up anthers of *Mouriri nervosa* to reach pollen grains further down, *Trigona williana* very rarely touched the glands (Renner, 1984, and unpubl.). Most often, *T. williana* cut off the anthers above the glands, then stopped and started cutting and robbing the pollen of another anther. This shows that this pollen robber, like the legitimate pollinators, does not regularly collect the glandular exudates. Buchmann & Buchmann (1981) have observed *T. pallens* manipulating the glands of *M. myrtilloides* with the front legs and mouth parts.

The secretion of the staminal glands is yellow, viscous, stains red in Sudan III, and tests positive

for fatty substances. That of the relatively large (0.8 mm long) glands of *M. lunatanthera* forms myelin figures in water after a drop of sodium hydroxide is added (pers. obs.; method from Vogel, 1974). The secretion in *M. myrtilloides* has been reported to be a lipoidal mixture of many compounds (e.g., phenolic compounds, small amounts of glucose and saponin, at least 13 fatty acids, and free fatty acids) and to be "extremely rich in non-lipid constituents" (Buchmann & Buchmann, 1981).

Since the secretions from the floral glands contain lipids, the relationship between *Mouriri* and oil-collecting bees is of particular interest. Floral oils are collected by bees belonging to relatively few genera of Anthophoridae (e.g., *Centris*, *Epicharis*, *Monoeca*, *Paratetrapedia*, *Tapinotaspis*, *Tetrapedia*; cf. Vogel, 1974; Neff & Simpson, 1981). Although many of these collect pollen from Melastomataceae (comp. Table 4), to date only a single anthophorid bee species, *Paratetrapedia calcarata*, has been observed on *Mouriri* (Buchmann & Buchmann, 1981). This bee, due to its small size (7–8 mm long), rarely vibrated more than two or three of the ten anthers in each flower and only rarely touched the stigma (l.c.). Also, Buchmann & Buchmann (1981) reported that *Paratetrapedia calcarata* was an infrequent visitor of *M. myrtilloides* (16 times during 50 hours) and not a legitimate pollinator.

The secretion of the staminal glands forms a shiny film on the gland cuticle and in this respect differs greatly from the lipid-filled blisters of other epithelial elaiophores (Vogel, 1974). *Paratetrapedia* has scrapers on the fore-basitarsi (Neff & Simpson, 1981) and ruptures the cuticle of the elaiophores from which it collects oils. While scrutinizing hundreds of stamens from *Mouriri nervosa* and *M. guianensis* under the stereoscope in order to collect their glandular secretions, I never found signs of the glands having been scraped. This was perhaps to be expected, since the secretion forms a film on the outside of the cuticle.

A further problem in understanding the role of the staminal glands is that they are so small and positioned in such a way that the collection of any exudate either with the fore-basitarsi or the mouth parts by the medium-sized bees that pollinate *Mouriri* is difficult to envisage. Visitors small enough to be attracted by the minute quantities of secretion offered (such as the *Paratetrapedia* species observed by Buchmann & Buchmann, 1981) are not large enough to touch the stigmatic surface when manipulating the glands, especially since the styles in *Mouriri* are always longer than the stamens and the stigmas are held well away from the anthers.

A possible role of the staminal glands suggested by Morley (1976) is odor production. *Mouriri* species often have a strong perfume scent (Buchmann & Buchmann, 1981; Renner, 1984). Perhaps a volatile oil would persist longer when mixed with the fatty oils and other compounds. Buchmann & Buchmann (l.c.) suggested that the glands, which absorb ultraviolet light, might visually guide the bees to the pollen. Extending this idea, one might ascribe a pseudonectary role to the staminal glands. It is interesting that in the Bonnetiaceae, at least 23 species of *Caraipa* and *Mahurea* have very similar minute urceolate glands positioned subapically on the connective (Kubitzki, 1978). The role of these glands, as of those of *Mouriri*, is obscure.

Seed Dispersal in Melastomataceae

Of the neotropical Melastomataceae, 40% have capsular fruits and wind-dispersed seeds (Renner, 1986). The remaining 60% have soft, juicy berries and endozoochorous seeds. Animal-dispersed Melastomataceae are most diverse in lowlands and montane forests, whereas the capsular-fruited tribes are richest in species in various types of savannas. Melastome capsules are often sturdy and persist on the plants for many months, during which the seeds are gradually shaken out. There are no data on dispersal distances in the wind-dispersed species; however, the many striking disjunctions observed in savanna melastomes (Renner, 1987b, and in press) probably attest to their good dispersability. Small herbaceous understory species with broadly conical capsules (*Salpinga*, *Monolena*, *Bertolonia*) may also have their seeds dispersed ballistically by raindrops.

Melastome berries range in size from five to ca. 35 mm in diameter. The smaller ones are of outstanding importance for small frugivorous birds throughout the Neotropics (Huber, 1910; Snow, 1965, 1971, 1981; Ricklefs, 1977; Skutch, 1980; Lumer, 1982; Wheelwright et al., 1984; R. Bierregård, pers. comm., and many additional references). Epiphytic Melastomataceae are mostly bird-dispersed (Renner, 1986), as are many of the most successful pioneer species, for example, *Clidemia hirta*, which has become a noxious weed in Africa, Asia, and Hawaii.

Fruit attributes, such as position, size, aroma, and color, indicate that different animal classes act as the principal dispersers in different species groups. For example, black spider monkeys are the predominant consumers and likely dispersers of the green, slightly astringent and relatively large berries of the tree *Bellucia grossularioides* in Surinam (Roosmalen, pers. comm.). In French Guiana,

this species is a favorite with the *Philander opossum* (Atramentowicz, 1982), which also eats *Henriettea* and *Loreya* fruits. However, a search of recent literature on feeding records (Renner, 1987a) showed that Melastomataceae are not among the preferred foods of either monkeys or bats (for bats, Fleming, 1986; but compare Foresta et al., 1984, and Fleming, 1988). Perhaps because the majority of Melastomataceae are shrubs or understory trees with terminally positioned infructescences, they are unsuited for foraging monkeys and bats. Also, the taste of the mostly sweet, watery melastome berries may not be to the liking of monkeys, which apparently prefer slightly acidic fruits (Sourd & Gautier-Hion, 1986).

Fruits that have fallen to the ground are often eaten by turtles (Moskowitz, pers. comm.; Roosmalen, pers. comm.), lizards (W. Magnusson, pers. comm.), rodents (Magnusson & Sanaiotti, 1987), tapirs (Huber, 1910), and ants (pers. obs.).

Seed Dispersal in Memecylaceae

All Memecylaceae have berries, ranging in size from 0.5 to 10 cm long; color at maturity is most commonly yellow to red, less often it is purple-black to black (Morley, 1976). The smaller-fruited species are surely bird dispersed; some larger-fruited ones are monkey-dispersed (Roosmalen, 1985). Fish eat the fruits of at least one riverine *Mouriri* species (Goulding, 1980), which is curious, since Morley (1976) reported that two other species are used for poisoning fish.

Reproductive Biology and the Evolution of Melastomataceae and Memecylaceae

Floral morphology in Melastomataceae and Memecylaceae can only be understood as the result of coevolution between the earliest ancestors of these groups and pollen-collecting bees. Flowers of the Old World members of both families have the same basic construction as those of their New World relatives and, although little information is available on their floral biology, van der Pijl's (1939) detailed description of the pollination mechanism in some species of *Osbeckia*, *Medinilla*, and *Melastoma* makes it likely that they are pollinated in the same manner as the New World ones. The pollen offered in the poricidal stamens of both families is accessible exclusively to bees, but not to many of the most common ones, such as the numerous species of *Trigona* and the paleotropical *Apis*, which apparently do not vibrate stamens. Most Melastomataceae and Memecylaceae have "modern" pollen flowers in the sense of Vogel (1978), in which the visitor is forced into a fixed position while harvesting the reward and in which the position of the stigma is of relatively little consequence because of the deposition of pollen on a large part of the visitor's surface.

There appears to be little opportunity for partitioning the bee body. Sharing of pollinators, noted rather frequently among sympatric buzz flowers (Linsley & Cazier, 1963; Macior, 1970, 1971; Thorp & Estes, 1975; Lumer, 1982; Renner, 1984), results in hybridization in the absence of genetic barriers. This is consistent with the fact that systematists working with Melastomataceae and Memecylaceae often notice hybrids (Kral & Bostick, 1969; Whiffin, 1973; Morley, 1976; Almeda, 1978; Solt & Wurdack, 1980; Renner, in press). The data on Melastomataceae breeding systems corroborate the suggestion that apomixis may be more widespread in the tropics than formerly thought (Kaur et al., 1978; Ashton, pers. comm., 1987). Apomictic seed production would make such species independent of pollinators, while retaining the advantages of producing seeds, i.e., the potential for dispersal and dormancy. Most notably, it would give them the capacity to build up a new population from a single propagule.

Statements that "details of the structure of the anthers doubtless relate to mechanisms of pollination" (Cronquist, 1981) or "in a family, such as the Melastomataceae, where floral evolution has been extensive, one may logically conclude that the diverse floral types represent adaptations to different pollination systems" (Almeda, 1977) are not corroborated by field data. Rather, Melastomataceae seem to confirm Macior's (1971) suggestion that buzz pollination is so successful a system that, once it is established, hardly any other pollination mechanism evolves, even in species-rich groups. Compared with other families, such as Lecythidaceae, Gesneriaceae, and Bignoniaceae, for which the overall pollination spectrum is fairly well known, Melastomataceae and Memecylaceae show little diversification in floral morphology and pollination strategies. In this they resemble Malpighiaceae (Anderson, 1979) and Solanaceae (Symon, 1979), which also have relatively specialized pollination systems and faithful bee pollinators. Such lack of diversification could be interpreted as the result of being stuck on an adaptive peak.

Melastomataceae that offer nectar are pollinated by a broader range of pollinator classes, namely by hummingbirds, bats, rodents, and bees; this statement applies to the individual species as well, several of which have more than one important pollinator type, for instance birds and bats in *Tibouchina grossa* and bees and rodents in *Blakea chlorantha*. Cruden (1972) suggested, as a possible

ecological significance for nectar production at higher altitudes, that under adverse climatic conditions the homoiothermic birds and mammals may be more reliable pollinators than bees. If valid, this explanation would apply to all now known nectar-producing Melastomataceae, except the species of *Miconia*.

Whether the thousands of pollen-only Melastomataceae derived from ancestors with nectar flowers or whether the proto-Melastomataceae never possessed nectaries (as suggested by Vogel, 1978) is a difficult question. Phylogenetically, the extant nectariferous species belong to groups not closely related: *Meriania* and *Centronia* are in the capsular-fruited Merianieae (as is *Axinaea*, which probably also has some nectariferous species, see above); *Brachyotum* and *Tibouchina* are in the likewise capsular-fruited Tibouchineae; *Chalybea*, *Huilea*, and *Miconia* are in the berry-fruited Miconieae; and *Blakea* is in the also berry-fruited Blakeeae. Thus nectar production occurs in at least five evolutionary lines: the first leading to *Meriania* and *Centronia* (which are not closely related to each other), the second to *Brachyotum* and *Tibouchina* (the first genus is a segregate of the second; Wurdack, 1954), the third to *Chalybea* and *Huilea* (two intimately related genera), the fourth to *Miconia* (with 1,000 species, only two of which to date are securely known to produce nectar), and the fifth to *Blakea*. Nectaries could have originated independently in all these lineages.

The problem is confounded by the slits observed in the filaments of some non-nectariferous Melastomataceae exactly in the same position as in some of the nectariferous species, where nectar is secreted through them. They occur in species of *Heterocentron* (Tibouchineae), *Bertolonia* (Bertolonieae), and *Centradenia* (Microlicieae) and in the paleotropical genera *Medinilla* and *Dissotis* (compare above under nectariferous melastomes) and may be rudimentary, nonfunctional nectaries. Thus, to date, only in two of the neotropical tribes—the small Rhexieae with 64 species and the Cyphostyleae with nine species—are nectar production or presumed rudimentary nectaries absent. In view of the presence of nectaries in at least five neotropical lineages and the indications of their former presence in two further ones, their parallel independent origin becomes hard to accept. Instead, I suggest that the capacity for developing nectaries is basic in the Melastomataceae but suppressed in most modern members.

To understand the origin of the memecyloid connective gland, whatever the chemical composition of its secretion, the following observations seem relevant. Functioning nectaries have been observed on the hypanthia of *Memecylon edule* Roxb. (= *M. ramiflorum* Desr.; Burck, 1891) and *M. floribundum* Blume (Zimmermann, 1932). Also, I have frequently seen ants on the hypanthia of *Mouriri nervosa*, which may be an indication that this neotropical Memecylaceae also secretes sugar, albeit in minute quantities. Evolutionarily, the capacity to secrete minute quantities of exudates directly through the hypanthium epidermis, without conspicuous morphological structures, may be correlated with the development of the staminal glands. However, data on the pollinators and the chemical composition of the exudates of paleotropical Memecylaceae are needed before the significance of the staminal glands in the family as a whole can be assessed. The Memecylaceae have ca. 340 Old World and 89 New World species, and it should be noted that, in the opinion of Morley (1953), the New World Memecylaceae are more basal than the Old World ones.

There is a great amount of parallelism between the Old World and the New World tribes in the Melastomataceae: the Oxysporeae, Sonerileae, Dissochaeteae, and Osbeckieae resemble more or less closely the Merianieae, Bertolonieae, Miconieae, and Tibouchineae, respectively, of the New World (Gleason, 1932). Based on wood anatomy, the differentiation into at least some of these tribes and into Melastomataceae and Memecylaceae occurred before the breakup of Pangaea (Vliet et al., 1981). However, the coevolutionary relationships between bees and proto-Melastomataceae, which are a conditio sine qua non for the evolution of the melastome androecium, can only have begun during the mid-Cretaceous when bees arose (Michener, 1979). The mid-Cretaceous may thus have been the time when the ancestors of these families switched from nectar-reward flowers to pollen-reward flowers (with the pollen presented in poricidal anthers and available only to bees). Likely, the Melastomataceae and Memecylaceae originated during Aptian times (lower mid-Cretaceous, 110 million years before present), when the gap between Brazil and Ghana was still very narrow; their east and west Gondwanian lineages, probably coevolved in parallel with the earliest bees. The oldest fossil melastome leaves are known from the early Eocene (Hickey, 1977), about 53 million years before present, and Eocene and Miocene leaves occur widely scattered throughout the Northern Hemisphere (Wurdack & Kral, 1982). Therefore, members of the family (and some of their pollinators?) at one time may have dispersed via Europe between North America and Africa.

The Melastomataceae, with two-thirds of their species in the Neotropics, have much of their di-

versity centered in areas of varied topography—the Andes, Guayana, and south-central Brazil. The neotropical Memecylaceae, on the other hand, are centered in the Amazonian lowlands, where they appear adapted to different soil types (pers. obs.). The very early shift from anemochory to zoochory in the Melastomataceae was probably one of the reasons for their success in the understory of closed forests, where animal dispersal is more advantageous than wind dispersal. (The capsular-fruited tribes are much more diverse in open habitats and have relatively few species in forests.) The crucial points in the radiation of large groups within the Melastomataceae, besides their different seed-dispersal strategies, have been the acquisition of particular plant architectural, indument, and leaf venation characters. Because adaptations to different pollinator types played such a limited role in the radiation within the two families, the floral biological data cannot be used to support either of the two suggested phylogenies for the Melastomataceae (Wurdack in Welle & Koek-Noorman, 1981; Vliet et al., 1981).

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FLORAL NECTARIES IN MELASTOMATACEAE AND THEIR SYSTEMATIC AND EVOLUTIONARY IMPLICATIONS[1]

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ABSTRACT

The vast majority of the 4,500–5,000 species in the primarily tropical family Melastomataceae do not produce floral nectar, instead relying on pollen as the pollinator reward. To determine the anatomical basis for nectar production in the relatively few nectar-producing taxa, we examined 40 species in 17 genera representing known nectar producers and genera and species not reported to secrete nectar. Our anatomical investigations included six species in three genera of Memecylaceae, a family traditionally placed within Melastomataceae. We also conducted field observations to clarify the site of nectar secretion in several genera. No structural nectaries (derived from differentiated parenchyma) were detected in any of the species examined. Rather, most nectar-secreting species appear to produce the nectar from a thickened staminal vascular bundle. Within the order Myrtales, this type of nonstructural androecial nectary is limited to Melastomataceae and is apparently very rare among angiosperms as a whole. Two additional methods of nectar production in Melastomataceae were revealed: secretion from the petal tips in *Medinilla*, and, although field confirmation is still required, from the stigma in *Miconia*. Given the ancestral myrtalean nectary type, it seems clear that structural nectaries were lost in the evolutionary lineage ancestral to Melastomataceae and Memecylaceae. In most nectar-producing Melastomataceae the re-evolution of nectaries appears to be related to a shift in pollinator interactions, specifically from vibratile-pollination bees at lower elevations to vertebrates at higher elevation. We consider the independent development of nectaries in several lineages of Melastomataceae to be the most parsimonious explanation for the diversity of nectary types within the family and for the scattered phylogenetic positions of nectar-producing taxa.

The family Melastomataceae, with ca. 200 genera and 4,500–5,000 species, is the largest in the order Myrtales. This primarily tropical family is distributed worldwide but particularly well represented in tropical and subtropical areas of the New World. Most members of the family produce no floral nectar, relying instead on pollen as the principal pollinator reward (for review see Renner, this volume). Species in at least two genera, *Tibouchina* (= *Purpurella*) (Ule, 1896) and *Brachyotum* (Lagerheim, 1899), however, have long been known to produce nectar. Additional observations of nectar production, or presumed production, have been made more recently on these and several other melastome genera, including *Blakea* (Lumer, 1980; Lumer & Schoer, 1986), *Huilaea* (Snow & Snow, 1980), and *Miconia* (Mori & Pipoly, 1984). Most reports that note the location of nectar secretion within the flower generally found the nectar to emanate from the stamens. This strongly contrasts with the situation in most myrtalean families in which floral nectaries are located either on the floral tube, the gynoecium, or at the floral tube–gynoecium junction.

Floral nectaries of Melastomataceae have been little studied, and nothing has been reported pre-

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viously about their anatomical structure. The primary purpose of this study is to elucidate the structure of Melastomataceae nectaries through anatomical examination and to confirm the unusual location of nectar secretion through field observations. Our investigation of floral nectary structure extends to representative genera of Memecylaceae, a family traditionally included in Melastomataceae as a tribe or subfamily. The anther connective of Memecylaceae contains a distinctive depressed gland structure that had previously been described as a nectary (Burck, 1891; Subramanyam, 1949). In *Mouriri*, however, these glands have recently been found to secrete a lipid-rich substance, suggesting that they are elaiophores (Buchmann & Buchmann, 1981).

Materials and Methods

We examined anatomically flowers of 40 species in 17 genera of Melastomataceae, representing known nectar producers and genera and species not reported to secrete nectar. In addition, six species of Memecylaceae in three genera were investigated. FAA-fixed collections were made by the authors and by numerous collaborators worldwide (Table 1).

After dehydration through a t-butyl alcohol series and embedding in Paraplast with MP 57–58 C°, flowers (and sometimes stamens alone) were sectioned transversely and longitudinally at 8–10 μm thickness; the sections were stained with hematoxylin, safranin, and fastgreen FCF and were mounted with Entellan. Dark staining by hematoxylin represents a concentration of cytoplasm in cells, indicating high metabolic activity such as seen in active nectaries. In other families of the Myrtales, this staining method has fully demonstrated the location and size of nectariferous tissue (Tobe, pers. obs.); if present, nectaries are thus easily distinguished from other tissue by their dense staining.

We noticed that certain species, particularly those known to secrete nectar, have a conspicuously thickened staminal vascular bundle. Thus, for comparative purposes, the thickness of the staminal vascular bundle is presented as a relative value (Table 1). The "relative thickness" of stamen vascular bundles is calculated as: radial thickness of the vascular bundle (t)/radial thickness of the filament (T). Calculations were made on the basis of two or three stamens. Relative thickness values are presented as a range, since the thickness of the filament and the vascular bundle can differ at varying points along the same filament.

Field observations of nectar secretion in *Brachyotum*, *Chalybea*, and *Tibouchina* were conducted while field collecting floral material for this study. Fresh flowers were examined for evidence of nectar, and the location of nectar secretion within the flower was noted. Nectar quantity and sugar concentration were measured using microcapillary tubes and a Reichert temperature-compensated hand refractometer (model 10431). Nectar sugar concentration measurements (% brix) were subsequently converted to sucrose-equivalents (weight by total weight).

Results

We did not detect densely staining structural nectaries in the flowers of any of the species examined of Melastomataceae and Memecylaceae. Three significant features were noted, however. First, stamens of some melastomes, particularly those known to secrete nectar, have a markedly thickened vascular bundle in relation to the filament or anther connective. Relative thickness of staminal vascular bundles of nectar-producing and non-nectar-producing species are presented in Table 1. The relative thickness values of staminal vascular bundles in nectar-producers normally exceed 0.3 (mean 0.34), whereas most other melastomes examined range between 0.1 and 0.3 (mean 0.23), a statistically significant difference ($P < 0.001$). Second, although no densely staining structural nectaries were found, many of these thickened vascular bundles showed relatively dark-staining phloem cells, indicating that they are cytoplasm rich and may be fulfilling a nectary function. Third, many of the nectar-secreting species have external slits that develop on or near the geniculum of the filament and that may represent a nectar emission pathway.

Information on the site of nectar secretion and on known or putative pollination vectors for nectar-producing Melastomataceae is summarized in Table 2. Examined genera that are known or strongly suspected to produce nectar are discussed individually below. Members of several other genera may also secrete nectar but were not examined. These include two additional Andean genera that hummingbirds have recently been observed visiting, *Centronia excelsa* (Bonpl.) DC. (Neill, pers. comm., 1987) and *Meriania tomentosa* (Cogn.) Wurdack (van der Werff, pers. comm., 1987).

MELASTOMATACEAE

Blakea. Three species of *Blakea* were examined anatomically, with *B. chlorantha* Almeda known

TABLE 1. Species examined anatomically. Relative thickness of staminal vascular bundles given at right. Tribal positions of genera essentially follow Cogniaux (1891) and van Vliet et al. (1981).

Species	Collection Voucher	Relative Thickness of Staminal Bundle, t/T (see Figs. 5 and 10)
Melastomataceae		
Tribe Microlicieae		
Rhynchanthera paludicola (J. D. Smith) Gleason	Costa Rica, *Grayum et al. 6009* (MO)	0.24–0.26
Tribe Tibouchineae		
Brachyotum campanulare (Bonpl.) Triana	Ecuador, *Stein & D'Alessandro 2709* (MO)	0.32–0.40
B. ledifolium (Desr.) Triana	Ecuador, *Stein et al. 2701* (MO)	0.39–0.45
B. ledifolium (Desr.) Triana	Ecuador, *Stein 2892* (MO)	0.32–0.37
B. lindenii Cogn.	Ecuador, *Stein 2890* (MO)	0.33–0.34
B. microdon (Naud.) Triana	Bolivia, *Solomon 13089* (MO)	0.33–0.36
B. sanguinolentum (Naud.) Triana	Bolivia, *Solomon 13859* (MO)	0.32–0.33
Heterocentron elegans (Schlecht.) Kuntze	Cultivated, Royal Botanic Gardens, Sydney, *Griggs 7145* (NSW)	0.16–0.23
Tibouchina bicolor (Naud.) Cogn.	Bolivia, *Solomon 13862* (MO)	0.30–0.36
T. clavata (Pers.) Wurdack	Cultivated, Mathias Botanical Garden, *Prigge 6525* (UCLA)	0.29–0.31
T. grossa (L.f.) Cogn.	Colombia, *Stein & McDade 3147* (MO)	0.38–0.41
T. heteromalla Cogn.	Cultivated, Mathias Botanical Garden, *Prigge 6445* (UCLA)	0.19–0.24
T. laxa Cogn.	Cultivated, Mathias Botanical Garden, *Prigge 6211* (UCLA)	0.32–0.33
T. multiflora Cogn.	Cultivated, Mathias Botanical Garden, *Prigge 6524* (UCLA)	0.24–0.28
T. semidecandra (DC.) Cogn.	Cultivated, Missouri Botanical Graden, *Tobe s.n.* (no voucher)	0.34–0.37
T. stenocarpa (DC.) Cogn. var. *boliviensis* Cogn.	Bolivia, *Solomon 13231* (MO)	0.32–0.35
T. urvilleana (DC.) Cogn.	Cultivated, Mathias Botanical Garden, *Prigge 6444* (UCLA)	0.32–0.34
Tribe Rhexieae		
Monochaetum floribundum (Schlecht.) Naud.	Mexico, *Breedlove & Almeda 56716* (CAS)	0.27–0.33
Tribe Sonerileae		
Sonerila picta Korth.	Thailand, *Maxwell s.n.* (PDA)	0.23–0.27
Sonerila sp.	Sri Lanka, *Jayasuriya 3009* (PDA)	0.22–0.25
Sonerila sp.	Sri Lanka, *Jayasuriya 3030* (PDA)	0.26–0.27
Sonerila sp.	Sri Lanka, *Jayasuriya 3094* (PDA)	0.24–0.25
Tribe Bertolonieae		
Bertolonia maculata DC.	Cultivated, Missouri Botanical Garden, *Zardini s.n.* (no voucher)	0.23–0.24
Monolena multiflora Warner ined.	Panama, *Churchill 4155* (MO)	0.17–0.23
Triolena hirsuta (Benth.) Triana	Costa Rica, *Schatz 999* (WIS)	0.17–0.20
Tribe Dissochaeteae		
Medinilla fuchsioides Gardn.	Sri Lanka, *Jayasuriya 3351* (PDA)	0.23–0.24
M. myriantha Merr.	Cultivated, Mathias Botanical Garden #78-069 (no voucher)	0.10–0.13
Tribe Miconieae		
Bellucia pentamera Naud.	Costa Rica, *Hammel et al. 14149* (MO)	0.08–0.10
Chalybea corymbifera Naud.	Colombia, *Stein et al. 3610* (MO)	0.26–0.33
Miconia dodecandra (Desr.) Cogn.	Mexico, *Breedlove & Almeda 57466* (CAS)	0.14–0.22

TABLE 1. Continued.

Species	Collection Voucher	Relative Thickness of Staminal Bundle, t/T (see Figs. 5 and 10)
M. melanotricha (Triana) Gleason	Panama, *McPherson 8060* (MO)	0.13–0.22
M. minutiflora (Bonpl.) DC.	Venezuela, *Berry 4417* (VEN)	0.26–0.29
M. reducens Triana	Panama, *Sytsma 4032* (MO)	0.18–0.19
Tribe Blakeeae		
Blakea chlorantha Almeda	Costa Rica, *Haber 1197* (MO)	0.21–0.27
B. foliacea Gleason	Panama, *Churchill 5463* (MO)	0.21–0.25
B. sp. nov.	Costa Rica, *Grayum et al. 3553* (MO)	0.18–0.23
Topobea pittieri Cogn.	Panama, *Churchill 5477* (MO)	0.11–0.13
Tribe Astronieae		
Astronia candolleana Cogn.	Philippines, *Hernaez 3829* (CAHP)	0.19–0.23
A. ferruginea Elmer	Taiwan, *Peng 5247, 5503* (HAST)	0.21–0.29
A. meyeri Merr.	Philippines, *Hernaez 3832* (CAHP)	0.17 0.20
Memecylaceae		
Tribe Memecyleae		
Memecylon cantleyi Ridley	Cultivated, Singapore Botanical Garden, *Maxwell s.n.* (no voucher)	0.23–0.25
M. caeruleum Jack.	Cultivated, Singapore Botanical Garden, *Maxwell s.n.* (no voucher)	0.15–0.23
Mouriri myrtilloides (Sw.) Poir.	Panama, *Hamilton 2883* (MO)	0.20–0.25
M. nervosa Pilger	Brazil, *Renner 249* (US)	0.16–0.18
Tribe Pternandreae		
Pternandra caerulescens Jack.	Cultivated, Singapore Botanical Garden, *Maxwell s.n.* (no voucher)	0.23–0.24
P. echinata Jack.	Cultivated, Singapore Botanical Garden, *Maxwell s.n.* (no voucher)	0.17–0.24

to produce nectar. Two additional nectar-producing species have recently been reported, *B. austin-smithii* Standl. and *B. penduliflora* Almeda (Lumer & Schoer, 1986). There is some disagreement concerning the site from which nectar is secreted in this genus. Lumer (1980, and pers. comm., 1985) stated that in *B. chlorantha* nectar appears to be secreted in the area at the base of the stamens, either at the junction of the filament and floral tube or at the base of the filaments. According to Haber (pers. comm., 1985), however, nectar is secreted on the abaxial surface of the filaments (the side facing the corolla wall), with the nectar forming thick droplets between the filament and the corolla.

Anatomical sections of *Blakea chlorantha* flowers do not show a densely staining nectary anywhere on the floral tube wall (Fig. 1), nor do stamens have an externally or internally differentiated nectariferous structure (Figs. 2, 3). Stamens are folded inward in bud, with a geniculum present just above the midpoint. Slitlike structures are present on the adaxial surface of the geniculum (arrows in Figs. 1–3). The relative thickness value of the vascular bundles is fairly low (0.21–0.27) compared with other nectar producers (Fig. 5). These vascular bundles, however, are relatively densely staining, particularly in the upper part of the filament and at the connective (Figs. 3–5). A major part of the staminal vascular bundle appears to consist of small, cytoplasm-rich phloem cells. Parenchyma cells surrounding the staminal vascular bundle are not specialized (Figs. 4, 5), suggesting that they are not nectariferous.

Stamens of *Blakea* sp. nov. (fide F. Almeda) and *B. foliacea* are folded inward in bud at the anther–filament junction, and filament slits are not present. Although, like *Blakea chlorantha*, they have a thin more or less densely staining vascular bundle, they differ in that the staminal vascular bundle is surrounded by a thick-walled tanniferous epidermis and by some underlying tanniferous cell layers. *Blakea* sp. nov. and *B. foliacea* stamens are unlikely to secrete nectar through such tanniferous tissue, and nectar production has never been reported in either of these two species.

Brachyotum. All *Brachyotum* species investigated in the field were found to produce nectar,

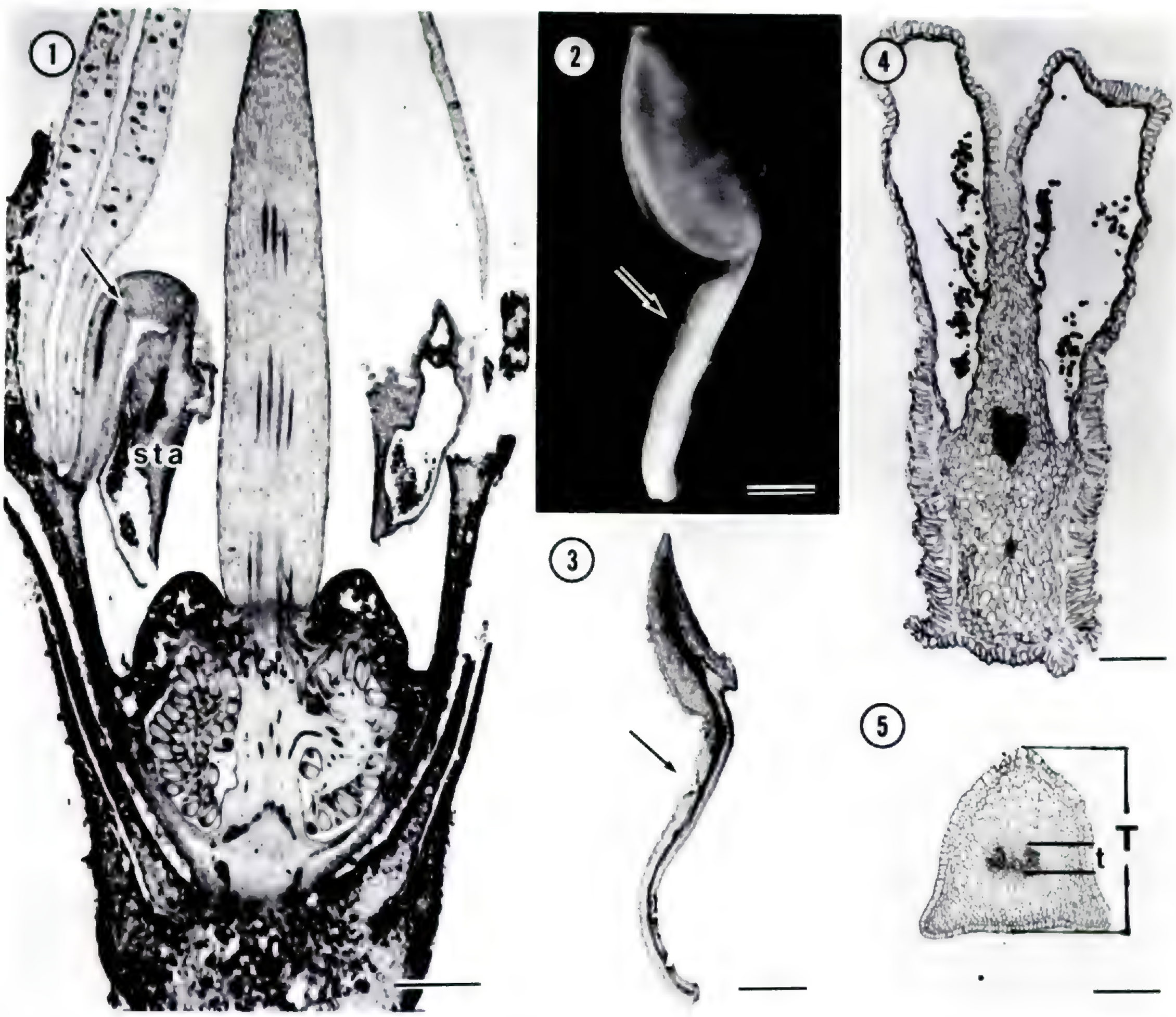
TABLE 2. Summary of data on nectar secretion and pollinators in nectar-producing Melastomataceae.

Species	Nectar Secretion Site	Time of Secretion	Pollinators	References
Blakea austin-smithii Standl.	Base of filaments	Nocturnal	Rodents	Lumer & Schoer, 1986
B. chlorantha Almeda	Abaxial surface or base of filaments	Nocturnal	Rodents	Lumer, 1980
B. penduliflora Almeda	Base of filaments	Nocturnal	Rodents	Lumer & Schoer, 1986
Brachyotum ledifolium (Desr.) Triana and other *Brachyotum* species	Adaxial surface of filaments	Diurnal	Hummingbirds	Lagerheim, 1899; Stein, pers. obs.
Chalybea corymbifera Naud.	Base of stamens? (see text)	Diurnal	Hummingbirds?	Stein, pers. obs.
Huilaea macrocarpa Uribe	Not known	Diurnal	Hummingbirds	Snow & Snow, 1980
Medinilla magnifica Lindl.	Tips of petals	Diurnal	Not known	Tobe et al., in prep.
Miconia minutiflora (Bonpl.) DC.	Not known (stigma?)	Morning	Bees	Mori & Pipoly, 1984
Tibouchina cleistoflora Ule	Adaxial surface of filaments	Not known	Bees	Ule, 1896; Renner, this volume
T. grossa (L.f.) Cogn.	Adaxial surface of filaments	Nocturnal/ Diurnal	Bats and hummingbirds	Vogel, 1957; Stein, pers. obs.
T. hospita (DC.) Cogn.	Adaxial surface of filaments	Not known	Bees	Ule, 1896; Renner, this volume
T. itatiaiae (Wawra) Cogn.	Adaxial surface of filaments	Not known	Not known	Ule, 1896

confirming previous reports (Lagerheim, 1899; Vogel, 1957; Wurdack, 1965), and it is likely that this entire Andean genus is nectariferous. From field observations, the nectar appears to be secreted by the filament at the slitlike structure located on or just below the geniculum on the adaxial filament face (Fig. 6) and forms large droplets suspended between adjacent pairs of filaments. Nectar concentration ranged from a high of 20–22% sucrose-equivalents in *B. ledifolium* (Desr.) Triana to a low of 15–16.5% in *B. campanulare* (Bonpl.) Triana, values consistent with most hummingbird-pollinated flowers (Baker, 1975).

Anatomical sections of stamens do not show any differentiated nectariferous structure in the filaments. Stamens of *Brachyotum ledifolium* have a thick vascular bundle running the length of the filament (Fig. 7) to the connective (Fig. 8). The staminal vascular bundle is densely staining and contrasts with the surrounding nonspecialized parenchyma cells. All other examined species of *Brachyotum* contain a similar thick, densely staining staminal vascular bundle: *B. campanulare* (Fig. 10), *B. lindenii* Cogn., *B. microdon* (Naud.) Triana, and *B. sanguinolentum* (Naud.) Triana (Fig. 9). This similarity in staminal anatomy suggests that all these species exude nectar from the filament.

Chalybea. *Chalybea* is a monotypic genus of the Colombian Andes closely related to, if not congeneric with, the nectar-producing genus *Huilaea*. Poorly known and consisting only of *C. corymbifera* Naud. (= *Pachyanthus corymbiferus* [Naud.] Cogn.), *Chalybea* recently has been resurrected on the basis of material newly collected for this study (Wurdack, 1988). We have observed nectar secretion from *C. corymbifera* and measured the nectar sugar concentration at 16.5% sucrose-equivalents. Pinpointing the site of secretion is problematic. Nectar was collected from the summit of the inferior ovary; however, the nectar was observed and measured several hours after the normally pendulous flowers were collected and could have migrated to this location. Stamens are bent inward in bud and have neither a pronounced geniculum nor filament slits (Figs. 11, 12). Anatomical sections do not show a differentiated nectariferous structure at the ovary summit (Fig. 11). While stamens do not have either externally differentiated structures or densely staining nectariferous tissue (Figs. 11, 12), they do contain a thick vascular bundle running through the filament (Fig. 14) to the connective (Fig. 13), suggesting staminal secretion. Tanniferous parenchyma cells surrounding the staminal vascular bundle appear unfavorable



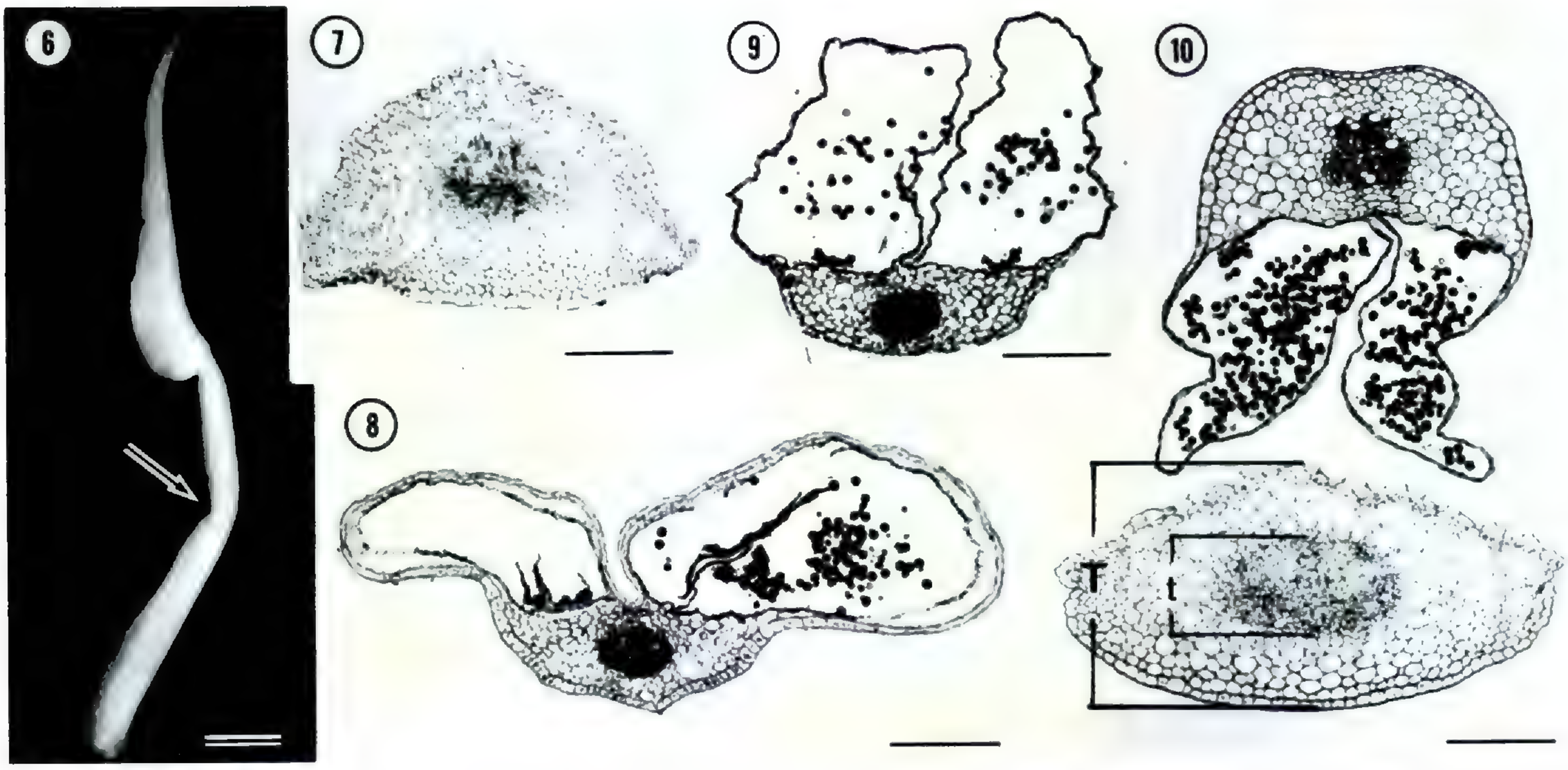
FIGURES 1–5. *Blakea chlorantha*.—1. Longitudinal section (LS) of flower. –2. Stamen.—3. LS of stamen. —4,5. Transverse sections (TS) of anther and of filament. Arrows in Figures 1–3 indicate a depression or break formed at the inner side of the bend. Abbreviation: sta, stamen. T and t in Figure 5 are thickness of filament and of vascular bundle respectively, which are measured for calculation of relative thickness of staminal vascular bundles (see text for explanation). Scale bars = 1 mm in Figures 1–3; 0.2 mm in Figures 4, 5.

for secretion of nectar. These tanniferous cells, however, are much less conspicuous in the lower part of the filament, and nectar thus may exude from the filament in this location, perhaps accounting for its observed presence on the ovary summit.

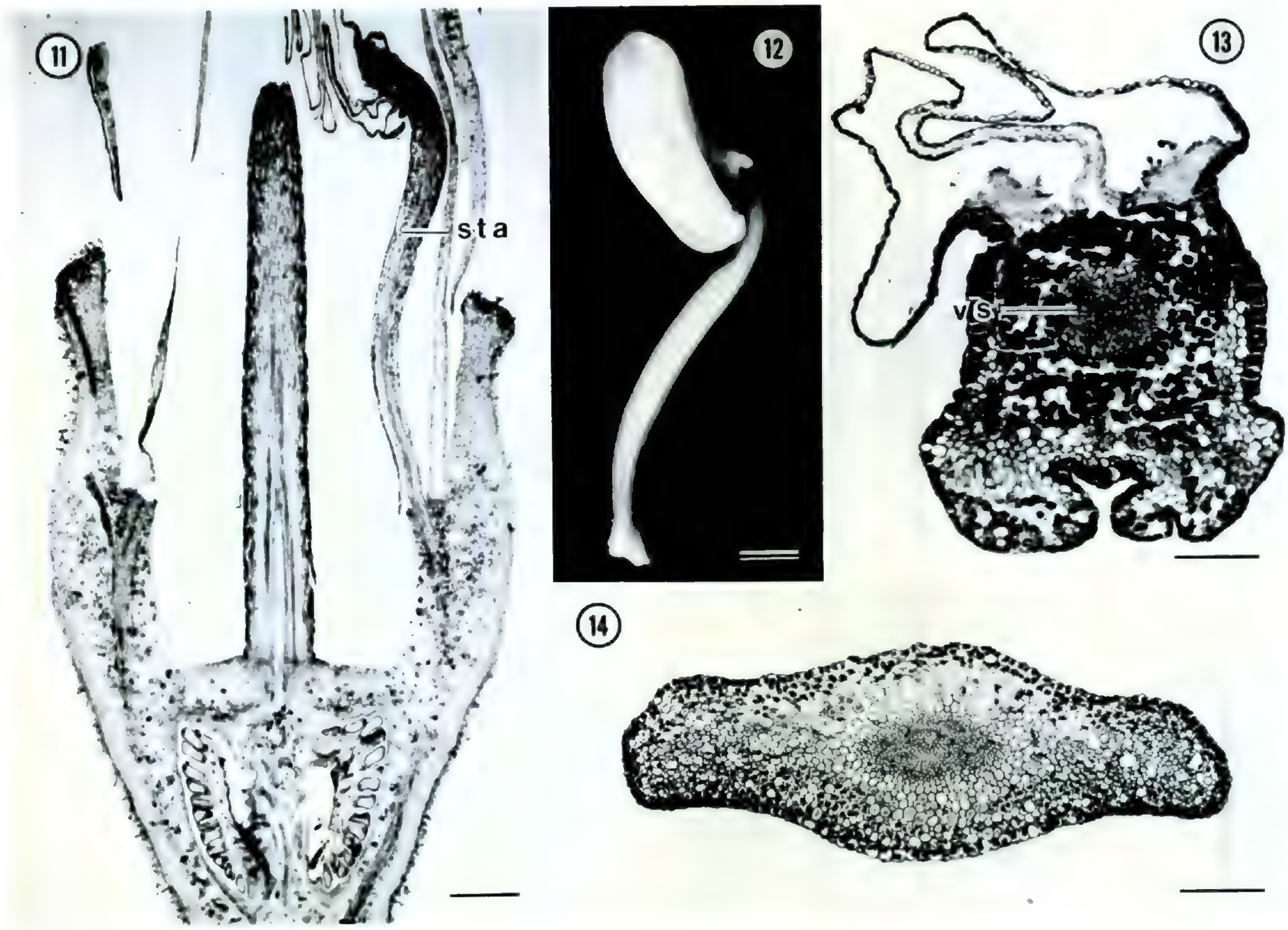
Huilaea. Snow & Snow (1980) reported nectar production by *Huilaea macrocarpa* Uribe and measured the nectar sugar concentration to range from 12 to 16% with a mean of 13.4%. No information was provided as to the precise location of nectar secretion in these pendulous flowers.

Tibouchina. Nine species of *Tibouchina* were examined, including the Andean *T. grossa*, which is known to produce nectar. Brazilian *Tibouchina* species reported to secrete nectar include *T. cleistoflora* Ule, *T. hospita* (DC.) Cogn., and *T. itatiaiae* (Wawra) Cogn. (Ule, 1896). Our observations of nectar secretion in *T. grossa* differ somewhat from those of Vogel (1957), who considered the nectar to exude from the inner wall of the floral tube below the insertion of the stamens. *Tibouchina grossa* flowers are open-campanulate and oriented horizontally with all stamens arranged in a half-circle in the lower side of the corolla. We observed nectar droplets forming on the adaxial surfaces of the filaments near the geniculum. The drops are at first suspended between adjacent filaments and occasionally between the filaments and style. The rather copious nectar then flows down the filaments to collect either in the floral tube or on the convex lower petals. We measured sugar concentration of *T. grossa* nectar at 14.5% sucrose-equivalents.

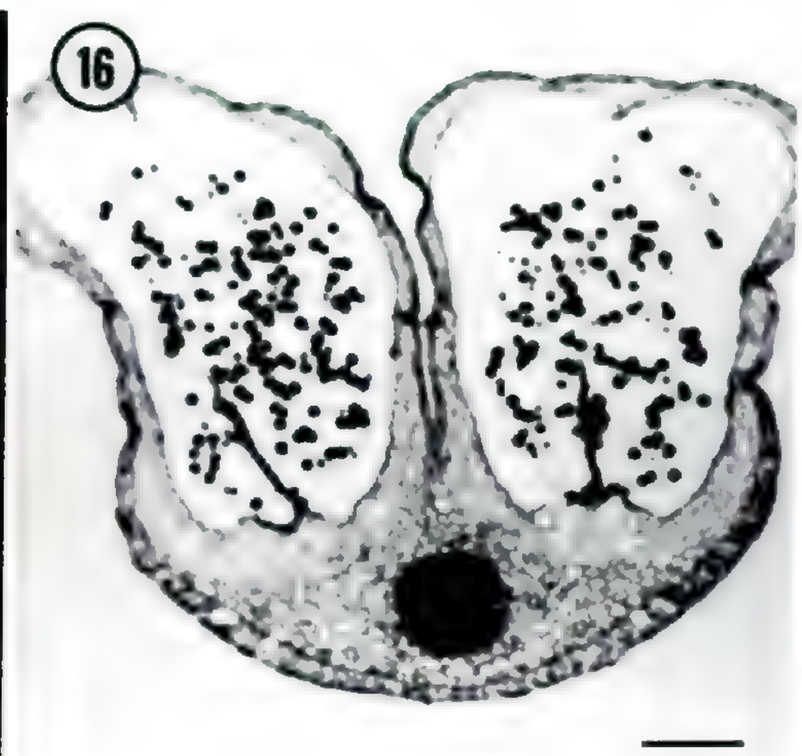
No densely staining differentiated structure was found in the filaments of *Tibouchina grossa* (Fig.

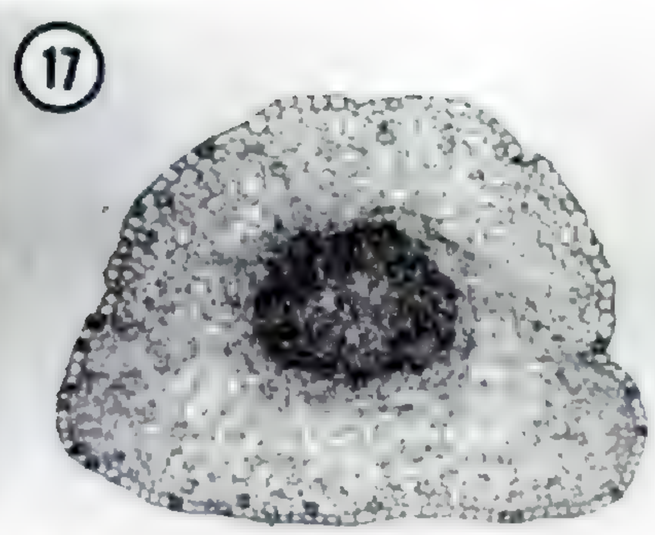


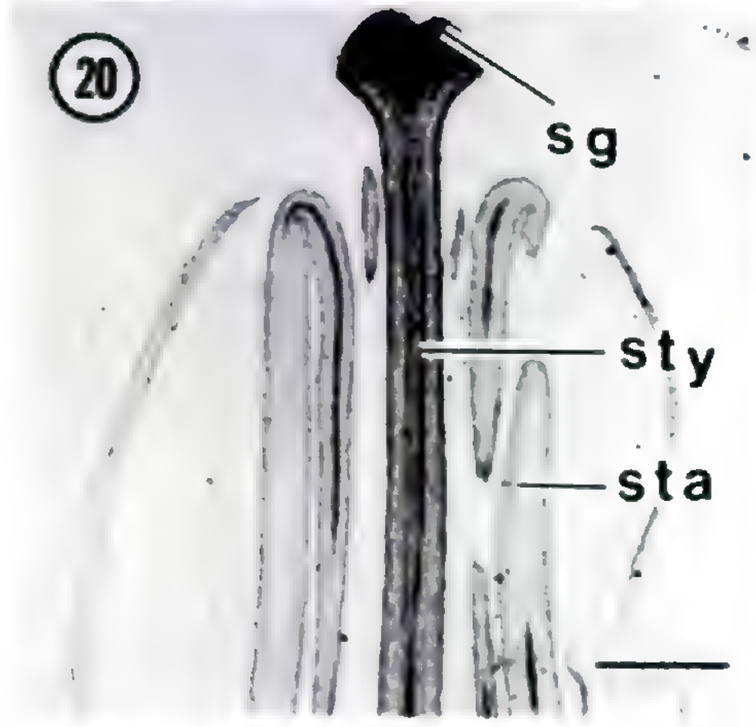
FIGURES 6–10. *Brachyotum.*—6. Stamen of *Brachyotum ledifolium.*—7, 8. Transverse sections (TS) of filament and of anther of *Brachyotum ledifolium.*—9. TS of anther of *Brachyotum sanguinolentum.*—10. TS of anther (above) and of filament (below) (the adaxial sides of which are opposite) of *Brachyotum campanulare.* Note thick staminal vascular bundles in all species. Abbreviations (T and t) in Figure 10 correspond to those in Figure 5. Scale bars = 1 mm in Figure 6; 0.2 mm in Figures 7–10.

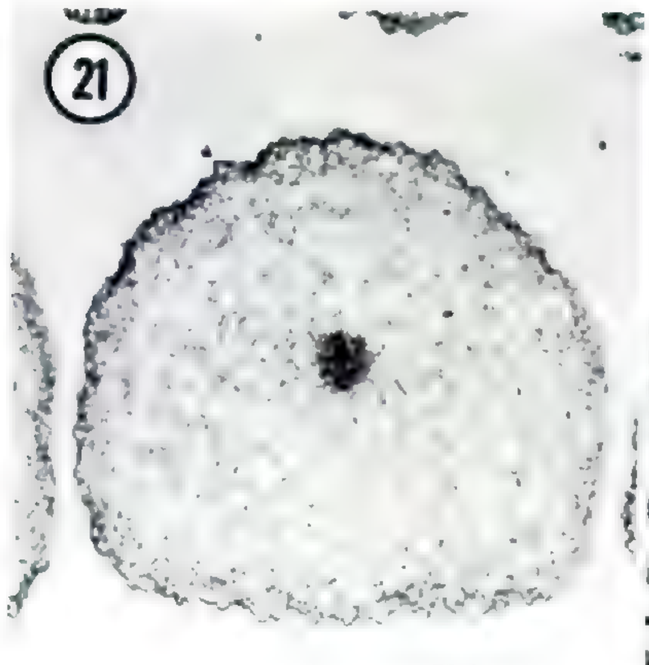


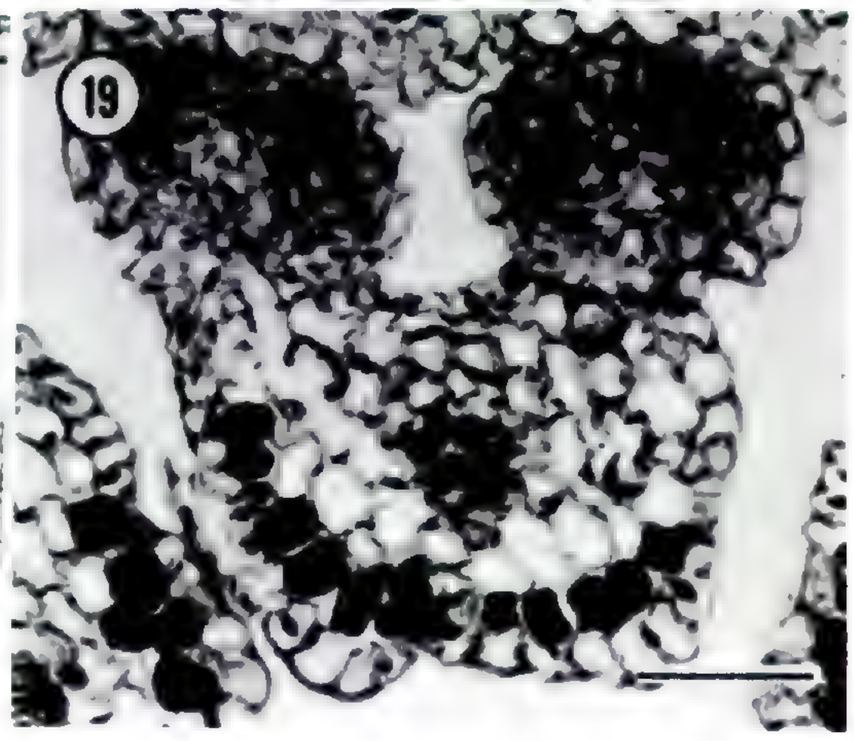
FIGURES 11–14. *Chalybea corymbifera.*—11. Longitudinal section of flower.—12. Stamen.—13, 14. Transverse sections of anther and of filament. Abbreviations: sta, stamen; vs, vascular bundle. Scale bars = 1 mm in Figures 11, 12; 0.2 mm in Figures 13, 14.











FIGURES 15–21. *Tibouchina* and *Miconia*. —15. Stamen of *Tibouchina grossa*, which is bent at a hinge. —16, 17. Transverse sections (TS) of anther and of filament of *Tibouchina grossa*, showing thick vascular bundle. —18. Longitudinal section (LS) of flower bud of *Miconia minutiflora*. —19. TS of young anther of *Miconia minutiflora*. —20. Upper half of LS of flower bud of *Miconia melanotricha*. —21. TS of filament of *Miconia melanotricha*. Abbreviations: sg, stigma; sta, stamen; sty, style. Scale bars = 1 mm in Figures 15, 20; 0.2 mm in Figures 16, 17, 18, and 21; 0.05 mm in Figure 19.

15). Instead, stamens of *T. grossa* have a thick, densely staining vascular bundle surrounded by nonspecialized parenchyma cells (Figs. 16, 17). Relatively thick staminal vascular bundles are observed in all *Tibouchina* species investigated (see Table 1), although nectar production has so far not been reported in those other species.

Medinilla. The Old World genus *Medinilla* includes certain species that morphologically appear to be good candidates for bird pollination. We examined anatomically one such species, *Medinilla fuchsioides* Gardn., but found the staminal vasculature to be unexceptional. Subsequent to this, however, we found cultivated material of *M. magnifica* Lindl. at the Berlin Botanical Garden to secrete nectar from the petal tips. Anatomical investigations of this very unique nectar secretion method are currently under way (Tobe et al., in prep).

Miconia. In discussing a mass flowering episode of *Miconia minutiflora* (Bonpl.) DC, Mori & Pipoly (1984) reported the presence of nectar as a pollinator reward in this species. In other localities, however, this lowland species has not been found to secrete nectar (Renner, 1983).

Only young buds of *Miconia minutiflora* were

available for the present study. Anatomical sections of this material indicate no structure likely to produce nectar in either the stamens or around the floral tube–gynoecium junction (Fig. 18). Flowers are very small, with the filaments supplied by a relatively thin vascular bundle (Fig. 19). Anatomical sections show, however, that *M. minutiflora* has a remarkably conspicuous stigma supplied by ample, densely staining vascular tissue (Fig. 18).

Hummingbirds have been observed visiting *Miconia melanotricha* (Triana) Gleason (Almeda, pers. comm., 1986), and this species may produce nectar. The flowers appear morphologically well suited for hummingbird pollination, given their large size (10–15 mm in diameter and 23–25 mm long) and red petals. This species also has longitudinally dehiscent anthers rather than the apically poricidal anthers typical of bee-pollinated melastomes. Anatomical sections do not show densely staining structures or tissue, and the stamens have a thin vascular bundle (Fig. 21). As in *M. minutiflora*, however, the stigma and supporting vascular tissue are unusually densely staining (Fig. 20).

Miconia robinsoniana Cogn. was reported to produce nectar in a survey of the foraging ecology of the Galápagos Islands carpenter bee, *Xylocopa darwinii* (Linsley et al., 1966). Subsequent observations of this species have not reconfirmed the presence of nectar (McMullen, pers. comm. in Renner, this volume). During our own field investigations of this species, no suitable material could be located to resolve this question. An additional, as yet unidentified, *Miconia* species from lowland Amazonia has recently been reported to produce nectar (Roubik, pers. comm. in Renner, this volume).

MEMECYLACEAE

Memecylon and *Mouriri* have a peculiar depressed gland on the backside of the anther connective (Figs. 22, 24). This structure was early described as a nectary (Burck, 1891; Subramanyam, 1949; Venkatesh, 1955) but recently has been hypothesized to be an elaiophore, or oil-producing gland (Buchmann & Buchmann, 1981). Anatomical sections reveal this gland to be composed of more or less radially enlarged epidermal cells, which are clearly distinguishable from other cells of the connective (Figs. 23, 25).

Pternandra is variously included in or excluded from the Memecylaceae. Its uncertain status is based largely on the absence of the anther connective glands found in other members of Memecylaceae. The two species examined in this study, *P. caerulescens* Jack. and *P. echinata* Jack., lack these gland structures on the surface (Figs. 26, 27) and in section (Fig. 28).

Discussion

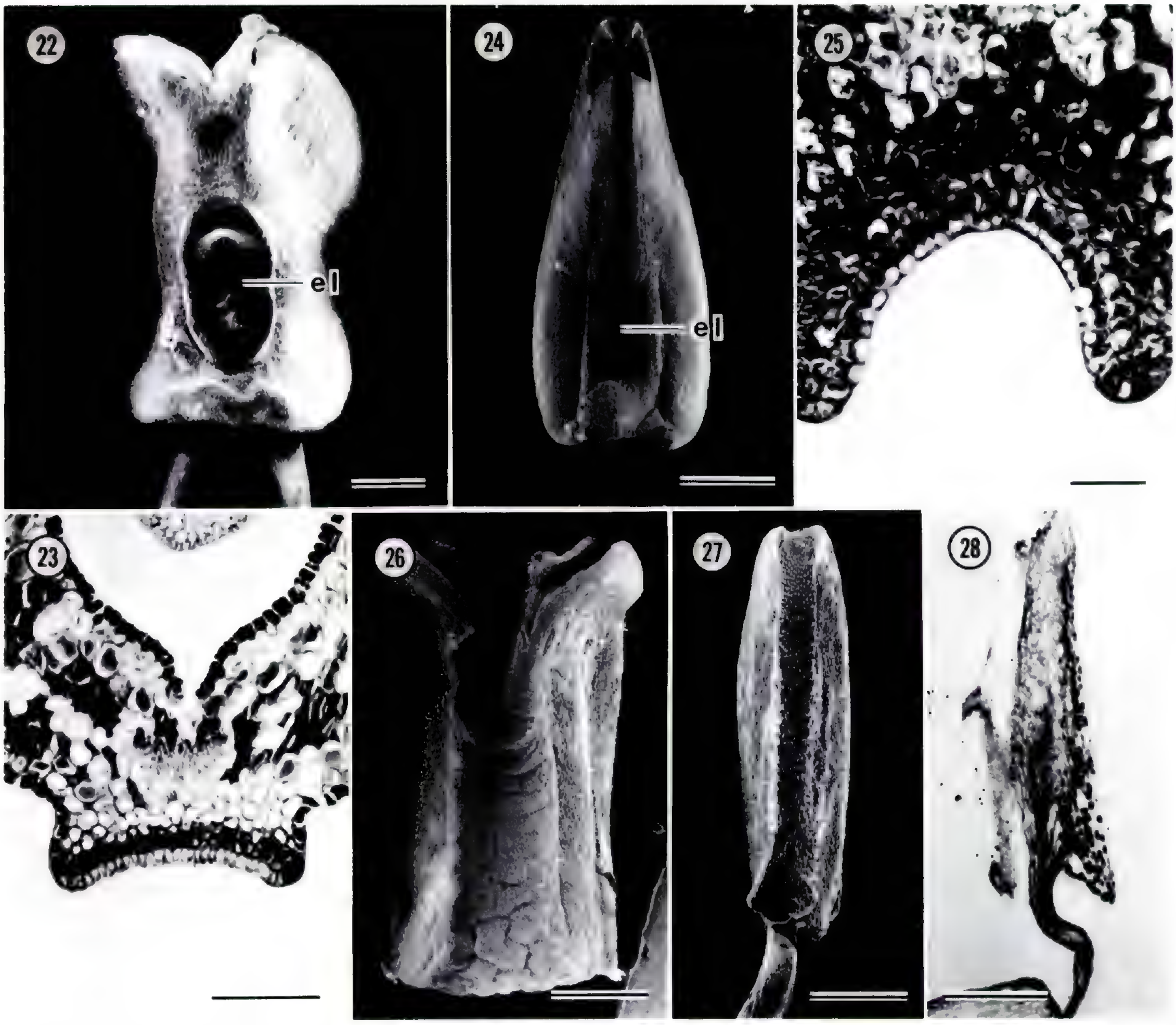
POSITION AND STRUCTURE OF FLORAL NECTARIES IN MELASTOMATACEAE

The present study shows that, in contrast to nearly all other myrtalean families, Melastomataceae lack histologically differentiated nectariferous tissue either on the inner surface of the floral tube, on the gynoecium, or at the floral tube–gynoecium junction. While nectar production in Melastomataceae is rare, a diversity of unusual nectary types are implicated, including secretion from the stamens, petals, and perhaps stigmas. Most documented nectar-producing melastomes secrete nectar from the stamens, although we did not find any differentiated nectariferous structures or tissue in that organ. On the basis of observations and anatomical structure, we thus conclude that in most nectariferous Melastomataceae nectar is produced by a nonstructural nectary consisting solely of the staminal vascular bundles.

Compared with melastome species generally, stamens of nectar-producers have a much thicker vascular bundle containing many small, densely staining cytoplasm-rich phloem cells. An ultrastructural survey of these cells could offer additional evidence of their nectar-secreting capability, since there is a clear connection between cytological constituents and processes of nectar secretion (for review of ultrastructural features see Fahn, 1979).

The nonlocalized nature of these androecial nectaries may help resolve the conflicting reports about the specific sites of nectar secretion (Table 2). If nectar is produced by the staminal vascular bundle, it could emanate from almost anywhere along the stamen. Additionally, if the direction of the nectar stream within a stamen is affected by gravity, the secretion site could differ between stamens and among individual flowers.

Several observers, including one of us (B.A.S.), have noticed that in certain genera (e.g., *Brachyotum* and *Tibouchina*) the location of nectar secretion appears to be closely associated with a small slit in the adaxial surface of the filament (see arrows in Figs. 1–3, 6). The development and significance of these slits is somewhat controversial. We found no anatomical differentiation of this structure. Since stamens in Melastomataceae are folded or bent inward in bud, becoming more or less straight at anthesis, the observed slitlike structures may form spontaneously and be unrelated to nectar secretion.



FIGURES 22–28. *Memecylon*, *Mouriri*, and *Pternandra*.—22, 24. Scanning electron micrographs (SEM) of anthers of *Memecylon caeruleum* and *Mouriri nervosa*, showing anther glands on backside of connective.—23, 25. Transverse sections of anther glands of *Memecylon caeruleum* and *Mouriri nervosa*.—26, 27. SEMs of anthers of *Pternandra echinata* and *P. caerulescens*, showing absence of glands on backside of connective.—28. Longitudinal section of stamen of *Pternandra caerulescens*. Abbreviation: el, anther elaiophore. Scale bars = 0.5 mm in Figures 24, 26, 27, and 28; 0.2 mm in Figures 22, 23; 0.05 mm in Figure 25.

Such slits are, in fact, reported in some species not known to secrete nectar (Renner, this volume). However, an apparent association of these slits with nectar-producing species, their absence in related non-nectariferous species (e.g., *Blakea chlorantha* vs. *B.* sp. nov. and *B. foliacea*), and field observations of nectar droplets formed precisely at these indentations strongly argue for a role in nectar secretion. These structures may form through a deterioration of a small amount of tissue on the inner side of the geniculum, providing an exit pathway for nectar produced by the staminal vascular bundle. Clearly, a systematic survey of the occurrence of these slits throughout the Melastomataceae would be useful in clarifying their role.

Although nectar production has been reported in *Miconia minutiflora* (Mori & Pipoly, 1984; Mori, pers. comm., 1986), Renner (this volume) has questioned whether the fluid observed was truly nectar. From our anatomical examination, *Miconia minutiflora* does not appear capable of secreting nectar from the stamens in the manner of the other confirmed nectar-producers we investigated. If nectar production in this species is reconfirmed, the conspicuous stigma, which is subtended by cytoplasm-rich vascular tissue, should be closely examined for a possible secretory role. Stigmatic nectar secretion is rare within the angiosperms but occurs in Asclepiadaceae and Araceae (Fahn, 1979).

EVOLUTION OF FLORAL NECTARIES IN MELASTOMATACEAE

Nectaries generally consist of an epidermis subtended by specialized parenchyma cells (Esau, 1977;

Fahn, 1979). The phloem-based nectaries we have found in Melastomataceae, which have no structurally differentiated parenchyma, are a rather extreme deviation from this typical structure. The nonstructural androecial nectaries found in Melastomataceae are particularly anomalous in Myrtales, where, of the 14 families currently included in the order (Dahlgren & Thorne, 1984), only Melastomataceae, Memecylaceae, and Rhynchocalycaceae lack densely staining structural nectaries. Eyde (1981) has discussed evolutionary shifts in the location of floral nectaries in flowers of various myrtalean families and concluded that the ancestral site of nectar secretion for Myrtales, as for many other dicots, is the junction between the gynoecium and the floral tube or, in tubeless flowers, the junction with the androecium. From this ancestral position, nectaries evolutionarily have migrated onto the floral tube, or even onto the androecium in some tubeless species of *Lopezia* and *Epilobium* of the Onagraceae (Eyde & Morgan, 1973; Eyde, 1981). Androecial nectaries are also found in other groups, including virtually all members of the Caryophyllales (Zandonella, 1977). However, the androecial nectaries in these other families are more typical differentiated structures and thus not comparable to the nonstructural androecial nectaries of Melastomataceae, which are certainly unique within the Myrtales and perhaps among angiosperms as a whole.

Given the ancestral myrtalean nectary type and position proposed by Eyde (1981), it seems clear that structural nectaries were lost in the evolutionary lineage ancestral to Melastomataceae and Memecylaceae. Such nectaries appear to have been lost independently in the lineage leading to Rhynchocalycaceae (a monotypic family consisting only of the South African *Rhynchocalyx lawsonioides* Oliver), since on many other grounds this family is more closely related to other members of the Myrtales than to Melastomataceae (Tobe & Raven, 1984).

Pollinator interactions appear to have played a key role in both the ancestral loss and subsequent re-evolution of nectaries within the Melastomataceae. Melastomataceae are, on the whole, a family uniquely suited for bee pollination. The distinctive poricidally dehiscent anthers are directly related to vibratile extraction of pollen by bees, a phenomenon known as buzz pollination. Bees foraging for pollen in this manner rarely forage simultaneously for nectar, and then only to mix it with the pollen to improve the pollen's handling properties (Buchmann, 1983). Although poricidal anthers are found in numerous angiosperms (for review see Buchmann, 1983), few plant families are so completely characterized by this feature as Melastomataceae. Given the widespread distribution of poricidal anthers within all lineages of Melastomataceae, this feature appears to be the ancestral condition for the family. Thus, if buzz pollination became established in the lineage ancestral to Melastomataceae, there would be little or no selective advantage in maintaining energy-expensive nectaries. By attracting undesirable and potentially destructive floral visitors, nectaries may even have been selected against in protomelastomes.

Nectaries appear to have re-evolved independently in several distinct lineages within the family, most of which share certain ecological and reproductive traits. Cruden (1972) has pointed out the potential reproductive advantage ensuing from a shift from bee to bird pollination in wet-tropical montane ecosystems. Similarly, Heinrich & Raven (1972) have noted the increased energy reward necessary to attract pollinators operating at higher elevations and to support vertebrate rather than invertebrate pollinators. Nectar, composed principally of carbohydrates, is a much richer energy source than pollen and is almost invariably the floral reward used to attract vertebrate pollinators. Not surprisingly, most confirmed nectar-producing Melastomataceae (species of *Blakea*, *Brachyotum*, *Chalybea*, *Huilaea*, and *Tibouchina*) occur at high or relatively high elevations, and are known or presumed to be pollinated by vertebrates (Table 2).

According to traditional and recent classification systems for the family (Cogniaux, 1891; van Vliet et al., 1981; Wurdack, 1980), confirmed nectar-producing Melastomataceae are found in at least four different tribes: Blakeae, Dissochaeteae, Miconieae, and Tibouchineae (see Table 1). The phylogenetic relationships among these tribes are not yet resolved, but they undoubtedly do not form a monophyletic lineage within the family. In addition, the majority of genera in these four tribes are not known to produce nectar. Except for the lowland species of *Miconia* discussed above, most of the nectar-producing taxa can be viewed as relatively derived within their respective tribes in terms of pollination systems and ecological/altitudinal preferences. With regard to the latter, the Central and northwestern South American montane terrains that are inhabited by many of these species (and, if the above interpretation is correct, may have provided the ecological impetus for the development of nectar rewards) are generally more recent (Zeil, 1979)

than the origin of the Melastomataceae, fossils of which are known from as early as Eocene times (Hickey, 1977).

Two hypotheses can be advanced to account for the unusual systematic distribution of nectaries within the family. The first is that such nectaries are the basal condition in Melastomataceae and have been lost in the vast majority of species. Given the structural nectaries present in other families of Myrtales and the rather specialized morphological state of most of the nectariferous species, however, such an interpretation is untenable. Renner (this volume) advocates a modified version of this hypothesis, suggesting that "the capacity for developing nectaries is basic in the Melastomataceae but suppressed in most modern members." This supposition seems equally difficult to accept. Rather, we propose a second hypothesis, which is that nectaries have evolved independently a number of times within the family and developmentally have followed the easiest course available. Two lines of evidence point to this. First, three different nectary types have developed within the family, each involving different floral organs (stamens, pistil, petals). Although rare within angiosperms, the most common melastome nectaries, nonstructural androecial nectaries, involve very little modification of existing structures and thus appear to be an easily developed solution to producing nectar. It is difficult, however, to reconcile this view of the ease of developing such nectaries with the relative rarity of nonstructural androecial nectaries in the angiosperms as a whole.

SYSTEMATIC IMPLICATIONS OF NECTARY ANATOMY FOR MEMECYLACEAE

Memecylaceae traditionally have been included in Melastomataceae as a tribe or subfamily (e.g., Cogniaux, 1891; Morley, 1976). Based on floral nectary characters, Memecylaceae agree with Melastomataceae in completely lacking densely staining structural nectaries. The term "disc" has sometimes been used to describe certain structures within the flowers of *Memecylon* (see Bremer, 1983). Given the complete lack of nectariferous tissue, this term should, however, be avoided. As previously discussed, loss of structural nectaries seems to be a feature ancestral for Melastomataceae, and this is probably also the case for Memecylaceae. We regard loss of structural nectaries as a synapomorphy uniting these two families.

Memecylaceae have generally been circumscribed to include the Old World *Memecylon* and the New World *Mouriri* and *Votomita*, all containing anther connective glands. Based on observations of *Mouriri myrtilloides* (Sw.) Poir, Buchmann & Buchmann (1981) suggested that the connective glands of *Memecylaceae* are elaiophores that secrete lipids for nutritional use by pollinating bees, primarily in larval provisioning. Although the secretion is lipid rich, its chemical complexity and the presence of components seemingly toxic to insects have led others to be cautious about this interpretation (Renner, this volume; Simpson & Neff, 1981).

Morley (1976) considered these distinctive but little-understood connective glands to be one of the most characteristic features of the "Memecyleae" (= Memecylaceae), even though they are occasionally lost, as in *Mouriri exadenia* Morley. Whatever its taxonomic rank, the group is now generally considered to include additional genera, among them *Pternandra*, which lacks connective glands (Dahlgren & Thorne, 1984). The present study reconfirms this observation: all examined species of *Memecylon* and *Mouriri* have anther glands on the backside of the connective, whereas all examined species of *Pternandra* lack them. Therefore, even if *Pternandra* is aligned with *Memecylon*, *Mouriri*, and *Votomita* at the familial level, evolution of the anther glands appears restricted to the lineage including the three last-mentioned genera. Available evidence from staminal anatomy does not resolve the correct familial placement of *Pternandra* but does suggest that if included in Memecylaceae, it should be regarded as the sister group to the rest of the family. This is generally the approach taken by van Vliet et al. (1981) in placing *Pternandra* in its own tribe Pternandreae of their "Memecyloideae" (= Memecylaceae).

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A SYSTEMATIC REVISION OF *FUCHSIA* SECT. *QUELUSIA* (ONAGRACEAE)[1]

Paul E. Berry[2]

Abstract

Fuchsia sect. *Quelusia* consists of nine closely related species, eight from southeastern Brazil and one from southern Chile and Argentina. This treatment recognizes *F. alpestris* and *F. glazioviana* as separate from *F. regia* and describes two new species from southern Brazil, *F. brevilobis* and *F. hatschbachii*. The section is defined by its shrubby-lianoid habit, opposite-whorled leaves, and distinctive floral pattern associated with hummingbird pollination. It is one of only two entirely polyploid sections in the genus. Unique characters of the section include the large, violet, convolute petals, strongly exserted stamens, and partially connate sepals that are longer than the floral tubes. All nine species occupy cool forest habitats that are remnants of the widespread Tertiary temperate forests of the Southern Hemisphere. With the Old World sect. *Skinnera* as the sister group of all the American species of *Fuchsia*, sect. *Quelusia* represents an early offshoot of the ancestral South American fuchsias, distinct from the tropical Andean and Central American sections in its polyploidy and derived, 3-porate pollen. The nearest relative and sister species of sect. *Quelusia* is *F. lycioides*, a specialized xerophyte and the sole member of sect. *Kierschlegeria*, which occurs in central Chile just north of the range of *F. magellanica*. The Andean and Brazilian populations of sect. *Quelusia* probably became isolated in the late Tertiary, when the austral temperate forests were broken up by increasing aridity to the east of the Andes, as these were strongly uplifted. While *F. magellanica* has not differentiated substantially throughout its range in the southern Andes, sect. *Quelusia* has radiated extensively in the subtropical mountains of southern Brazil, where five of the eight species are restricted to high, isolated mountain peaks. *Fuchsia regia*, on the other hand, is widespread at lower altitudes throughout the planalto and coastal mountains of southeastern Brazil; it is differentiated into three mostly allopatric but intergrading series of populations which are treated here as subspecies. Two of these subspecies are newly described, *F. regia* subsp. *reitzii* and *F. regia* subsp. *serrae*. *Fuchsia regia* is the only species now found to occur sympatrically with other members of the section, and it forms natural hybrids with at least five different species. The only naturally occurring octoploid populations in the genus occur in *F. regia* and appear to be recently derived.

Fuchsia is a distinctive genus of Onagraceae with close to 105 species belonging to ten sections (Berry, 1982; Berry et al., 1988). The genus consists mostly of mesic shrubs confined to cool, moist habitats, with nearly ¾ of the species concentrated in the tropical Andes. The remaining species occur in Mexico and Central America, Hispaniola, southeastern Brazil, the southern Andes, New Zealand, and Tahiti.

In recent years, *Fuchsia* has been the subject of a series of studies designed to refine the taxonomy and to improve our understanding of the evolutionary relationships within the group. A comprehensive analysis of leaf flavonoids (Averett et al., 1986) confirmed the distinctiveness of the New Zealand species of the widely disjunct sect. *Skinnera* from their American congeners. Studies of pollen morphology and ultrastructure in a broad

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array of species have helped to define sectional limits by detecting consistent differences in viscin thread types, aperture number, and grain size (Skvarla et al., 1976, 1978; Nowicke et al., 1984; Praglowski et al., 1983). Systematic revisions for seven of the ten sections in the genus have been completed, based on broad cytological surveys, a thorough review of the major collections of herbarium specimens, and extensive field examination of natural populations (Breedlove, 1969; Berry, 1982, 1985; Breedlove et al., 1982; Berry et al., 1988). The present study uses the same methodology to produce a revision of the species of sect. *Quelusia*, a group centered in southeastern Brazil and forming the largest section outside of the tropical Andes.

A better understanding of the systematics of sect. *Quelusia* is particularly desirable, as the species form a closely related, yet unspecialized group that may have retained many of the primitive characters of the genus. Biogeographically, the section is confined to ancient forest areas in the southern Andes and in southeastern Brazil that show clear austral-Antarctic affinities. Ultimately, this may have been the source area from which other sections differentiated and spread both to Australasia, when more or less direct overland connections were possible across Antarctica until the mid-Tertiary, and to Central America, where several small sections presently occur.

Horticulturally, most of the hundreds of hybrid *Fuchsia* cultivars have been derived primarily from members of sect. *Quelusia* (Reiter, 1944), yet there has been much confusion as to which taxa were involved in the early crosses. Accurate information on the different native species of sect. *Quelusia* can also be expected to stimulate interest in their preservation, cultivation, and use in hybridization for new ornamental cultivars.

In the only recent monograph of *Fuchsia*, Munz (1943) recognized five species in sect. *Quelusia*, together with *Fuchsia hybrida* Hort. ex. Vilm., a name used to encompass most of the common garden hybrids. *Fuchsia magellanica* and *F. regia* included three and four varieties, respectively; these species have the broadest geographical distributions in the genus and also show complex patterns of morphological variation. In this study, *Fuchsia magellanica* is treated as a single, cytologically uniform, polymorphic species with no clear geographical pattern of differentiation. *Fuchsia regia*, on the other hand, has tetraploid and octoploid populations, with geographically differentiated variants that are treated here as comprising three intergrading subspecies. Both *F. alpestris* and *F. glazioviana* are reinstated as distinct species, and two previously unrecognized species are described, *F. brevilobis* and *F. hatschbachii*. As herein delimited, sect. *Quelusia* consists of 11 taxa, with nine different species.

Habitat and Distribution

Fuchsia sect. *Quelusia* is an entirely Southern Hemisphere group of species, with a latitudinal range extending from 18°S to 55°S. It occurs in South America in two large but widely disjunct areas: the southern, temperate Andes of Chile and Argentina, and the coastal mountains and high plains of southeastern Brazil (Fig. 1).

The only species occurring in the southern Andes is *F. magellanica*, which is characteristic of the wet, temperate, Valdivian forests that are centered in the Región de Los Lagos of Chile. These forests are considered to be relicts of an ancient vegetation type that includes many taxa of Australasian affinity, such as *Nothofagus*, *Drimys*, *Podocarpus*, and *Araucaria* (Rambo, 1951; Hueck, 1972; Lötschert, 1981). *Fuchsia magellanica* also extends farther north into drier areas in Chile, where it occurs in moist microhabitats as far north as Santiago and Valparaíso, and then southward to the subantarctic scrub forests of Tierra del Fuego. Throughout its range, *F. magellanica* occurs as low as sea level, but only at its northernmost range does it reach its upper altitudinal limit of 1,750 m. Seasonality increases southwards, so that in Tierra del Fuego, flowering is restricted to the summer months of December to March, and plants are strongly deciduous in the freezing winter months.

The other eight species of the section all occur in the highlands of southeastern Brazil. A single species, *F. regia*, is widespread and covers the entire range of the section in Brazil, from 18°20′S to 29°30′S. The remaining species have much more restricted distributions, several occurring on a single mountain range.

Fuchsia regia consists of three largely allopatric subspecies. Subspecies *serrae* occurs mainly in dense cloud forests at the crests and on the seaward-facing escarpments of the coastal mountains from Rio Grande do Sul to northern São Paulo state, at elevations of 500–1,450 m. In Santa Catarina, however, it is also found in enclaves of montane vegetation on the summits of the isolated "morros" that emerge just 100 to 300 m above the Atlantic lowland forest in the Itajaí Valley (Klein, 1978). It has also been found at sea level in restinga forests near the Santa Catarina–Rio Grande do Sul border,

where Reitz (1961) found a number of other plants typical of the high inland serras.

Fuchsia regia subsp. *reitzii* is restricted to thickets and low forest on the drier planalto, or southern highlands, that occupies much of the interior of Paraná, Santa Catarina, and Rio Grande do Sul. It occurs at altitudes between 900 and 1,700 m in areas subject to strong winter frosts (Klein, 1984). The range of subsp. *reitzii* in this area coincides quite closely with *Araucaria angustifolia*, the dominant element of the planalto forests (Hueck, 1953). In Rio Grande do Sul and southern Santa Catarina, the planalto ends abruptly to the east at the "Aparados" or "Taimbés," sheer cliffs that drop down hundreds of meters to the Atlantic coastal plains. At these sites, subsp. *reitzii* reaches its eastern limit, growing sympatrically along a narrow band with the westernmost populations of subsp. *serrae*.

Fuchsia regia subsp. *regia* occurs further north in a series of separate mountain systems, from northern São Paulo to Rio de Janeiro, Minas Gerais, and Espírito Santo. It grows in cloud forests beginning at 1,000 m and reaches open campos above treeline as high as 2,400 m on Mt. Itatiaia.

Several species are restricted to high altitudes and are known from just one area. *Fuchsia bracelinae* grows only between 2,300 and 2,850 m, above treeline in the "campos de altitude" of a few peaks of the Serra do Caparaó. This is the highest mountain range of southern Brazil, situated along the Minas Gerais–Espírito Santo border. Similarly, *F. campos-portoi* occurs only in campos around Mt. Itatiaia, in the Serra da Mantiqueira, between 2,100 and 2,550 m. *Fuchsia coccinea* occurs naturally only at the summit of four of the highest mountains in Minas Gerais, between 1,400 and 2,000 m.

Two species are endemic to several of the high, granitic "morros" characteristic of the Serra do Mar in Rio de Janeiro state. *Fuchsia alpestris* grows among bushes at the base of granitic outcrops in the Serra dos Orgãos and around Santa Maria Madalena. *Fuchsia glazioviana* is found as high as 2,100 m in open campo vegetation on morros around Nova Friburgo and Santa Maria Madalena. It also descends into cloud forest as low as 1,500 m on the same mountains.

Two newly described species from Paraná and southern São Paulo states have broader ranges. *Fuchsia brevilobis* occurs in forests of low, inland mountain ranges at 600–900 m, but on the eastern slopes of the Serra do Mar in Paraná, it is found from 400 m to sea level. *Fuchsia hatschbachii* occurs further inland in Paraná, in drier forests than the coastal mountains, and is apparently restricted to limestone and sandstone outcrops between 950 and 1,150 m.

Reproductive Biology

The members of sect. *Quelusia* all conform to a very similar pattern of floral biology. The flowers are hermaphroditic and self-compatible, as well as protogynous and herkogamous. Consequently, the genus has been characterized as "modally outcrossing" (Raven, 1979a). Blossoms are always pendent, with the stigma exserted well below the anthers, a prime example of "approach herkogamy" (Webb & Lloyd, 1986), where the stigma is contacted as the visitor enters the flower prior to picking up pollen. Protogyny is incomplete, however, because the anthers begin to dehisce within a day after anthesis, while the stigmas remain receptive from the onset of anthesis until flower senescence several days later. Despite the presence of these outcrossing mechanisms, geitonogamous pollen transfer may still lead to effective selfing. Automatic selfing can also occur, since pollen usually hangs down in clumps joined by viscin threads, which are able to contact the stigmatic surface before the flower senesces.

The flowers of sect. *Quelusia* are highly specialized for pollination by hummingbirds. Each species has red, odorless, hanging, tubular flowers with copious nectar secreted at the base of the floral tube, all standard features in hummingbird-pollinated plants (Faegri & van der Pijl, 1979). Unlike other bird-pollinated fuchsias, however, the petals are much larger and strongly convolute; they thus act functionally as a prolongation of the floral tube, further restricting the access of insects to the nectary. The deep blue-violet color of the petals of sect. *Quelusia* is unique in the genus, although its significance in pollination is not clearly understood. The abundance of viscin threads in *Fuchsia* is among the most copious in the family and has been considered a probable adaptation to bird pollination (Nowicke et al., 1984).

Hummingbirds are commonly observed visiting the flowers of sect. *Quelusia* throughout its native range, but few published accounts have identified the species of the hummingbird visitors. Curtis (1836) cited an early account by J. Anderson, the botanist on Philip King's voyage to the Magellan Straits, who observed numerous hummingbirds visiting *F. magellanica* around Port Famine, even after days of constant rain and sleet at near-freezing temperatures. Hauman-Merck (1912) reported frequent visits of *Eustephanus galeritus* (Mol.) on

F. magellanica near Corral, in Valdivia, Chile. In Brazil, Ruschi (1982) reported *Colibri serrirostris* (Vieillot) visiting flowers of *F. regia*. A Plovercrest hummingbird, *Stephanoxis lalandi* (Vieillot), was observed visiting *Fuchsia* in the open campos area of Mt. Itatiaia, Rio de Janeiro state by Mitchell (1957), as well as by Ruschi (1982) in Teresópolis at 900 m. Three hummingbird species, *Colibri serrirostris*, *Stephanoxis lalandi*, and *Leucochloris albicollis*, were common around *F. bracelinae* in the Serra do Caparaó, at 2,400 m, during a visit in February 1985 (L. Gonzaga, pers. comm.). It is unlikely that any strong pollinator discrimination exists between the different species of *Fuchsia* in Brazil, since the flowers are very similar in size and overall floral pattern. On both *F. campos-portoi* and *F. brevilobis*, I have seen two different hummingbird species visiting flowers of the same bush in rapid succession, and I also watched an individual hummingbird visit flowers of *F. brevilobis* right after leaving flowers of a neighboring plant of *F. regia* subsp. *serrae*.

Besides hummingbirds, several insect species have also been observed visiting flowers of sect. *Quelusia* in their native habitat. *Apis mellifera* was a common visitor to flowers of *F. coccinea* at Serra da Piedade, Minas Gerais, during our visit in February 1985; it was also observed on *F. campos-portoi* at Mt. Itatiaia in January 1985. Hauman-Merck (1912) described the visits of *Bombus chilensis* to *F. magellanica* in southern Chile, and thought it to be a more important visitor there than hummingbirds. Both of these bee species hang from the anthers to collect pollen and may attempt to reach the nectary at the base of the tube; *Bombus*, especially, is able to make contact with the stigma and acts as an effective pollinator. I also saw a butterfly visiting *F. regia* subsp. *serrae* near Mogi das Cruzes, São Paulo, Brazil; it grasped the stamens attempting to enter the floral tube for nectar and made contact with both the anthers and the stigma in the process. When species of sect. *Quelusia* are cultivated outside their native range in areas where hummingbirds do not occur, such as England, they are frequently visited by honey bees and bumblebees (J. Wright, pers. comm.).

Seed dispersal is probably effected by frugivorous birds, although no direct observations or published reports have been made.

Morphology

Habit and stems. Plants of sect. *Quelusia* are all shrubs or lianas. Stems are usually flexuous and require the support of neighboring vegetation, but low, densely branched shrubs are common in such species as *F. coccinea* and *F. bracelinae*. *Fuchsia regia* can become a large, forest liana, with stems to 20 cm in diameter climbing as high as 15 m into the tree canopy, but it can also be found growing as a compact shrub in open situations. On large, climbing plants of *F. regia* and *F. alpestris*, it is common to find hanging branches several meters long. Short, divaricating side shoots are typical of young plants of *F. regia* subsp. *serrae*.

Vegetative reproduction occurs in most taxa through stem-layering, especially when long, flexuous stems lay over ground litter. *Fuchsia bracelinae* and *F. coccinea* reproduce locally by underground, stoloniferous stems, and some populations of *F. regia* subsp. *serrae* produce aerial roots on shoots well above the ground, as described by Lindley (1841) for *F. radicans*.

Leaves. Phyllotaxis in sect. *Quelusia* is opposite or whorled. The most common condition in the section is ternate leaves, but individual plants often combine leaves in pairs, threes, and fours on different shoots. Exceptions are *F. alpestris*, almost always with opposite leaves, and *F. regia* subsp. *reitzii*, with leaves all in whorls of 3, 4, or 5. *Fuchsia glazioviana* has unusually short internodes, just 3–12 mm long, with the leaves densely packed on the stems.

The texture of the leaves of most species is membranous, but *F. regia* subsp. *serrae* has coriaceous leaves, and those of *F. regia* subsp. *regia* are mostly subcoriaceous. Leaf surface is a useful character in some taxa; it is smooth and lustrous in *F. regia* subsp. *serrae*, with a dark green color above and a paler tone below. Leaf surfaces of *Fuchsia glazioviana* and *F. hatschbachii* are similar, but the surface is less brilliant. Impressed leaf veins are especially characteristic of *F. bracelinae*, and to a lesser degree in *F. brevilobis*. Secondary venation in leaves of *F. campos-portoi* can be almost imperceptible, while in *F. regia* subsp. *reitzii* a conspicuous tertiary venation is usually evident.

Leaf size and shape vary considerably within taxa, but some differences can be readily distinguished. The leaves of *Fuchsia glazioviana*, *F. bracelinae*, and *F. campos-portoi* are small, mostly less than 4 cm long, and very narrow in *F. campos-portoi*. The largest leaves occur in *F. alpestris* and *F. regia* subsp. *regia* and are mostly 6–14 cm long. Ovate leaves with cordate bases are diagnostic of *F. coccinea*.

Leaf margins are characteristically gland-denticulate, but in *F. campos-portoi* and *F. regia*

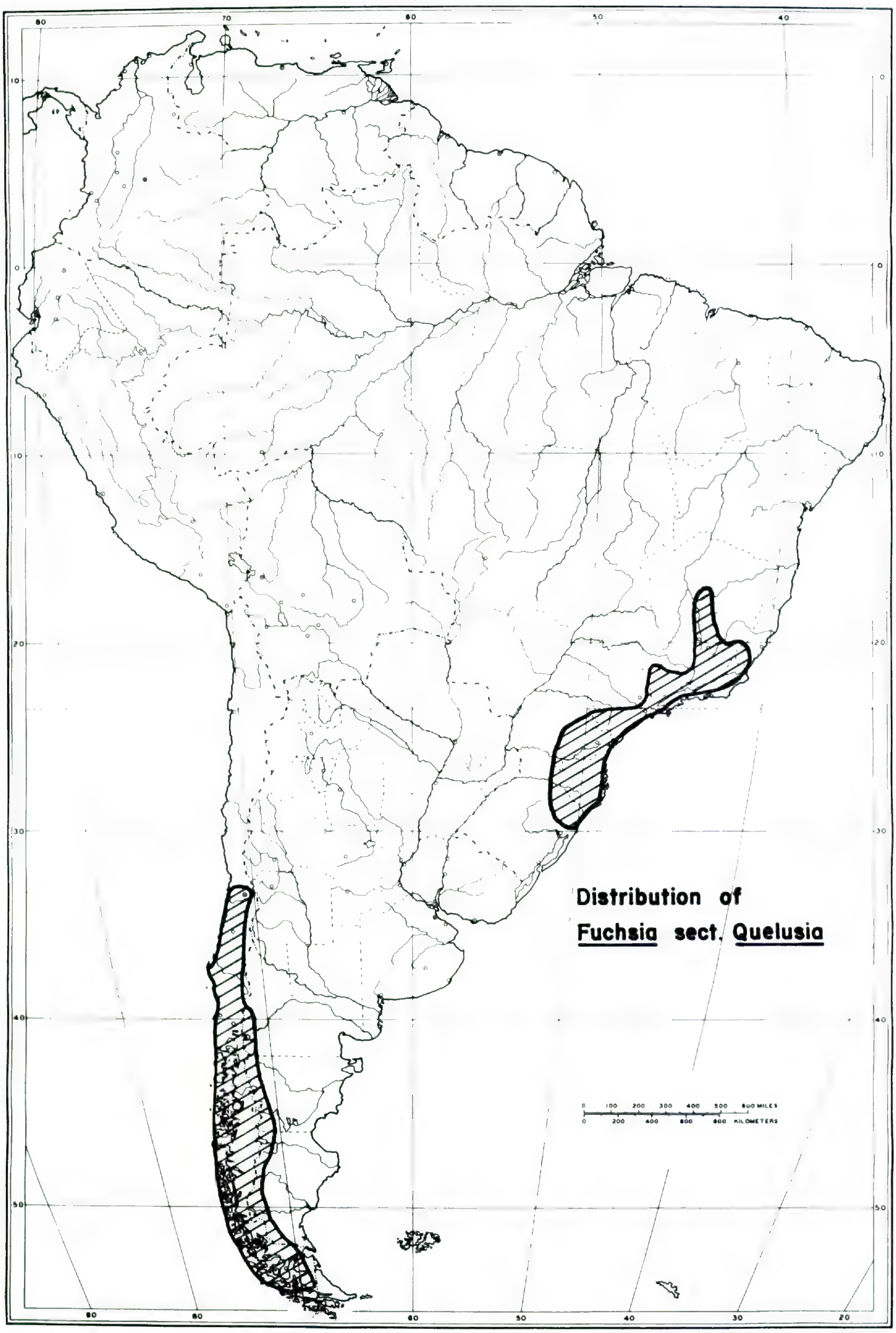

FIGURE 1. Native distribution of *Fuchsia* sect. *Quelusia*.

subsp. *reitzii* they are conspicuously gland-serrulate, with the teeth angled towards the leaf apex. *Fuchsia magellanica* has mostly serrulate margins, but they are sometimes crenate, with shallow lobes between the teeth.

Petiole length is useful in discriminating taxa in sect. *Quelusia*. *Fuchsia coccinea* and *F. bracelinae* have nearly sessile leaves, with petioles 1–3 mm long, while they exceed 10 mm in *F. regia* subsp. *regia* and *F. regia* subsp. *serrae*. Often the proportion of the petiole to the blade length is very informative: high (> 1 : 4) in *F. regia* and *F. magellanica*, and low (1 : 8 <) in *F. hatschbachii* and *F. alpestris*. Petioles are stout and over 1 mm thick in *F. alpestris*, *F. coccinea*, *F. regia* subsp. *serrae*, and *F. regia* subsp. *regia*; they are slender in *F. magellanica*.

Stipules in all but one taxon are small, lanceolate, and deciduous. *Fuchsia regia* subsp. *serrae* is unique, with prominent, persistent stipules that are thick and recurved, usually fused in pairs between adjacent leaves, and give a characteristic nodose appearance to the stems.

Flowers. Flowers are all borne singly or rarely in pairs in the axils of young leaves near the branch tips. Rarely more than two or three whorls of leaves bear flowers at the same time on a single stem. The pedicels are pendulous, except in *F. coccinea*, where they are divergent from the stem before hanging down in the distal half.

Section *Quelusia* is the only group in the genus where the sepals are much longer than the floral tube. In addition, the sepals are always connate to varying degrees at their base, which in effect lengthens the tubular portion of the flower. The petals are strongly convolute and form a cone around the stamens and stigma. The nectary consists of a smooth to slightly lobed band ca. 1 mm thick lining the inner, basal portion of the floral tube. A flower from sect. *Quelusia* is illustrated diagrammatically in Figure 2.

The floral tubes of most species are cylindrical-fusiform, but *F. campos-portoi* is distinct with its short, subrhombic tubes. Sepal connation is only 3–6 mm in most taxa. *Fuchsia brevilobis* is exceptional, with sepals connate for 10–16 mm, almost completely concealing the corolla and longer than either the free sepal lobes or the true floral tube. *Fuchsia regia* subsp. *serrae* also has sepals joined for over ⅓ their length; the buds are noticeably four-ridged, and the free lobes sometimes recurve after anthesis.

Fruits. Berries in sect. *Quelusia* are generally oblong-ellipsoid and dark purple to black when ripe. In *F. regia* subsp. *reitzii*, the berries are mostly globose, while in *F. magellanica* they are much more elongate than in the other species. Ovules are biseriate in each locule and number between 60 and 120 per fruit.

Cytology and Palynology

Cytology. Concurrently with this revision, Hoshino & Berry (1989) made an extensive cytological survey of all 11 taxa of sect. *Quelusia*, examining 103 individuals from natural populations and 11 cultivated plants. Their results showed the section to be entirely polyploid, predominantly tetraploid ($n = 2x = 22$), but with octoploidy ($n = 4x = 44$) found in two species. All other sections in the genus, except for the tetraploid, monotypic sect. *Kierschlegeria*, are entirely or mostly diploid ($n = x = 11$).

Tetraploidy was found in all specimens examined of six Brazilian species and in the more than 40 populations that were studied from the widespread *F. magellanica* of the southern Andes (see Hoshino & Berry, 1989, Table 1). Normal bivalent formation was observed in all of these collections.

Octoploidy was limited to the three subspecies of *F. regia* and a single cultivated individual of *F. alpestris*. *Fuchsia regia* subsp. *reitzii* and *F. regia* subsp. *serrae* were consistently octoploid, but tetraploid individuals were also found in *F. alpestris* and *F. regia* subsp. *regia*. In all octoploids examined, varying numbers of quadrivalents were present at meiotic Metaphase I and Anaphase I. Although tetraploid and octoploid plants occurred sympatrically in several localities, no hexaploid individuals were detected. The chromosome numbers of the individuals examined by Hoshino & Berry are indicated in this paper under the specimen citations of the respective taxa.

Palynology. Pollen grains of *Fuchsia* have distinctive, onagraceous features such as viscin threads, paracrystalline-spongy ektexine, protruding apertures, and a solid endexine. The genus is unique, however, in possessing predominantly two-aperturate, bilaterally symmetrical pollen grains. Radially symmetrical, three-aperturate grains also occur in the genus but are confined to polyploid species and are clearly derived from two-aperturate ancestors, a result of the increased cell volume of polyploid cells. Most sections of the genus can be distinguished by a combination of aperture number, viscin thread ultrastructure, and type of exine sculpture elements. Detailed pollen descriptions of the different sections are provided in Praglowski et al. (1983) and Nowicke et al. (1984).

The members of sect. *Quelusia* have radially symmetrical and three-aperturate pollen grains, a condition consistent with the polyploidy found in all species of the section. Viscin threads are segmented-beaded, and the exine has globular sculpture elements. Praglowski et al. (1983) reported a size range of 33–60 μm for P (polar axis length) and 59–85 μm for E (equatorial axis) for the seven taxa they examined. Rare four-aperturate grains have been found in *F. coccinea* and *F. regia*; occasional two-aperturate grains were also found in *F. magellanica* and were considered to be reversions to the ancestral condition of the genus (Praglowski et al., 1983; Nowicke et al., 1984). Octoploid individuals of *F. regia* cannot be distinguished from tetraploids by differences in pollen morphology, although octoploid pollen grains may be significantly larger (Hoshino, pers. comm.).

The only other section of *Fuchsia* characterized by three-aperturate pollen is the monotypic sect. *Kierschlegeria* (*F. lycioides*). Its pollen can be distinguished from that of sect. *Quelusia*, however, by the smooth viscin threads with elongated sculpture elements (Nowicke et al., 1984).

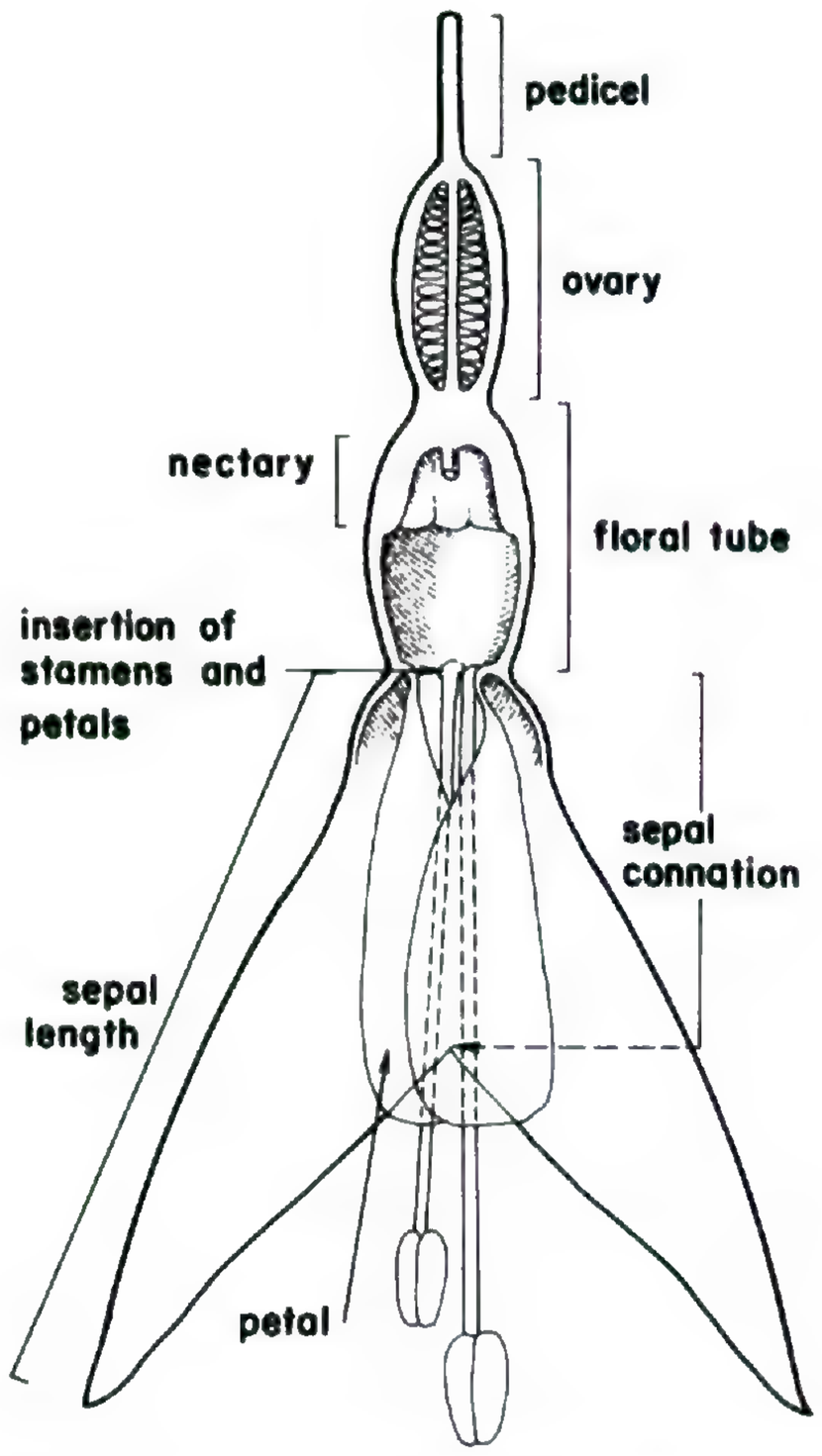

FIGURE 2. Schematic longitudinal section of a flower from *Fuchsia* sect. *Quelusia*, with terminology used in the species descriptions.

FLAVONOID COMPOUNDS

Because of the ornamental appeal of *Fuchsia*, several studies have examined the role of anthocyanins in the different flower colors in the genus (Harborne, 1963; Yazaki & Hayashi, 1967; Nozzolillo, 1970; Yazaki, 1976; Crowden et al., 1977). Flower colors are determined almost entirely by the 3-glucosides and 3,5-diglucosides of all six common anthocyanins. Red coloration in the sepals and floral tube is due mostly to cyanidin and peonidin pigments, whereas the characteristic blue-violet color of the petals of all members of sect. *Quelusia* is due to the dominance of malvidin derivatives, with peonidin in much lesser concentrations (Nozzolillo, 1970; Yazaki, 1976; Crowden et al., 1977). Yazaki (1976) indicated that the intense blue-violet color of some cultivars is due to the simultaneous presence of other co-pigments in the cell, particularly quercetin glycosides. In some cultivars, the petals change color from blue-violet to purple-red with age; Yazaki (1976) has shown this to be due to the combined effect of the flavonoid co-pigments, together with a decrease in the pH of the cell sap brought about by the accumulation of organic acids.

Averett et al. (1986) carried out a comprehensive survey of the foliar flavonoids in 80 taxa of *Fuchsia* and reported the flavonoid profiles of four taxa belonging to sect. *Quelusia*. Current taxonomic changes in the section, however, have modified these results, and a revision is presented in Table 1. Based on the same samples examined by Averett et al. (1986), two additional taxa are now included, *F. brevilobis* and *F. regia* subsp. *serrae*. From these changes, it is apparent that it is *F. brevilobis*, not *F. regia*, that has a distinctive flavonol diglucoside. *Fuchsia magellanica* remains the only species in the section known to possess flavones (compounds 12 and 15), which could be used as excellent markers for detection of the parentage of this species in cultivars of uncertain origin, although flavones might not be expressed in all *F. magellanica* hybrids. Otherwise, the remaining flavonol monoglucosides are all of common occurrence in other taxa of the genus.

NATURAL HYBRIDIZATION

Because of the restricted distributions of most of the Brazilian species of *Fuchsia*, there is no range overlap among them, except with the widespread *F. regia*. *Fuchsia regia* occurs sympatrically with five other species, and in each case, morphologically intermediate, putatively hybrid individuals have been detected (Table 2). Populations of *F. regia* subsp. *serrae* also occur together with each of the other subspecies of *F. regia*, forming extensive hybrid swarms in areas of sympatry.

TABLE 1. Foliar flavonoids in species of *Fuchsia* sect. *Quelusia*.[1]

Taxa Examined	Compounds[2]									
	1	2	3	5	6	7	8	9	12	15
F. brevilobis	+		±	+	+			±		
F. campos-portoi	+		+		+	+	+	+		
F. coccinea	+				+	+	+	+		
F. magellanica	+	+	+		+	+	±		+	+
F. regia subsp. *regia*	+	±	+		+	±	+	+		
F. regia subsp. *serrae*	+	±	+		+	±	+	+		

[1] Based on the same samples as reported in Averett et al. (1986); changes in identifications are as follows: *Davidse et al. 10904*, *Hatschbach & Ramamoorthy 42974* (*F. brevilobis*), *Conrad & Dietrich 2055*, *Hatschbach & Ramamoorthy 42976*, *Ramamoorthy & Reitz 1163*, and *Ramamoorthy & Vital 685* (*F. regia* subsp. *serrae*); *Ramamoorthy & Vital 673, 674, 676, 680* (*F. regia* subsp. *regia*).

[2] + = present in all collections sampled, ± = present in some collections but absent in others. Same numerical codes as in Averett et al. (1986): 1 = K-3-O-glu; 2 = K-3-O-gal; 3 = K-3-O-rham; 5 = K-3-O-rham-glu; 6 = Q-3-O-gluc; 7 = Q-3-O-gal; 8 = Q-3-O-rham; 9 = Q-3-O-ara; 12 = A-7-O-glu; 15 = L-7-O-glu. Abbreviations: K = kaempferol, Q = quercetin, A = apigenin, L = luteolin, glu = glucose, gal = galactose, rham = rhamnose, ara = arabinose.

The morphological intermediacy of several characters was the main criterion used in detecting hybrids between different taxa; in most cases, both putative parents were growing sympatrically close by. Details of the different hybrid combinations found are provided in the Appendix.

Natural hybridization among sympatric taxa of sect. *Quelusia* appears to occur readily, as there are no major differences in pollinators, flowering time, or habitat in mixed populations. The only indication that reduced fertility might occur in hybrids was from one artificial cross between a tetraploid individual of *F. regia* subsp. *regia* and an octoploid individual of *F. regia* subsp. *serrae*, where the hexaploid progeny showed low pollen fertility (Hoshino & Berry, 1989). More experimental work is needed on the chromosomal behavior of crosses between tetraploid and octoploid taxa in sect. *Quelusia*.

In most cases, the area where two species overlap is small, and the frequency or abundance of hybrids is low compared with the parental populations. *Fuchsia campos-portoi*, *F. coccinea*, and *F. glazioviana* are all high-altitude species that grow in the open "campos de altitude" at or above treeline. Hybrids between these species and *F. regia* occur where they descend into the upper forest zone, or when *F. regia* extends beyond its normal limit into the open campos. *Fuchsia brevilobis* has the inverse of this pattern, generally occurring at lower altitudes than *F. regia* subsp. *serrae*, with probable hybrids in limited areas where their ranges overlap. *Fuchsia bracelinae* may have grown sympatrically with *F. regia* until the past century, when extensive cutting and burning eliminated the upper forest belt of most of the Serra do Caparaó.

The situation among the subspecies of *F. regia* is notably different. These taxa are much more widespread and overlap more extensively than any of the other species in the section. *Fuchsia regia* subsp. *reitzii* is typical of the planalto region in Rio Grande do Sul and southern Santa Catarina states, but it contacts populations of the more mesic *F. regia* subsp. *serrae* along the easternmost edge of the planalto near the crests of the Serra Geral, producing large, widely variable, intermediate populations. Extensive intergradation between *F. regia* subsp. *regia* and *F. regia* subsp. *serrae* occurs

TABLE 2. Sympatric occurrence and natural hybridization among the native taxa of *Fuchsia* sect. *Quelusia* in Brazil. An X indicates that both sympatry and natural hybridization occur. Abbreviations are of the first three letters of the specific (capitals) or subspecific (lower case) epithets.

Subspecies of *F. regia*									
subsp. *regia*	X	—	—	X	X	X	—		
subsp. *reitzii*	—	—	—	—	—	—	—	—	
subsp. *serrae*	—	—	X	—	—	—	—	X	X
	ALP	BRA	BRE	CAM	COC	GLA	HAT	reg	rei

along the eastern edge of the Serra da Bocaina and the Serra do Mar in northern São Paulo state.

Although *F. regia* is the only species presently found in widespread contact with other species of sect. *Quelusia*, the numerous hybrid combinations detected indicate that interspecific genetic recombination may have been an important mechanism in providing a rich source of novel, adaptive genotypes in the fuchsias of southern Brazil.

Evolution of Section *Quelusia*

Various lines of evidence, including chloroplast DNA restriction fragment analysis (Sytsma & Smith, 1988) and leaf flavonoid analyses (Averett et al., 1986), have suggested the Old World sect. *Skinnera* to be the earliest offshoot of the genus and the sister group of all the American sections of *Fuchsia*. The oldest fossil pollen grains of the genus have been found in New Zealand and Australia from Oligocene and Miocene deposits (Pocknall & Mildenhall, 1984; Berry et al., in prep.). Despite the early divergence of this group, the members of sect. *Skinnera* exhibit several specialized features for the genus, including the derived condition of male sterility, reduced petals, presence of flavone sulphates, and a variety of unusual life forms, such as large trees and procumbent creepers.

The most likely area of origin of *Fuchsia* is South America, where the greatest concentration of species as well as the sections with the most generalized features in the genus occur (Raven, 1979a; Berry, 1982). Whereas the large Andean sections appear to have arisen and radiated during the Neogene uplift of the tropical Andes (Berry, 1982, 1985), the areas now occupied by sect. *Quelusia* have changed little since the mid-Tertiary, when temperate forests were much more widespread in southern South America (Simpson, 1973). With the current Australasian fossil record, it is now apparent that *Fuchsia* formed part of the *Nothofagus* and podocarp-dominated temperate forests that occurred more or less continuously across southern South America, Antarctica, and Australia until at least the late Eocene (Zinmeister, 1987; Truswell, in press). The wet, temperate forests of the southern Andes and the montane forests of southeastern Brazil are now the only remnants of these austral temperate forests in South America, which, like *Fuchsia*, share a large number of disjunct plant groups that also have close relatives in Australasia (Raven, 1979b).

Although there are no fossil records to indicate an early presence of sect. *Quelusia* in South America, the section follows a pattern consistent with other relicts of the southern temperate forests. It is ecologically conservative, with most individuals restricted to moist sites in cool, forest habitats. Morphologically, there is little divergence in the section, with species differentiated by relatively minor variations on a common pattern of floral and vegetative characters. Many of the features of sect. *Quelusia* are unspecialized in the genus, including the axillary, bisexual flowers, well-developed petals, numerous seeds, and segmented-beaded viscin threads. It is possible that some of the primitive characters in sect. *Quelusia* were preserved through the buffering effects on evolutionary divergence caused by paleopolyploidy in the group (Stebbins, 1985; Hoshino & Berry, 1989).

The ancestor of the modern-day species of sect. *Quelusia* was probably tetraploid, with derived, three-porate pollen (Hoshino & Berry, 1989). As such, it could not have given rise directly to the other, mostly diploid, sections of the genus, but rather represents an early offshoot of the ancestral stock of *Fuchsia* in South America. Early on, sect. *Quelusia* developed its own floral syndrome for hummingbird pollination: the relatively short, nectar-holding floral tube; large, attractive sepals; and petal cone and sepal tube that further extend the tubular portion of the blossom.

Section *Kierschlegeria*, containing only *F. lycioides* restricted to the dry coastal scrub of central Chile, is the only other section of *Fuchsia* that is entirely polyploid and has three-porate pollen grains. Because of this similarity and its geographic proximity to *F. magellanica*, Berry (1982) and Raven (1988) postulated that it is related to sect. *Quelusia*. Using chloroplast DNA restriction fragment analysis, Sytsma & Smith (1988) demonstrated that sects. *Quelusia* and *Kierschlegeria* form a distinct lineage from the rest of the genus, defined by three synapomorphies. Furthermore, within this lineage *F. lycioides* could not be distinguished from the two species of sect. *Quelusia* studied, *F. magellanica* and *F. regia*. This evidence of a close relationship is remarkable, since *F. lycioides* has a high number of specialized features, such as functional dioecy, spinose leaf bases, low seed number, smooth viscin threads, small flowers, and summer deciduousness. Evidently, the evolutionary shift of sect. *Kierschlegeria* to a xeric habitat in the southern Andes entailed a large number of morphological changes corresponding to a much smaller degree of genotypic divergence.

Within sect. *Quelusia*, we are faced with the question of why there is just one species in Chile and Argentina, while in Brazil there are eight species

in an area of comparable size. *Fuchsia magellanica* is a classic example of the lack of differentiation that is characteristic of the *Nothofagus* forests of Chile. These habitats presumably have been stable and continuous for long periods of time, providing little opportunity for speciation to occur. Most taxa inhabiting these areas have retained primitive characters for their respective groups (Simpson, 1973). Although the current distribution of *F. magellanica* extends beyond the *Nothofagus* forests, virtually all of the area now occupied by this species south of 44°S latitude was covered by ice during the Pleistocene (Vuilleumier, 1971).

In contrast to the temperate latitudes of Chile and Argentina, the Brazilian members of sect. *Quelusia* are centered in the subtropics. There, *Fuchsia* is limited to the cool, moist habitats of the coastal mountains and the interior planaltos. Most of the cold-adapted taxa of Brazilian fuchsias are vicariant species that are now restricted to just a few high mountain peaks. Allopatric speciation in this group of species was likely enhanced by the joining and subsequent separation of populations caused by the cycles of Pleistocene glacial and interglacial events (Simpson, 1979; Klein, 1984).

Two of the Brazilian species have adapted to warmer, lower-altitude habitats that are more continuous over much of the southeastern part of the country. *Fuchsia regia* extends over the entire range of the section in Brazil and forms a broad taxonomic complex treated here as comprising three subspecies, each adapted to a slightly different set of environmental conditions. This species shows an intermediate stage in the morphological differentiation of populations between the more uniform *F. magellanica* in the southern Andes and the distinct, high-altitude species of Brazil. *Fuchsia regia* overlaps geographically with most of the other species in the section and hybridizes with them whenever they come into contact; these hybrids may constitute an important source of genetic recombination for new adaptive genotypes in the section. It is also the only species in the genus with naturally occurring octoploid populations, which may lead to partial reproductive isolation with the other tetraploid taxa in the section.

Two newly described species from Paraná, Brazil both consist of tetraploid populations that occur within the range of the octoploid subspecies of *F. regia*. The different ploidy levels may afford sufficient reproductive isolation for these species to remain distinct. One of the new species, *Fuchsia hatschbachii*, is the only species in the section that appears to be edaphically specialized, occurring on limestone and sandstone substrates on the eastern edge of the southern planalto. Populations of *F. regia* subsp. *serrae* occur within 15 km of *F. hatschbachii* near Curitiba, Paraná, but the two have never been observed to grow together under natural conditions. The other new species, *Fuchsia brevilobis*, is specialized in its small flowers with elongate sepal tubes, and it has become adapted to lower altitudes than most neighboring populations of *F. regia*.

Overall, the evolutionary scenario of sect. *Quelusia* differs significantly from the two, more speciose, Andean sects. *Fuchsia* and *Hemsleyella*. Those species radiated recently into a broad expanse of new, cool montane habitats that were created with the recent uplift of the tropical Andes (Berry, 1982, 1985). Section *Quelusia*, on the other hand, has occupied a more ancient and stable vegetation type in which disruptive selection may have played less of a role in the divergence of populations.

Cladistic Analysis

This section examines the relationships of the taxa of sect. *Quelusia* and the closely related *F. lycioides* by means of a formal cladistic analysis. The advantages of this approach are that it provides clearly stated hypotheses about evolutionary relationships based on shared, derived character states, and it is based on an objective, repeatable methodology.

The data were analyzed on an ATT 6300 microcomputer by the Wagner parsimony method of the PAUP software package (version 2.4.1., Swofford, 1985), using the branch and bound algorithm (Hendy & Penny, 1982). Character polarity was determined by outgroup comparison (Hennig, 1966; Watrous & Wheeler, 1981), using sect. *Skinnera* as the outgroup. In two characters, however, the character states in sect. *Skinnera* are almost certainly apomorphic in the genus; so in these cases the other genera of Onagraceae were used as the outgroup.

Twenty-two characters were used in the phylogenetic analysis, with the character states listed in the data matrix (Table 3).

Fifteen equally parsimonious trees were produced, each with 29 steps and a consistency index of 0.931. Topologically all the trees are identical, as they represent arbitrary resolutions of a single tetrachotomy that appears in the trees. The unique topology of these trees is presented in Figure 3. According to these results, sects. *Kierschlegeria* and *Quelusia* form a monophyletic group defined by five synapomorphies, but within this clade *F.*

TABLE 3. Data matrix for characters of taxa used in the cladistic analysis of *Fuchsia* sects. *Quelusia* and *Kierschlegeria*. Sect. *Skinnera* is used as the outgroup. Characters 9, 16, and 17 are unordered. A zero represents the plesiomorphic states, and higher numbers represent the apomorphic states. In those characters where no zero appears, the plesiomorphic conditions are uncertain, and the character states were coded as unordered.

	Characters																					
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
sect. *Skinnera*	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	1	0	0	?	0	?
F. lycioides	1	1	1	0	0	0	0	0	2	1	0	1	1	0	1	2	2	0	0	0	0	?
F. alpestris	1	?	0	?	1	1	1	1	3	0	0	0	0	0	0	3	3	0	0	1	1	0
F. bracelinae	1	1	0	?	1	1	1	1	3	0	0	0	0	0	0	3	3	0	1	0	1	0
F. brevilobis	1	1	0	1	2	1	1	1	3	0	0	0	0	0	0	3	3	0	0	1	1	0
F. campos-portoi	1	1	0	1	1	1	1	1	3	0	0	0	0	0	0	3	3	0	0	0	0	1
F. coccinea	1	1	0	1	1	1	1	1	3	0	0	0	0	0	0	3	3	0	1	0	1	0
F. glazioviana	1	1	0	?	1	1	1	1	3	0	0	0	0	0	0	3	3	0	0	0	0	1
F. hatschbachii	1	1	0	1	1	1	1	1	3	0	0	0	0	0	0	3	3	0	0	0	0	0
F. magellanica	1	1	0	0	1	1	1	1	3	0	0	0	0	0	0	3	3	0	0	0	0	0
F. regia:																						
subsp. *regia*	1	?	0	1	1	1	1	1	3	0	0	0	0	0	0	3	3	0	0	1	0	0
subsp. *serrae*	1	2	0	1	2	1	1	1	3	0	0	0	0	0	0	3	3	1	0	1	0	0
subsp. *reitzii*	1	2	0	?	1	1	1	1	3	0	0	0	0	0	0	3	3	0	0	0	0	0

1. *Pollen grains:* 0 = 2-porate, 1 = 3-porate
2. *Ploidy level:* 0 = diploid, 1 = tetraploid, 2 = octoploid
3. *Viscin threads:* 0 = segmented-beaded, 1 = smooth
4. *Flavones:* 0 = present, 1 = absent
5. *Sepals:* 0 = unfused, 1 = fused < ¼ of length, 2 = fused > ⅓ of length
6. *Leaves:* 0 = alternate, 1 = opposite/whorled
7. *Stamens:* 0 = included within sepals, 1 = exserted beyond sepals
8. *Floral tube : sepal length:* 0 = (sub)equal, 1 = sepals noticeably longer
9. *Nectary:* 1 = smooth band around lower part of floral tube, 2 = thick lobes at base of tube around style, 3 = protruding from lower part of floral tube
10. *Stigma:* 0 = subentire, 1 = 4-lobed (on functional female flowers)
11. *Pollen color:* 0 = cream, 1 = blue
12. *Seed number per fruit:* 0 = > 50, 1 = < 40
13. *Petiole bases:* 0 = deciduous, 1 = persistent and spinose
14. *Sexual system:* 0 = hermaphrodite, 1 = male sterility determined by dominant gene
15. *Sexual system:* 0 = hermaphrodite, 1 = male sterility present and determination unknown
16. *Petal color:* 1 = dark maroon, 2 = pink or pale purple, 3 = blue-violet
17. *Petal imbrication:* 1 = separate, 2 = slightly overlapping, 3 = strongly convolute
18. *Stipules:* 0 = small and deciduous, 1 = thick-crassate and persistent
19. *Petioles:* 0 = > 3 mm long, 1 = < 3 mm long
20. *Habit (branch type):* 0 = shrubby, 1 = lianoid
21. *Pubescence:* 0 = plant glabrous or sparsely pubsecent, 1 = parts of plant densely pilose
22. *Internodes:* 0 = > 16 mm, 1 = < 16 mm

lycioides is the sister group to all of sect. *Quelusia*. Section *Quelusia* is well delimited by the presence of four synapomorphies, and *F. lycioides* possesses eight unique, derived character states (autapomorphies). Within sect. *Quelusia*, *F. magellanica* appears as the sister group of all the Brazilian taxa, which are grouped by a single character, loss of flavones. The Brazilian taxa of *Fuchsia* are poorly differentiated by the cladistic analysis, forming a polychotomy with four different lineages. *Fuchsia hatschbachii* is an isolated line in Brazil, differing from *F. magellanica* only by the loss of flavones. The three subspecies of *F. regia* form a separate, mainly octoploid lineage, supporting the monophyly of *F. regia* sensu lato. *Fuchsia glazioviana* and *F. campos-portoi* are sister species within the third lineage. The fourth lineage includes four species, which are divided into two species pairs, the high-altitude *F. bracelinae* and *F. coccinea*, and *F. alpestris* and *F. brevilobis*. Two homoplasies (parallelisms) occur in the cladogram: long-connate sepals in *F. brevilobis* and *F. regia* subsp. *serrae*, and lianoid habit in two species pairs.

The paucity of characters that discriminate between the taxa of sect. *Quelusia* makes the results of the cladistic analysis within the section quite tentative, but it is also a reflection of the very close relationship of the species. The proposed sister-

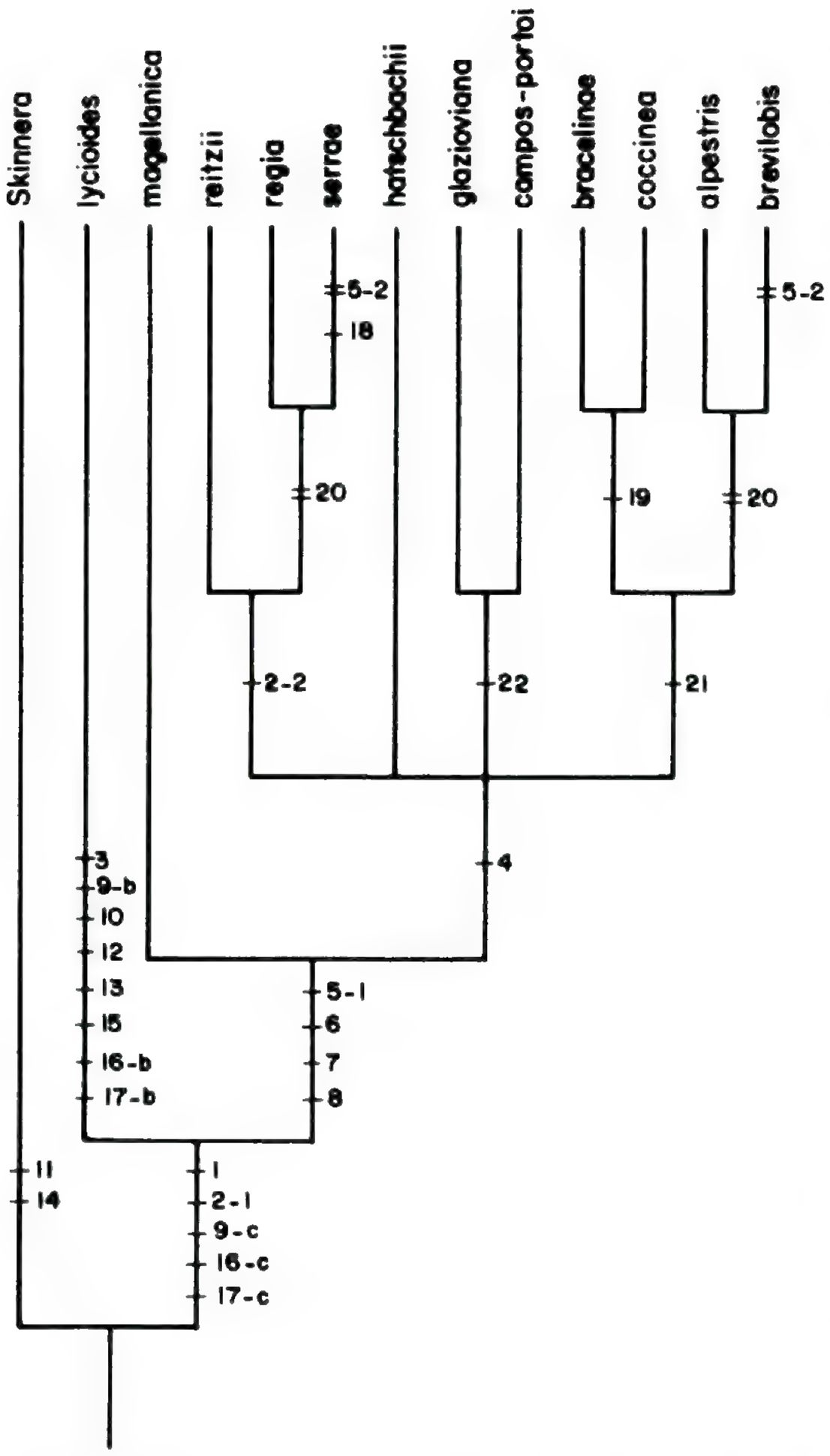

FIGURE 3. Cladogram of *Fuchsia* sects. *Quelusia* and *Kierschlegeria* (*F. lycoides*). Sect. *Skinnera* is used as the outgroup. Double crossbars indicate homoplasies. See Table 3.

group relationship of *F. magellanica* to the Brazilian members of the section is consistent with the biogeography of the group and the evolutionary hypotheses discussed previously, specifically the southern origin of the genus in South America and the secondary radiation of the section in the highlands of southeastern Brazil. According to this hypothesis, the Brazilian taxa differentiated, after their separation from the Andean *F. magellanica*, from an ancestor that had lost flavones. The occurrence of two parallelisms between *F. brevilobis* and *F. regia* subsp. *serrae* is remarkable and may be the result of past hybridization between the two species.

History of Cultivation

Members of sect. *Quelusia* were by far the most important species used in the early stages of fuchsia breeding. For the most part, however, fuchsia breeders in the past century kept few records about the parentage of their introductions. As a result, it is impossible to determine with certainty which species have been involved in the parentage of most of the modern cultivars (Reiter, 1944). Ancestry of sect. *Quelusia* can be assumed in cultivars that share the following exclusive "quelusioid" traits: fairly large, axillary flowers with sepals equal to or longer than the floral tube, and large, violet, rounded, and strongly convolute petals.

Following Reiter (1944), one can distinguish three stages in the history of fuchsia breeding during the past century. First, a variety of species and natural varieties were accumulated in cultivation. Next, these were crossed to select desirable combinations and produce a few, selected strains. This second stage began mostly with crosses between different introductions from sect. *Quelusia*, and then in a more important step, these were crossed with Mexican and Central American species of sect. *Ellobium*. Some of the resulting strains were further crossed with species of other sections, such as *F. boliviana* (sect. *Fuchsia*) and *F. lycioides* (sect. *Kierschlegeria*). Although some other crosses were made that did not involve species of sect. *Quelusia*, these were far fewer and less popular than the quelusioid crosses. The final stage involved the exploitation and selection of mutations, which no longer depended upon the introduction of native material. In the remainder of this section, I will review the role of sect. *Quelusia* in the first two stages of fuchsia breeding, then summarize the present-day situation of sect. *Quelusia* species in cultivation.

Species introductions. With the possible exception of a short-lived introduction of *F. triphylla* in the early 18th century (Wright, 1975), *F. coccinea* was the first species of *Fuchsia* introduced into cultivation in Europe. Plants of this species were growing at Kew Gardens in London in 1788 (Aiton, 1789), and an illustration of it was published by Sims (1789). Hooker (1869) suggested that Sims's figure might have represented *F. magellanica* rather than *F. coccinea*, because of the prominent petioles on the lower leaves. This is clearly not the case, however, as the figure accurately represents the unique arching pedicels and ovate, subsessile upper leaves of *F. coccinea*, and Sims's own specimen deposited at Kew is *F. coccinea* (pers. obs.). Although Dryander stated that the plants he described were introduced from Chile (Aiton, 1789), the species is native to just a few mountains in Minas Gerais, Brazil.

The next introduction from sect. *Quelusia* was *F. magellanica*. An array of different variants of this species appeared in England in the 1820s

under several names, starting with *F. gracilis*, which was reported from the Edinburgh Botanic Garden in 1822 (Lindley, 1824). *Fuchsia conica* and *F. gracilis* var. *multiflora* were both introduced into England from Chile in 1824 (Lindley, 1827a, b). *Fuchsia discolor* was introduced from Port Famine in the Magellan Straits around 1830 (Lindley, 1835). I have seen no other evidence, such as old herbarium specimens from cultivated individuals, to indicate that *F. magellanica* was present in Europe prior to 1822. Soon after *F. magellanica* was introduced, however, it was confused with *F. coccinea* and was often cited as *F. coccinea* (see de Candolle, 1828, and Hooker, 1869).

Fuchsia regia was first grown in England between 1838 and 1840, under the name *F. radicans* (Lindley, 1841), and *Fuchsia alpestris* was cultivated in the Glasgow Botanic Garden as early as 1842 (Gardner, 1843).

Interspecific crosses. Interspecific hybridization among members of sect. *Quelusia* must have begun in the mid-1820s, but the first evidence for this was the appearance of *F. globosa* in a Horticultural Society exposition in London in 1832 (Lindley, 1833). Although the origin and parentage of this plant were not known to Lindley, the illustration and the description strongly suggest that it was a cross between *F. magellanica* and *F. coccinea*. A great proliferation of names of cultivars that were either variants of *F. magellanica* or crosses with *F. coccinea* followed in the next decades, including *F. riccartonii*, *F. tenella*, *F. recurvata*, and *F. corallina*. The history of these plants is unfortunately too poorly documented to determine their precise parentage, and names such as *riccartonii* have been applied to quite different cultivated strains (J. Wright, pers. comm.).

A major step in the search for novel, interesting traits in *Fuchsia* cultivars was the use of *F. fulgens*, a diploid species of the Central American section *Ellobium*, in crosses with selections from sect. *Quelusia*. One of the first such hybrids produced was exhibited in London in 1839, a cross of *F. fulgens* with *F. globosa* called "Standish's Fuchsia" (Lindley, 1840), which must have been either triploid or a spontaneously doubled hexaploid. Harrison (1841) also made a large number of crosses of *F. fulgens* with sect. *Quelusia* hybrids, publishing figures of the flowers of several of the different hybrids he selected. A hybrid between *F. cordifolia* (= *F. splendens*, sect. *Ellobium*) and *F. globosa* was grown in 1842, under the name *F. exoniensis* (Paxton, 1843). *Fuchsia regia* was also used in a series of crosses starting in 1840, leading to the development of darker petal color and improvement of flower shape (Wright, 1979). *Fuchsia boliviana*, a member of sect. *Fuchsia* from South America, may also have been used in the early crosses with selections of sect. *Quelusia* (J. Wright, pers. comm.).

The 19th-century crosses between members of sect. *Quelusia* and sect. *Ellobium* can be considered the "mainstream" fuchsias later treated collectively under the names *F. hybrida* Hort. (Siebert & Voss, 1896; Munz, 1943) and *F. speciosa* Hort. (Bailey, 1900). In the strictest sense, these names have been attributed to crosses between *F. magellanica* and *F. fulgens*. At the other extreme, they have been used to include almost all garden fuchsias. Reiter (1944) suggested that *F. hybrida* might best be treated as a horticultural complex including all cultivars of sects. *Quelusia* × *Ellobium* ancestry, including many of complicated origin.

Chaudhuri (1956) made cytological observations that suggest how crosses between *F. magellanica* and *F. fulgens* might have facilitated the rapid advances in fuchsia breeding during the mid-1800s. In his crossing experiments, the tetraploid ($n = 2x = 22$) *F. magellanica* and the diploid ($n = x = 11$) *F. fulgens* yielded triploid progeny in which a high percentage of unreduced gametes were produced. As a result, the F_1 crosses were partially fertile, and hexaploids ($6x$) were produced in the F_2 generation, as well as tetraploid ($4x$) and pentaploid ($5x$) individuals in the respective backcrosses. All of these crosses retained some degree of fertility. Crosses between *F. magellanica* and other diploids, such as *F. splendens* and *F. denticulata*, did not have the same propensity for unreduced gametes as *F. fulgens*, and their hybrids were largely sterile. Thus, *F. fulgens* may have been a critical species that helped prevent total sterility in crosses with the polyploid members of sect. *Quelusia* and with later cultivars of even higher ploidy levels.

More recently, J. O. Wright in England has confirmed Chaudhuri's findings, producing a complete set of $3x$ to $9x$ progeny, entirely by selfing and backcrossing the original *F. magellanica* × *F. fulgens* hybrids (J. Wright, pers. comm.). Wright further reports that none of these hybrids showed any obvious similarity to *F. fulgens*.

Fuchsia magellanica is the only species in sect. *Quelusia* able to withstand winter conditions with long periods of freezing temperatures, so that all of the hedge plants of fuchsia grown outdoors in England and Ireland are variants of this species or crosses with a strong *F. magellanica* parentage.

Many of the recent introductions from Brazil, however, such as *F. campos-portoi* and *F. coccinea*, are proving to be frost-resistant as well (J. Wright, pers. comm.).

Native species in cultivation today. Many of the early species introductions have been maintained for long periods of time in cultivation without crossing. Thus, Hooker (1869) was able to trace plants of *F. coccinea* found in the Oxford Botanic Garden in 1867 back to the original introduction of that species at Kew in 1788. Although this species may have been later lost from cultivation in England and Europe, it was successfully established on several of the Atlantic islands off the north African coast, such as Madeira, St. Helena, and the Canary Islands, in the early 1800s, persisting to present day (Hansen, 1969; A. Calero, pers. comm.). Plants of *F. alpestris* grown today in England and continental Europe have particularly small leaves similar to Gardner's type specimen and may well date back to his original introduction in 1842. Wild strains of *F. magellanica* are apparently still present in England, and the species has become widely naturalized in parts of Ireland, New Zealand, Hawaii, South America, and eastern and southern Africa.

As a result of the author's collections of native fuchsias in Brazil between 1985 and 1987, and seeds of different strains of *F. magellanica* obtained from Chile and Argentina, many new species and strains from sect. *Quelusia* have been recently introduced into cultivation. All the taxa recognized in this treatment, except *F. bracelinae* and *F. glazioviana*, are now in cultivation, with the most complete collections grown at the University of California Botanical Gardens at Berkeley and in the private garden of Mrs. Drude Reiman-Dietiker in the Netherlands. Other important collections include those of Mr. J. O. Wright in England, members of the different amateur fuchsia societies on the west coast of the U.S., and the Nederlandse Kring van Fuchsia-Vrienden in the Netherlands.

Systematic Treatment

Taxonomic history. The earliest known specimens of *Fuchsia* from South America were collected in the Magellan Straits around 1690 by George Handisyd, who was surgeon aboard the British ship *Modena* (Middleton, 1909). These collections correspond to *F. magellanica* and are deposited in the eighth volume of Hans Sloane's herbarium at BM. Louis Feuillée published the first description and illustration of this species under the name *Thilco* (Feuillée, 1725), but it was not taken up by Linnaeus, who described *Fuchsia* in 1753 in *Species Plantarum*. More specimens of *Fuchsia* were collected in the Magellan Straits in January of 1768 by Philibert Commerson, naturalist on the French survey expedition led by Louis de Bougainville. Commerson's specimens were examined by Lamarck, who designated them the type collection for *F. magellanica*, which he described in 1788. Another early collection of this species was made by Ruiz and Pavón between 1778 and 1788, near Concepción, Chile; they later described it as *F. macrostema* (Ruiz & Pavón, 1802).

Domingo Vandelli published the genus *Quelusia* in 1788, based on Brazilian plants. He did not name a species, and his description and illustration dealt mostly with the flower, making it difficult to distinguish which of the Brazilian species he was treating. José M. da C. Vellozo, a contemporary of Vandelli, described *Quelusia regia* from Brazil, providing locality information and an illustration that included leaves and flowers. Due to political problems, however, Vellozo's name for the species was not published until 1829 (Borgmeier, 1937; Carauta, 1973).

Jonas Dryander described *Fuchsia coccinea* in 1789 based on cultivated plants that had been introduced in England the previous year. The source of his plants remains unclear, however, since Aiton (1789) attributed their introduction from Chile by a Captain Firth, while Salisbury (1791) stated that they were brought from Brazil by Vandelli around 1787. In reprinting Vandelli's publication of *Quelusia*, Roemer (1796) added a footnote wherein he stated that Vandelli's genus was the same as Dryander's *F. coccinea*. Meanwhile, Salisbury (1791) had already synonymized *Quelusia* under *F. coccinea*.

In the first conspectus of the genus, de Candolle (1828) designated *Quelusia* as a section of *Fuchsia*; by that time, the identity of *F. magellanica* and *F. coccinea* were already badly confused, and de Candolle considered them to be synonymous.

Collections made in Brazil by Auguste de Saint-Hilaire between 1816 and 1822 resulted in the description of four new species by Jacques Cambessèdes in 1830. None of these species have been maintained in the present treatment, but the name *F. integrifolia* Camb. was long used for *F. regia*.

During the 1820s and 1830s, there was a sudden surge of collections of *Fuchsia* from Brazil and Chile, and many plants were shipped for cultivation in Europe. Several new taxa, most of them now included under *F. regia* and *F. magellanica*, were described by John Lindley, George Gardner, and Karel Presl. During the second half of the 19th

century, Auguste Glaziou made extensive collections in eastern Brazil, when this area was off limits to most foreign botanists. The rare *F. glazioviana* was described from one of his finds.

During the first half of this century, Curt Brade and Ynes Mexia collected fuchsias from the two highest peaks of southern Brazil, Pico da Bandeira and Itatiaia. Their collections led to the description of two local endemics, *F. bracelinae* and *F. campos-portoi*.

The leading figure in *Fuchsia* taxonomy was Philip Munz, who published a comprehensive revision of the genus in 1943. He refined the sectional concepts and limited sect. *Quelusia* to a closely knit group of species from Brazil and one from the southern, temperate Andes. He recognized five species in the section, as well as *F. hybrida*, which covered most of the cultivated hybrids. Two of his species were polytypic: *F. magellanica* had three varieties, and *F. regia* four.

Since Munz, many new collections have accumulated, especially from the southern states of Brazil, where Balduíno Rambo, Raulino Reitz, Roberto Klein, and Gert Hatschbach have made significant contributions. Their collections have led me to recognize four new taxa of *Fuchsia* from the south of Brazil in this treatment. During two field trips in 1985 and 1987, I was able to collect and study field populations of all the Brazilian taxa.

Criteria for taxonomic rank. In distinguishing species within the section, I attempted to recognize basic, morphologically definable units that are also correlated with geographical, ecological, or cytological discontinuities between populations. It is assumed that these units also reflect the evolutionary divergences that have taken place in the group, but such hypotheses must be subjected to much more rigorous testing methods before they can be substantiated.

Subspecific rank was used when a wide-ranging species exhibited geographically or ecologically distinct morphological variants, but these were linked by intermediate populations along localized areas of sympatry.

Although different varieties have been recognized in the past for some species of *Fuchsia*, there is little biological basis for recognizing varieties. Similar pale color variants, for example, have appeared independently in a series of geographically distinct populations of *F. magellanica*, and they are probably the result of a single, recessive gene mutation (Chaudhuri, 1956). I do not consider this kind of variation worthy of formal taxonomic recognition in a biosystematic revision such as this, although I do recognize the utility of assigning names to such plants for horticultural purposes.

In widespread species, such as *F. regia* and *F. magellanica*, it has not been feasible to distinguish the genetic basis for the many minor variants that exist from environmentally induced variations or inherent plasticity in the plants. Most likely, genetically determined variations will best be recognized through careful observation of plants cultivated under uniform growing conditions. In this way, amateur and professional nurserymen can make valuable contributions to our taxonomic understanding of sect. *Quelusia* in the future, especially if they maintain well-documented records of the provenance of their stock and the constancy and inheritance patterns of the different characters.

In view of the uncertain phylogeny of the species of sect. *Quelusia*, they are listed as follows in alphabetical order.

Fuchsia section **Quelusia** (Vandelli) de Candolle, Prodr. 3: 36. 1828. *Quelusia* Vandelli, Fl. Lusit. Brasil., 23, fig. 10, 1788; Roemer, Script. Pl. Hisp. Lusit. Brasil., 101, tab. 7, fig. 10. 1796. LECTOTYPE: *Fuchsia coccinea* Dryander. *Quelusia* was published without the protologue naming a species, but Vandelli's original text and engraving were reproduced by Roemer, who stated in a footnote that the description corresponded to *F. coccinea*. Salisbury (1791) and de Candolle (1828) treated *F. coccinea* as the type of *Quelusia*. Therefore, Munz's (1943) choice of *F. magellanica* as the lectotype of *Quelusia* and Berry's (1982) designation of *F. regia* as the lectotype cannot be upheld.

Erect, scandent or climbing shrubs, subshrubs, or lianas. Leaves opposite or whorled. Flowers hermaphroditic, pendulous and axillary near the branch tips. Sepals normally reddish, longer than the floral tube and connate at the base. Petals purple, strongly convolute, erect, shorter than the sepals. Stamens erect, exserted beyond the sepals, the antisepalous filaments longer than the antipetalous ones. Pollen grains triporate or occasionally 4-porate, with segmented-beaded viscin threads. Nectary adnate to the base of the floral tube, smooth or ridged. Stigma clavate to subglobose, obscurely 4-cleft at the apex. Berries with ca. 60–120 seeds. Gametic chromosome number $n = 22, 44$.

Distribution (Fig. 1). Southeastern Brazil, from Minas Gerais to Rio Grande do Sul, and the Andes

of southern Chile and Argentina from 33°S to 55°S latitude.

Etymology. The name *Quelusia* was given by Vandelli after Queluz, the summer palace of Portuguese royalty located outside of Lisbon (Don, 1832).

Common names. Chile: chilco, chilca, palo blanco, fucsia, tilco. Brazil: brinco de princesa.

KEY TO THE SPECIES OF *FUCHSIA* SECTION *QUELUSIA*

Note: Leaf measurements are based on mature, fully expanded leaves. Dimensions are intended to cover the full range of dry and fresh specimens.

1a. Petioles mostly 1–3 mm long, pilose.
  2a. Leaves elliptic, with acute to rounded base, pilose on all veins below; pedicels hanging, 12–20 mm long ..... 2. *F. bracelinae*
  2b. Leaves ovate, with subcordate base, pilose mostly on lower ⅓ of midvein below; pedicels divergent from stems and pendent only in distal ⅓, 18–50 mm long ..... 5. *F. coccinea*
1b. Petioles mostly more than 3 mm long, glabrous to pilose.
  3a. Sepals connate at the base (from the point of petal insertion) for ≥ 8 mm and ≥ ⅓ of their total length.
    4a. Petioles mostly 4–8 mm long, leaves 10–25 mm wide, upper surface lightly sulcate-nerved; stipules inconspicuous ..... 3. *F. brevilobis*
    4b. Petioles mostly 10–25 mm long, leaves 25–45 mm wide, upper surface smooth; stipules crassate and persistent ..... 9. *F. regia* subsp. *serrae*
  3b. Sepals connate at the base for 2–7 mm and ≤ ¼ of their total length.
    5a. Leaves 2–6 mm wide, narrowly lanceolate; floral tube subrhombic, 4–6 mm long ..... 4. *F. campos-portoi*
    5b. Leaves ≥ 8 mm wide, less than 5 times as long as wide; floral tube cylindrical-fusiform, 5–35 mm long.
      6a. Leaves 15–30 mm long, 8–15 mm wide, densely grouped on branches with internodes 3–12 mm long; floral tube 5–7 mm long and glabrous ..... 6. *F. glazioviana*
      6b. Leaves longer or wider than above, internodes > 12 mm long; *or* floral tubes pubescent or > 7 mm long.
        7a. Petioles ≤ 6 mm long, leaf blade > 8 times as long as the petiole, leaves mostly opposite.
          8a. Plants glabrous, leaves 8–15(–30) mm wide; floral tube 10–15 mm long ..... 7. *F. hatschbachii*
          8b. Plants densely pilose, leaves 20–70 mm wide; floral tube 5–9 mm long ..... 1. *F. alpestris*
        7b. Petioles (3–)5–35 mm long, leaf blade < 6 times as long as the petioles, some or all leaves ternate or whorled.
          9a. Mostly erect shrubs; leaves membranous, usually glabrous, 15–60 mm long; margin serrulate and often shallowly lobed between teeth; petioles 0.3–1 mm thick; floral tube mostly 2–3.5 mm wide; berry narrowly oblong, 4–7 mm thick when ripe; southern Chile and Argentina ..... 8. *F. magellanica*
          9b. Mostly scandent shrubs or lianas; leaves membranous to coriaceous, glabrous to pilose, 20–140 mm long; margin entire to gland-serrate; petioles 1–3 mm thick; floral tube 3–7 mm wide; berry oblong, ellipsoid, or globose, 9–13 mm thick when ripe; Brazil ..... 9. *F. regia*

1. Fuchsia alpestris Gardner, Bot. Mag. 69: tab. 3999. 1843. TYPE: Brazil. Rio de Janeiro: Organ Mountains, "in moist, bushy, rocky places," 1,570 m, Mar. 1841, *George Gardner 5706* (holotype, OXF; isotypes, BM, CGE—2 sheets, G, GH, K—2 sheets, NY, P, UC, W). Figure 4.

Fuchsia mollis Krause, Engl. Jahrb. 37: 600. 1906. TYPE: Brazil. Rio de Janeiro: in forest near Nova Friburgo, 900 m, Oct. 1896, *E. Ule 4418* (holotype, B, destroyed in World War II, photograph at F; isotypes, CORD, R—#41706, RB).

Scandent shrubs 1–5 m tall, branches generally long and hanging, up to 5 m long. Branchlets reddish tan, densely pilose with erect, whitish hairs ca. 1 mm long. Leaves opposite, occasionally ternate, membranous, oblong, broadly ovate or narrowly elliptic-ovate, (55–)60–140 mm long, 20–70 mm wide, apex acute to acuminate, base rounded to subcordate or subauriculate, moderately pilose above, densely pilose below, sometimes purple-flushed when young, often yellowing before dehiscing; margin entire to subdenticulate, secondary veins 5–9(–10) per side. Petioles densely pubescent, 3–6 mm long, stout and 2–4 mm thick on older leaves, canaliculate above. Stipules narrowly triangular, 1–2 mm long, 0.8–1.5 mm wide, adjacent ones sometimes fused, generally covered by hairs. Flowers few and solitary in upper leaf axils; pedicels pendulous, 25–40 mm long. Ovary

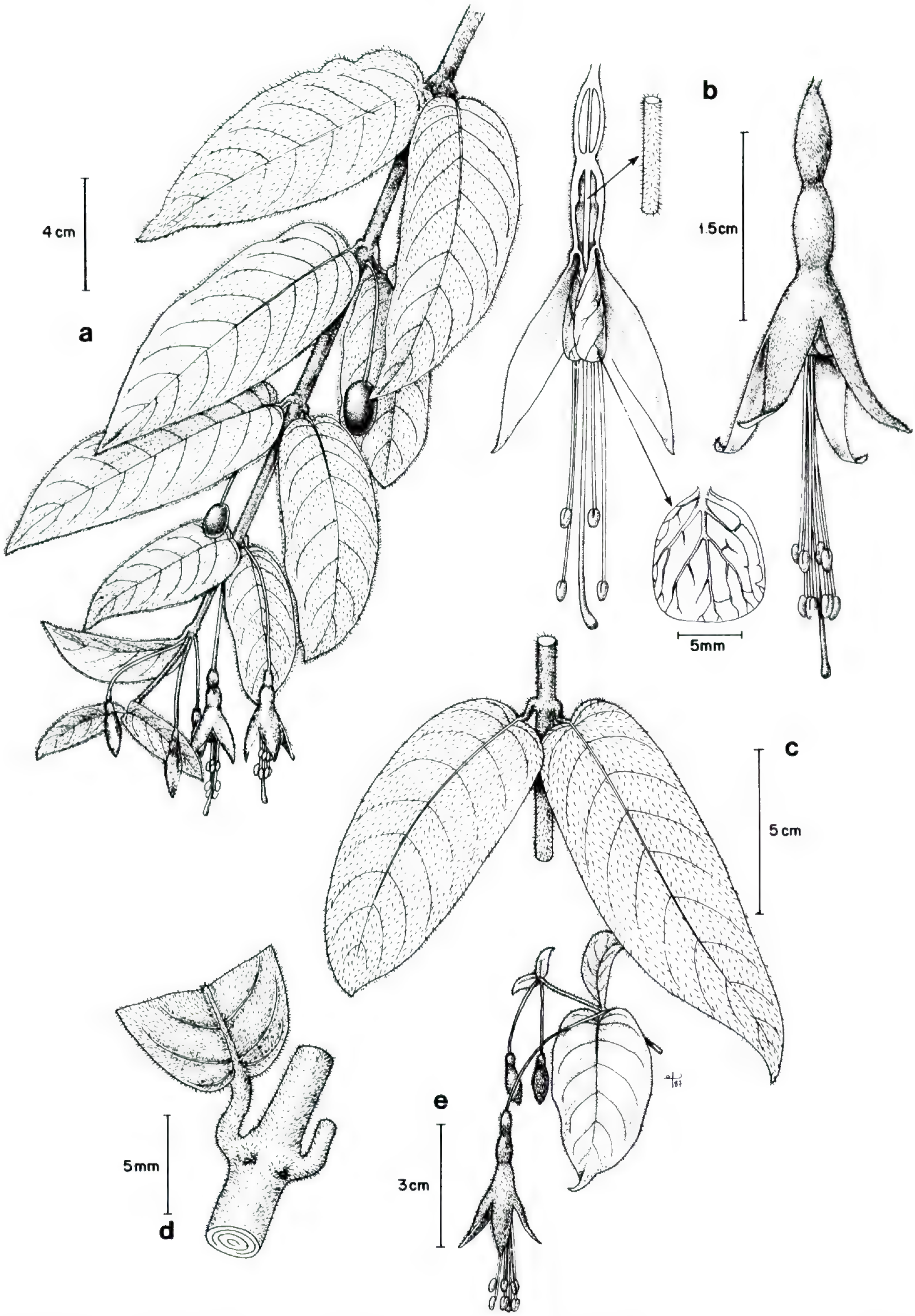

FIGURE 4. *Fuchsia alpestris.*—a. Flowering branch.—b. Details of entire and longitudinally split flower.—c. Pair of large leaves from basal portion of stem.—d. Detail of young stem with stipules and petioles.—e. Tip of flowering shoot with nearly sessile leaves. From *Berry et al. 4418.*

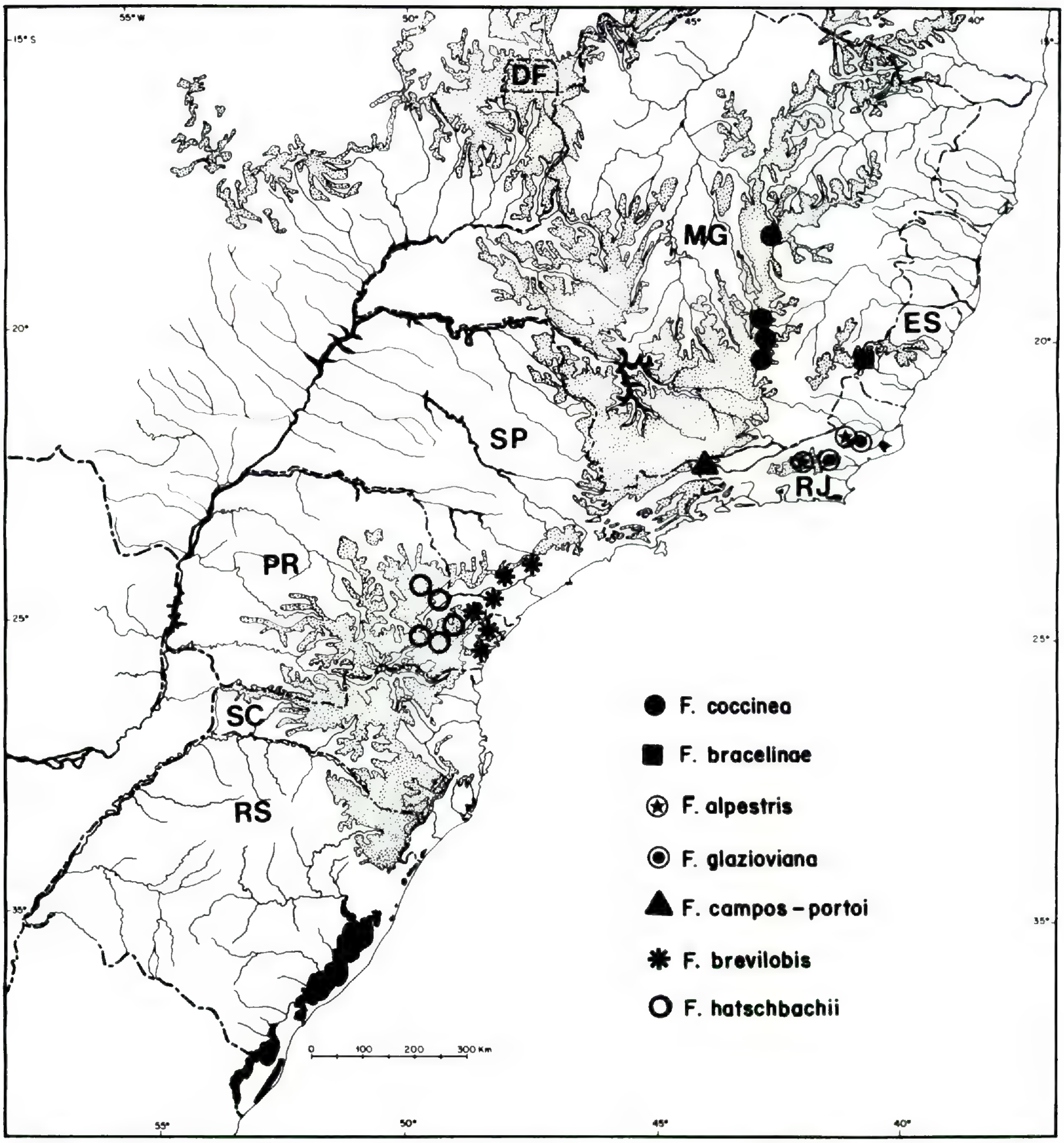

FIGURE 5. Geographical distributions of the Brazilian species of *Fuchsia* sect. *Quelusia*, except for *F. regia*. Contours higher than 800 m are indicated by the stippled areas. Capital letters are state abbreviations. MG = Minas Gerais, ES = Espirito Santo, RJ = Rio de Janeiro, SP = São Paulo, PR = Paraná, SC = Santa Catarina, RS = Rio Grande do Sol.

subquadrangular, pilose, 6–8 mm long, 2–3.5 mm wide. Floral tube cylindrical-fusiform, (5–)6–8(–10) mm long, 3–4 mm wide, pubescent outside, pilose inside; nectary 4–6 mm high, 1 mm thick, irregularly ridged. Sepals 18–26(–28) mm long, connate for 4–6 mm at the base, pilose outside; free lobes 3.5–4.5 mm wide at base, spreading at anthesis. Tube and sepals red to dull pink. Petals violet, broadly obovate, 10–14 mm long, 8–9 mm wide. Filaments red, 26–35 mm and 24–32 mm long; anthers red, oblong, 2.5–3.5 mm long, 1.2–1.6 mm wide. Style red, pilose in basal ⅓; stigma red, clavate, 2.5–3.5 mm long, 1.1–1.6 mm wide. Berry oblong-ellipsoid, 14–16 mm long, 8–10 mm wide, purple when ripe; seeds oblong, 1.8–2.2 mm long, 1–1.5 mm wide. Gametic chromosome number $n = 22, 44$.

Distribution (Fig. 5). In thickets and low forest near granitic outcrops of several morros in north-central Rio de Janeiro state, Brazil: near Nova Friburgo, Santa Maria Madalena, and in the

Serra dos Órgãos between Teresópolis and Petrópolis, (1,100–)1,400–1,600 m. Flowers mainly from November to March.

Additional specimens examined. BRAZIL. RIO DE JANEIRO: Teresópolis, *Bailey & Bailey 1296* (BH), *von Bayern 19539* (F, NY), *von Bayern in Sep. 1888* (M); 26 km SE of Itaipava, road from Teresópolis to Petrópolis, *Berry et al. 4418* (MO, RB; $n = 22$); Fazenda Portugal, Serra dos Órgãos, *Brade 19467* (RB); Canoas, Sítio Sumare II, Teresópolis to Nova Friburgo, *Braga 1535* (RB); Petrópolis, *Rgl. 55-11, 56.9* (LE); Morro do Sertão, Petrópolis, *Goés & Dionisio 427* (RB); Araras, Mun. Petrópolis, *Martinelli & Sucre 216* (RB); Araras, Morro Bolo de Milho, *Sucre & Braga 2808* (RB); Nova Friburgo, *Riedel 534* (LE), *Fomnov 4418* (CORD); Pedra Dubois, Santa Maria Madalena, *Anderson 11724* (MO).

Cultivated specimens. U.S.A. CALIFORNIA: Berkeley, from Brazilian plant, *Bracelin 2575* (RSA). THE NETHERLANDS: Hollandsche Rading, *Berry & Brako 001-86* (MO; $n = 44$). Also seen cultivated in England and France.

Munz (1943) treated *Fuchsia alpestris* as a variety of *F. regia*, but the former can be readily distinguished from *F. regia* by having large, mostly opposite, short-petioled leaves. The older leaves have a characteristic subcordate base, and the entire plant has characteristic dense, pale pubescence. The flowers are considerably smaller and often much paler than those of the subspecies of *F. regia* that occurs in the same area.

This species is rare in nature and is apparently confined to shrubby patches bordering exposed rock on the flanks of large, granitic domes. *Fuchsia regia* subsp. *regia* always occurs nearby, and some intergradation between the two species has been found at Pedra Dubois, near Santa Maria Madalena (see Appendix).

2. Fuchsia bracelinae Munz, Proc. Calif. Acad. Sci., Ser. 4, 25: 7, pl. 1, fig. 2. 1943. TYPE: Brazil. Espírito Santo: Serra do Caparaó, rocky open campo, 2,650 m, 25 Nov. 1929, *Ynes Mexia 4013* (holotype, GH, photograph at BH; isotypes, A, BM, CAS, G—DEL, GH, MO, NY, P, S, UC, US, Z). Figure 6.

Few- to many-branched subshrubs 10–60 cm tall, or occasionally scandent shrubs to 2 m high in dense shrubbery. Branchlets terete, generally reddish purple, densely pilose with erect, whitish hairs ca. 1 mm long; older branches with freely exfoliating bark. Leaves 3–5-verticillate, membranous, narrowly elliptic-lanceolate, 20–50 mm long, 7–17 mm wide, apex narrowly acute, base rounded, green and slightly strigose above with conspicuously impressed veins, paler and usually purple-flushed below and densely pilose on the sulcate veins and margins; margin subentire to gland-denticulate, secondary veins 4–7 per side. Petioles green to reddish, pilose, 1–3 mm long. Stipules lanceolate, with a thick base, 1.5–2 mm long, adjacent ones often fused basally, subpersistent. Flowers solitary in upper leaf axils; pedicels slender, pilose, pendulous, 12–20 mm long. Ovary oblong, strigillose to pilose, 4.5–8 mm long, 2–3 mm wide. Floral tube cylindrical-fusiform, 3.5–7 mm long, 2–4 mm wide, lightly strigillose to pilose outside, glabrous inside; nectary 2.5–3.5 mm high, ca. 1 mm thick and slightly ridged. Sepals 19–26 mm long, narrowly lanceolate to elliptic-ovate, connate at the base for 3–5(–6) mm; free lobes 5–8 mm wide at the base, apex acuminate, spreading at anthesis. Tube and sepals light red to pink. Petals deep violet, broadly obovate, 10–15 mm long, 6.5–9 mm wide, apex rounded. Filaments reddish purple, 24–30 mm and 17–21 mm long; anthers elliptic, 2.5–3 mm long, 1.2–1.6 mm wide. Style light red, glabrous; stigma reddish, clavate to subglobose, 1.5–3 mm long, 1–1.5 mm wide, exserted 5–14 mm beyond the anthers. Young fruits oblong, mature ones not seen. Gametic chromosome number $n = 22$.

Distribution (Fig. 5). Endemic to the highest peaks of the Serra do Caparaó (Pico da Bandeira, Pico do Cristal, Pico do Cruzeiro, and Pico do Calçado) along the border of the states of Minas Gerais and Espírito Santo. Grows in open campo above treeline, between 2,280 and 2,850 m, most common at 2,700–2,800 m. Flowers in the summer, principally from November until March.

Additional specimens examined. BRAZIL. ESPÍRITO SANTO: Pico da Bandeira, *Berry 4524* (MO, RJ; $n = 22$), *4530, 4532, 4533, 4534, 4535* (MO, RJ; $n = 22$); *Irwin 2745* (F, MICH, NY, R, TEX, UC). MINAS GERAIS: Pico da Bandeira, *Berry 4525* (MO, RJ), *4531* (MO, RJ; $n = 22$); Campos de Caparaó, *Ule in 8 Feb. 1890* (R #41703); *Schwacke in 8 Feb. 1890* (R #41702); Serra do Caparaó, *Torgo 6* (HB, MBM).

Fuchsia bracelinae is distinguished from other members of the section by having dense, stiff pubescence and small, narrow, verticillate leaves. It inhabits only the rocky, open campos of the highest peaks of southern Brazil, in the Serra do Caparaó. Individuals are found along rocks, in meadows, or in protected shrub and bamboo patches. This area is subject to frequent and severe winter frosts, and *F. bracelinae* is found to within 60 m of the 2,897-m-high summit of Pico da Bandeira. Extensive winter dieback of the above-ground stems probably accounts for the small stature of most plants, but underground stems lead to extensive vegetative reproduction in areas with good soil accumulation.

Fuchsia regia occurs lower down on the same mountain range, but there is no sympatry at pres-

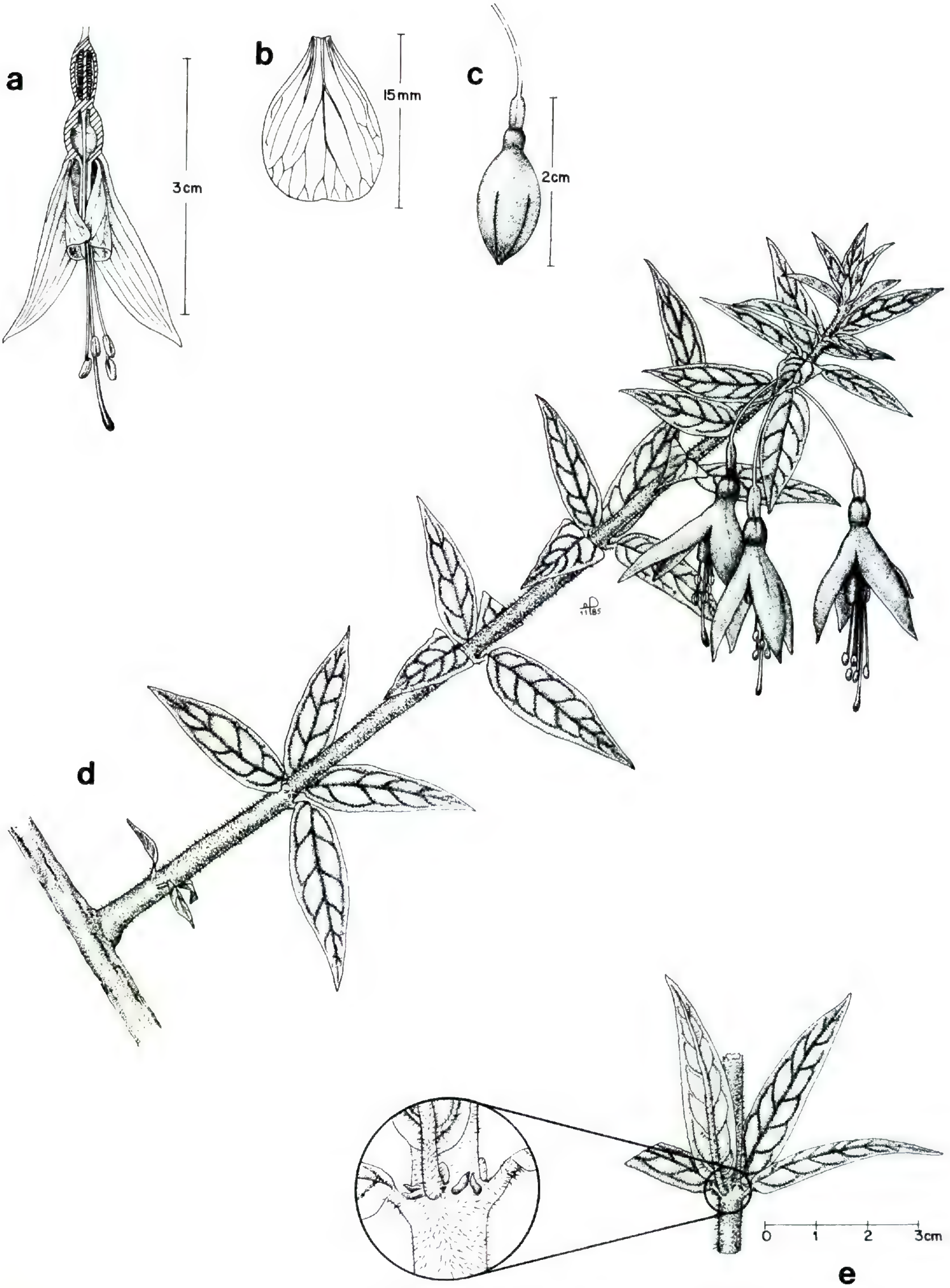

FIGURE 6. *Fuchsia bracelinae.*—a. Detail of flower in longitudinal section.—b. Petal, spread open.—c. Floral bud just prior to anthesis.—d. Flowering branch.—e. Leaf whorl and detail of stipules and petioles. From *Berry et al. 4524.*

ent; extensive forest areas at intermediate elevations existed until the past century but have been eliminated by cutting and fires. The collection *Irwin 2808* (US #2324661; Serra do Caparaó, 2,600 m) has narrow, moderately dentate leaves that resemble *F. campos-portoi*, but the Irwin collection is probably just a stunted individual of *F. bracelinae*.

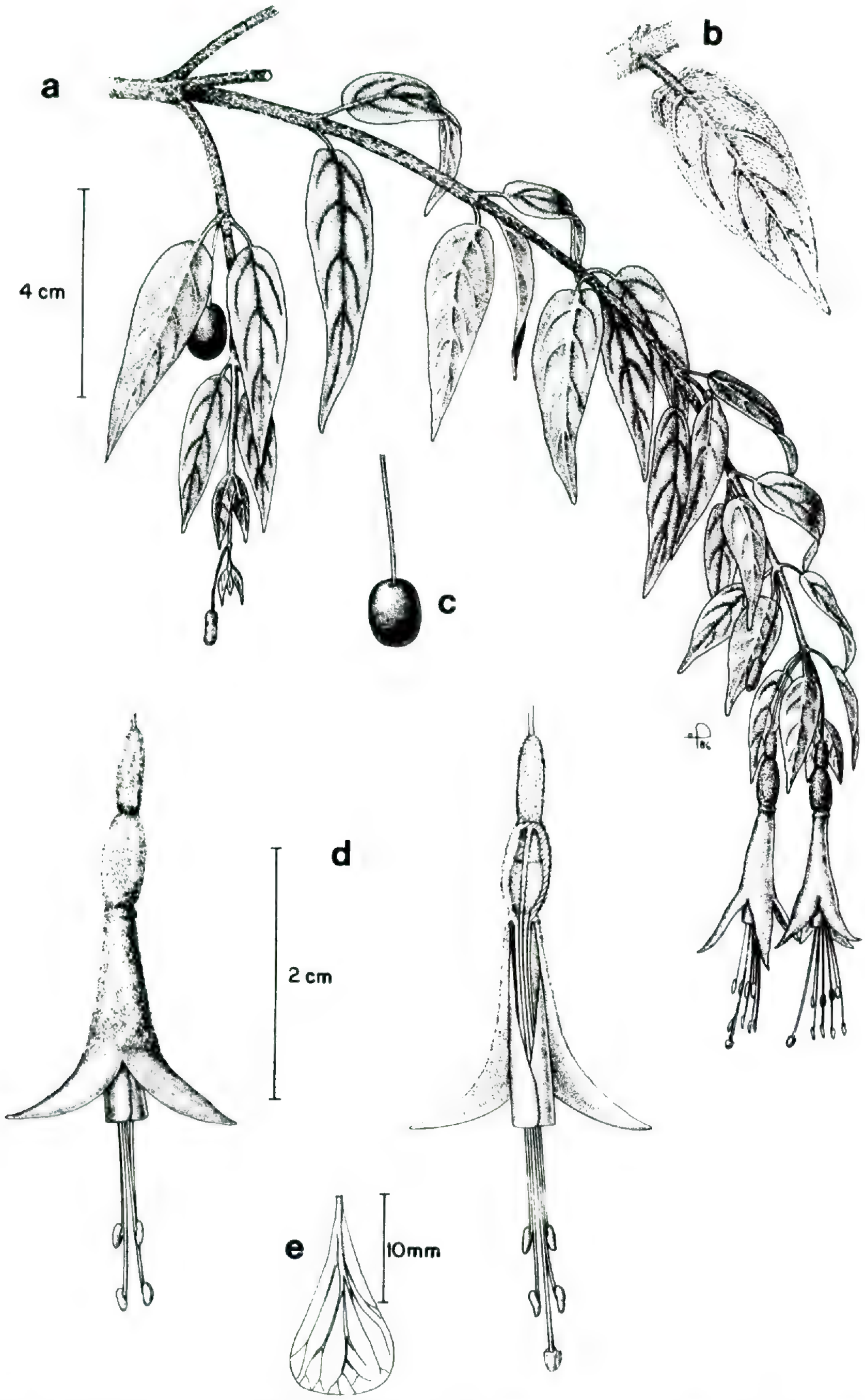

FIGURE 7. *Fuchsia brevilobis.*—a. Flowering branch.—b. Leaf detail.—c. Ripe fruit.—d. Detail of entire and longitudinally split flower.—e. Petal, spread open. From *Berry et al. 4441.*

3. Fuchsia brevilobis P. Berry, sp. nov. TYPE: Brazil. São Paulo: 38 km NE of the São Paulo–Paraná border near the 267 km post on Highway 116, bamboo forest on marshy ground, 680 m, 8 Mar. 1976, *Gerrit Davidse, T. P. Ramamoorthy & D. M. Vital 10902* (holotype, MO #2931564; isotype, SP (under *Davidse & D'Arcy 10902*); $n = 22$, $2n = 44$. Figure 7.

Frutex scandens, ramulis foliisque junioribus puberulentibus vel pilosis. Folia membranacea, lanceolata vel elliptico-ovata, basi rotundata, apice acuta, 2–7.5 cm longa, 1–3 cm lata, nervis secundariis 3–6; petiolis (2–)4–8(–14) mm longis. Tubi florales fusiformes 7–10

mm longi. Sepala 17–25 mm longa, basi (8–)11–16 mm connata, lobis liberis 5–11(–13) mm longis. Petala spathulata 12–18 mm longa, 5–7 mm lata, a tubo sepalorum fere occulta. Numerus gameticus chromosomatum $n = 22$.

Scandent shrubs 2–6 m tall, or occasionally lianas in trees to 8 m high, with basal stems 1–6 cm in diameter; branches scandent or drooping to 3 m long. Young growth densely pilose to puberulent, older stems exfoliating. Leaves opposite, ternate or occasionally in whorls of 4, firmly membranous, lanceolate to narrowly ovate, 20–75 mm long, 10–25(–30) mm wide, acute to occasionally acuminate at the apex, rounded at the base, subglabrous to sparsely pubescent above with impressed veins, sparsely puberulent to villous below, especially along nerves; margin entire to remotely denticulate, secondary veins 3–6 per side. Petioles usually dull purple, (2–)4–8(–14) mm long, subglabrous to densely pilose. Stipules 0.5–1.1 mm long, 0.7–1.2 mm wide, purplish, broadly triangular, thick-stubby and divergent, deciduous. Flowers solitary in upper leaf axils; pedicels pendulous, 17–28(–42) mm long. Ovary oblong, 5–10 mm long, 2–4 mm wide, loosely pilose, green. Floral tube subcylindric to fusiform, 7–10 mm long, 2–3 mm wide at the base, 3.5–4.5 mm wide in the middle, often constricted to ca. 3 mm wide at the point of insertion of the stamens beneath the widening of the sepal tube, glabrous to pilose outside, pilose inside; nectary green, slightly ridged, 1–1.2 mm thick and 2.5–3 mm high. Sepals 17–25 mm long, connate for (8–)11–16 mm at the base and forming a tube, this enlarging to 8–10 mm wide before the separation of the sepals; the free lobes narrowly triangular, 5–11(–13) mm long, 3–5 mm wide at the base, acute to acuminate at the apex, spreading to slightly recurved at anthesis. Tube and sepals red to red-pink. Petals almost entirely enclosed by the sepal tube, light to dark purple, spathulate, 12–18 mm long, (5–)6–7 mm wide, rounded at the apex, the base slender and adnate to the sepal tube in the basal 3–4 mm above the insertion of the filaments. Filaments reddish pink, 22–38 mm and 19–35 mm long; anthers red-purple, oblong, 2.5–3 mm long, 1–1.5 mm wide. Style reddish, pilose in lower half; stigma clavate, purple, 1.2–1.6 mm long, ca. 1 mm wide, exserted 5–10 mm beyond the anthers. Berry oblong-ellipsoid, 15–22(–26) mm long and 7–10(–16) mm wide at maturity, black when ripe; seeds oblong-triangular, 2–2.6 mm long, 1–1.6 mm broad, ca. 0.5 mm thick. Gametic chromosome number $n = 22$.

Distribution (Fig. 5). In montane forest of the Serra de Paranapiacaba in southern São Paulo state; in Paraná state in the Serra da Virgem Maria and Rio Capivari drainage, and then on the lowermost slopes of the Serra do Mar and in coastal restingas, from sea level to 900 m. Flowers throughout the year, principally from November to March.

Additional specimens examined. BRAZIL. SÃO PAULO: Reserva Carlos Botelho, between São Miguel Arcanjo & Sete Barras, *Prance et al. 6860* (MBM, SP, UEC); Reserva Capão Bonito, 70 km S of Itapetininga, *Sakane 543* (SP); 50 km S of Itapetininga, *Gibbs et al. 3279* (SP, UEC); Juquía to Tapiraí (on BR-478 S of Piedade), *Yamamoto 14653* (UEC); 38 km NE of SP-PR border, km 267 of BR-116, *Davidse & D'Arcy 10904* (MO); Apiaí-São Paulo, km 294, *Vianna in 5-5-64* (ICN #2820). PARANÁ: Prainhas, Mun. Morretes, *Hatschbach et al. 13412* (MBM, U); *Cordeiro et al. 215* (MBM; $n = 22$); below Eng. Lange train station to Prainhas, *Cordeiro et al. 218* (MBM; $n = 22$); Porto da Cima, Mun. Morretes, *Berry et al. 4495* (MBM, MO; $n = 22$); *Dusén 11964* (S), *14133* (G—DEL, K, S, US), *14340* (A, S); *Hatschbach 43303* (MBM); Sesmaria, 2–5 km W of Rio Capivari, Mun. Bocaiúva do Sul, *Berry & Juarez 4441* (MBM, MO; $n = 22$), *4442*, *4443*, *4444*, *4445* (MBM, MO); *Hatschbach 20936* (HB, MBM, UC); *Hatschbach & Ramamoorthy 42973* (MBM, MO), *42974* (MBM); 10 km E of Curitiba, *Lindeman & Haas 2539* (MBM, U); Estrada da Graciosa, Serra do Mar, 850 m, *Lindeman & Haas 5879* (U); road Rio Taquary–Rio Divisa, Mun. Campina Grande do Sul, *Hatschbach 7009* (MBM); Serra Virgem Maria, Mun. Campina do Sul, *Hatschbach 20284* (M, MBM, MO, UC); Rio Guaraguaçu, Mun. Paranaguá, *Hatschbach 7056* (MB); Rio São Joãozinho, Mun. Paranaguá, *Berry et al. 4496* (MBM, MO); *Falkenberg 2234* (ICN); Sapitanduva (cultivated), *Berry et al. 4494* (MBM, MO); *Falkenberg 2222* (FLOR); Mun. Antonina, Cacatu, *Hatschbach et al. 50788* (MBM; $n = 22$); Mun. Campina Grande do Sul, Rodovia BR-2, Ribeirão do Cedro, *Hatschbach 8946* (MBM).

Fuchsia brevilobis is distinguished by its remarkably long sepal tube, which almost entirely encloses the petals, and by the membranous, pubescent, narrowly ovate leaves. There are two distinct areas where this species occurs, with notable morphological differences in their populations. In the low ramifications of the Serra do Mar in northern Paraná and southern São Paulo states, plants grow between 700 and 900 m and are very pubescent, with especially long sepal tubes. Another group of populations is found on the lower, eastern flanks of the Serra do Mar in central Paraná, from 400 m to sea level. Most plants from these populations have longer petioles than those of higher altitude, and they vary considerably from population to population in color (dull pink to bright red), degree of sepal connation, and leaf shape and texture.

Several populations of *F. brevilobis* occur in the restinga or swamp forest close to sea level, a very

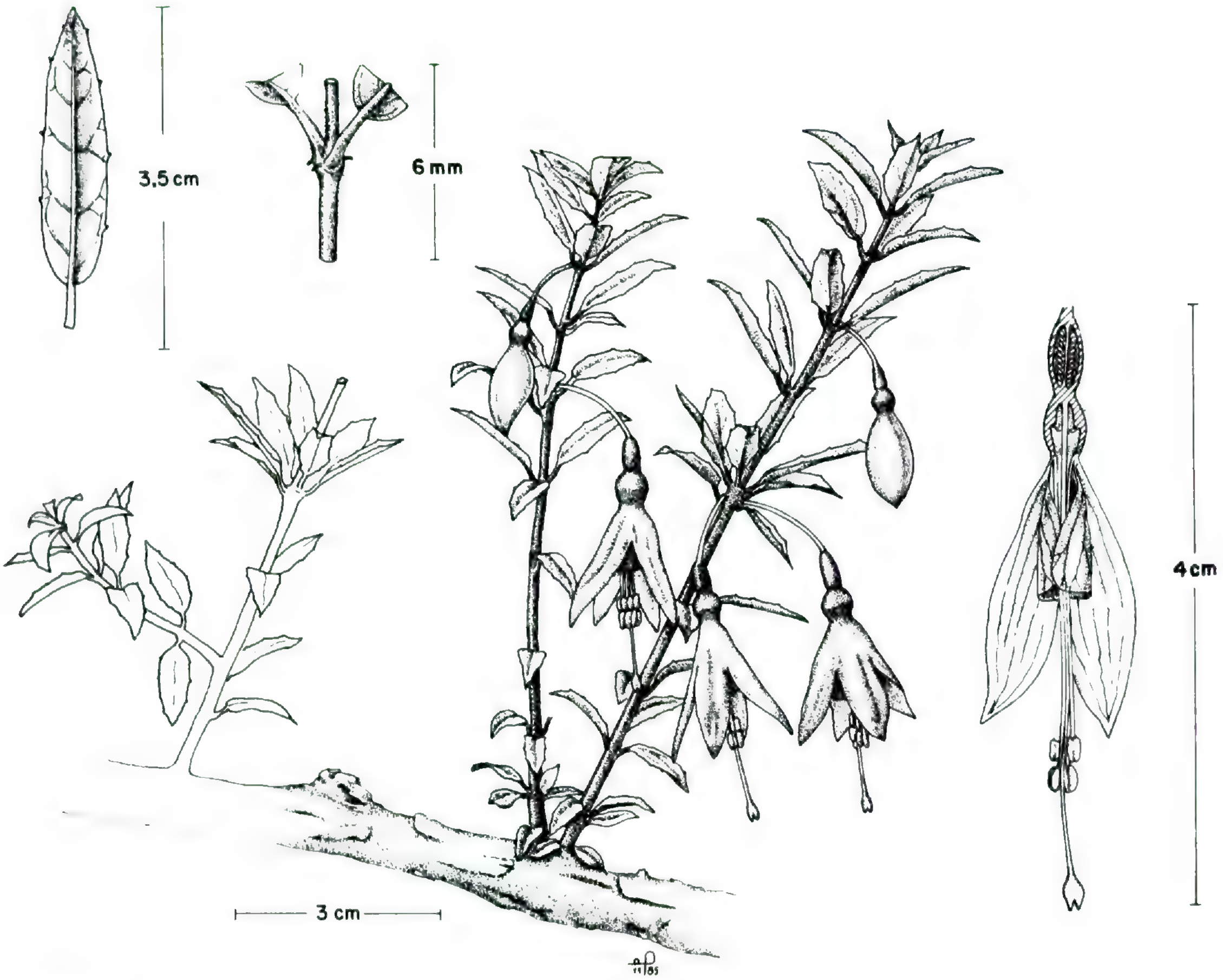

FIGURE 8. *Fuchsia campos-portoi*. Flowering shoots with details of an individual leaf underside, a leaf node with stipules, and a longitudinally divided flower. From *Berry et al. 4435*.

unusual habitat for Brazilian fuchsias. These plants grow as lianas and are found along rivers or streams, perhaps enabling them to withstand the heat and high evapotranspiration of the Atlantic lowlands. The population from Cacatu has unusually narrow, lanceolate leaves with acuminate tips.

Throughout most of its range, this species is sympatric with *F. regia* subsp. *serrae*. The presence of plants morphologically intermediate between the two taxa indicates that hybridization has occurred between them (see Appendix). The populations of *F. regia* subsp. *serrae* in northern Paraná have exceptionally long sepal tubes, which may be the result of introgression with *F. brevilobis*.

4. **Fuchsia campos-portoi** Pilger & Schulze, Notizbl. Bot. Gart. Berlin-Dahlem 12: 470. 1935; Rodriguésia 2: 94, figs. 1–5. 1935. TYPE: Brazil. Rio de Janeiro: Itatiaia, Serra da Mantiqueira, 2,200 m, 27 Dec. 1934, *Robert Pilger & Curt Brade 31* (holotype, B, destroyed in World War II; lectotype, RB, here designated; isotype, BH). Figure 8.

Subshrubs to woody scandent bushes 0.3–2 (–3) m tall, often growing among rocks. Young growth subglabrous to finely canescent or pilose; older stems 1–4 cm thick, with flaky, coppery brown bark. Leaves mostly ternate, occasionally opposite or 4–5-whorled, firmly membranous, narrowly elliptic-lanceolate, 12–40 mm long, 2–6(–8) mm wide, narrowly acute at the apex, acute to cuneate at the base, dark green and subglabrous above, paler and mostly glabrous below or with villous hairs along veins and margins; margin gland-serrulate, with teeth angled towards the apex, secondary veins 3–7 per side, at times inconspicuous; internodes short, mostly 10–16 mm long. Petioles (2–)3–8 mm long. Stipules 0.5–1 mm long, narrowly lanceolate or filiform, deciduous. Flowers solitary in upper leaf axils; pedicels slender, pendulous, (4–)8–20 mm long. Ovary oblong, 4–5 mm long, ca. 2 mm wide, strigose to strigillose. Floral tube subrhombic, 4–6 mm long, 3.5 mm wide in the middle and ca. 2.5 mm wide at the base and summit, glabrous to strigose outside, glabrous inside; nectary 2.5–3 mm high, shallowly 8-lobed. Sepals 12–20 mm long, lance-elliptic, con-

nate for 3–5 mm at the base; free lobes 4–7 mm wide at base, spreading at anthesis. Tube and sepals red to dark pink. Petals violet, broadly obovate, 9–12 mm long, 7–8 mm wide, rounded to slightly retuse at the apex. Filaments red, 15–28 and 13–25 mm long; anthers purple-red, elliptic-oblong, 1.5–2 mm long, 1–1.5 mm wide. Style glabrous, exserted 5–10 mm beyond the anthers; stigma clavate, 1.2–2 mm long, 0.7–0.9 mm wide. Berry cylindrical-oblong, 14–16 mm long, 7–8 mm thick; seeds 1.3–1.6 mm long, 0.7–1.1 mm wide. Gametic chromosome number $n = 22$.

Distribution (Fig. 5). Endemic to the open campos of the Itatiaia mountain massif, in the Serra da Mantiqueira, Rio de Janeiro and Minas Gerais border, from 2,100 to 2,550 m. Flowers mainly during the summer, from November to March.

Additional specimens examined. BRAZIL. RIO DE JANEIRO: Ayuruoca, *Glaziou 15948* (K, P); Itatiaia (Planalto), *Andrade & Emerich 626* (R); *Aparicio & Edmundo 826* (MO, RB); *Badini 22993* (OUPR); *Berry et al. 4435* (MO, RB; $n = 22$), *4436*, *4438* (MO, RB), *Brade 15160* (R, RB), *15676* (RB, POM, photos at NY, R, UC), *18008* (R, RB, S), *20335* (R); *Campos Porto 2705* (R, RB), *Duarte 826* (US); *Dusén 178* (R); *Gounelle in Jan. 1899* (G—BOIS); *Glaziou 4801* (P), *6522* (K, R); *Hatschbach et al. 35833* (MBM, UC, Z); *Hoehne 11918* (POM); *Koyama et al. 13701* (SP); *Lindeman & de Haas 4120* (MBM, U); *Lobo 4* (R); *Loefgren 5775* (SP); *Lutz in Nov. 1950, in Jan. 1957, in Nov. 1958* (R); *Lutz & Sampaio in Feb. 1954* (R); *Merxmuller 25591* (M); *Pabst 9308* (HB, K, M, MBM); *Pereira 7037* (HB, MBM, PEL); *Pereira & Pereira 7578* (B, HB, R, RB); *Ramamoorthy 104* (MO), *814* (MBM, MO), *s.n.* (MO; $n = 22$); *Santos 5169* (DS); *Sucre 4645* (MO, RB); *Ule 118* (R); *Vianna 771* (R).

Fuchsia campos-portoi is readily distinguished from other fuchsias by its small and very narrow, gland-serrulate leaves. It also has unusual, small flowers; the floral tube is nearly rhombic and very short, whereas the sepals are up to four times as long and are noticeably inflated in bud.

This species inhabits the high-elevation campos of the Itatiaia massif, where it grows in shrubby patches or in open, rocky sites. Winter frosts are common in this area. Populations of *F. regia* subsp. *regia* grow together with *F. campos-portoi*, and several intermediate plants have been found that indicate the occurrence of local hybrids (see Appendix).

5. Fuchsia coccinea Dryander in Aiton, Hort. Kew., 1st edition, 2: 8. 1789. Sims, Bot. Mag. tab. 97. 1789. Mordant de Launay, Herb. Gen. Amat. 2: 89, fig. 1817. Hook., Bot. Mag. 94: tab. 5740. 1868. *Nahusia coccinea* (Dryander) Schneevoogt, Icon. Pl. Rar. 1: 21. 1792. *Fuchsia elegans* Salisbury, Ic. Stirp. Rar., 13, tab. 7. 1791, nom. illeg. (Salisbury thought he would avoid confusion in renaming *F. coccinea*, since all species known at the time had red flowers.) *Fuchsia pendula* Salisbury, Prodr., 279. 1796, nom. illeg. (based on *F. elegans* Salisbury). TYPE: From a plant cultivated in 1788 at Kew Gardens, London, England, "*Oct. 1788, Hort. Kew*" (lectotype, LINN #670.3, Smith Herbarium, here designated: see Fig. 9; isolectotype, BM). Figures 9, 10.

Fuchsia montana Cambessèdes in St. Hilaire, Fl. Brasil. Merid. 2(17): 275, tab. 135. 1830. TYPE: Brazil. Minas Gerais: near the summit of the Serra da Caraça, Dec. 1816–Mar. 1818, *Auguste St. Hilaire B1 449* (holotype, P; isotype, P).

Erect shrubs 0.5–1.5 m tall, or scandent to 7 m high, often with extensive underground stems. Young growth puberulent to densely pilose, older stems 5–20 mm thick, with exfoliating bark. Leaves mostly ternate, sometimes opposite or in 4s, membranous or rarely subcoriaceous, narrowly ovate to ovate, 15–55 mm long, 7–25 mm wide, acute to subacuminate at the apex, subcordate or sometimes rounded at the base, generally dull, light green, paler below, sometimes strongly purple-flushed, subglabrous to puberulent on both sides, but generally densely pilose along the basal ⅓ of the midvein below; margins serrulate or occasionally subentire, secondary veins 4–6 per side. Petioles short and stout, ca. 1 mm thick, 1–3 mm long, occasionally longer on basal leaves, usually densely pilose or hirsute. Stipules narrowly lanceolate, 0.8–1.4 mm long, deciduous. Flowers solitary in the upper leaf axils; pedicels slender, pubescent, 18–42(–50) mm long, divergent or arching from the stems and pendent only in the distal third. Ovary oblong-ellipsoid, 5–9 mm long, 2.5–3 mm thick. Floral tube fusiform, 5–10 mm long, 2.5–3 mm wide at the base, 3.5–4.5 mm wide in the middle and 3–4 mm wide at the top, subglabrous to puberulent outside, puberulent inside; nectary smooth, 2–3 mm high. Sepals 15–24 mm long, oblong-lanceolate, lightly pubescent, connate at the base for 4–7 mm; free lobes 3.5–6 mm wide, acute at the apex, spreading at anthesis. Tube and sepals red to dark pink. Petals violet, obovate, 7–10 mm long, 6–8(–9) mm wide. Filaments red-purple, 18–38 mm and 13–30 mm long; anthers purplish, 2–2.5 mm long, ca. 1.5 mm wide. Style puberulent, red; stigma clavate, 1.5–2 mm long, exserted 5–15 mm beyond the anthers. Mature berry ellipsoid,

14–17 mm long, ca. 12 mm thick, purple; seeds oblong-triangular, 1.4–1.9 mm long, 0.8–1.2 mm wide. Gametic chromosome number $n = 22$.

Distribution (Fig. 5). Occurs in rocky, open campo near the summits of several of the highest mountains in Minas Gerais: Serra da Piedade, Serra da Caraça, Serra do Itacolomi, and Pico do Itambé, from 1,400 to 2,000 m. Flowers throughout the year, mainly from November to March.

Additional specimens examined. BRAZIL. MINAS GERAIS: E slopes of Pico do Itambé, Serra do Espinhaço, *Anderson et al. 35832* (HB, MICH, MO, NY, U, W); Serra do Gavião, Pico do Itambé, *Windisch & Gillamy 183* (HB); ascent to Pico do Itambé, Mun. San Antônio do Itambé, 18°24′S, 43°21′W, *Furlan et al. 3058* (SPF); Serra da Piedade, N of Caete, *Badini, Herb. #21373, 21374* (OUPR); *Berry et al. 4553* (MO, RB; $n = 22$), *4554, 4555, 4556, 4557* (MO, RB), *4558* (MO, RB; $n = 22$); *Glaziou in 19 Nov. 1893* (P); *Hoehne 6278, 6281* (POM), *6279, 6280* (R); *Irwin et al. 28777* (K, MICH, MO, NY, RB, US), *30326* (MO, NY, RB, U, US); *Landrum 4275* (MBM); *Magalhães Gomes 1451* (R); *Mello Barreto 7158, 7162, 8803* (F, BHMH), *7159* (BHMH, R), *7160* (F), *7161* (BHMH); *Pereira & Pabst 2662* (MO); *St. Hilaire 2276* (P); *Warming in 1907* (P); collector unknown *(#3000) in Nov. 1839* (LE), unknown *in Sep. 1824* (LE); Ouro Preto: Planalto do Pico Itacolomi, *Badini, Herb. #26275* (OUPR); *Barboza 1056* (R); *Bello 249* (R); *Berry et al. 4547, 4548* (MO, RB); *Damazio 1337* (G—BOIS, HB, RB); *Falkenberg 3381, 3382, 3383, 3385, 3386* (FLOR); *Glaziou 14703* (K, LE); *Hoehne 19661* (POM); *Magalhães Gomes 3027, in 28 June 1896, in 20 Nov. 1893* (OUPR); *Mello Barreto 9168* (BHMH, F); Morros de Vila Rica (Ouro Preto), *Martius s.n.* (M—2 sheets); Serra da Caraça, next to Pico do Sol, *Martinelli & Tavora 2742* (RB); Serra da Caraça, *Pereira & Pabst 2589* (MBM, RB), *2622* (HB, MBM, RB), *Silveira in July 1896* (R). No locality: *Clausen 44 in Oct. 1839* (G), *88 in 1840* (BM); *Hausmann 267E* (RB); *Langsdorff in Sept. 1829, s.n.* (LE); *Netto in 1862* (R); *Schwacke 13665* (MO, RB); *Vasconcellos in 25 Jan. 1901* (POM); *Vellozo?* (LE).

Cultivated specimens. AZORES: Flores, Bena Mao, *Pryor 79* (BM); Flores, Ponta Delgada, *Gonçalves 4256* (BM); Pico, Landroal, *Gonçalves 4436* (BM); Faial, Horta Alagoa, *Gonçalves 2278* (BM); São Jorge, Toledo, *Gonçalves 3630* (BM). CANARY ISLANDS: Tenerife, Orotaoa, *Burchard 177* (G—DEL, Z). JAMAICA: Green Hill, *Harris 5824* (US); near Cinchona, *Harris 9130* (BM), *Nichols in 16 July 1903* (NY). MADEIRA: Funchal, *Bornmüller 605* (PH, W, Z); above São Jorge, *Pickering 40* (PH); Jardim da Serra, *Mandon in July 1865-6* (G, G—BOIS, G—DEL). SUMATRA: Karo Highlands, E of Berastagi, *Hamel & Toroes 624* (G). U.S.A. KENTUCKY: *Short in 1864* (PH).

The type sheets of *F. coccinea* are the earliest known specimens of this species, and both were taken from the plant at Kew Gardens upon which Dryander based his description (Hooker, 1869). The source of the plants is unclear; both Sims and

FIGURE 9. Photograph of the lectotype of *Fuchsia coccinea* from the Smith Herbarium at LINN.

Dryander described the species as a native of Chile, introduced to Kew by a Captain Firth. Salisbury (1791), on the other hand, stated that Vandelli introduced the species from Brazil around 1787.

Fuchsia coccinea is a rare species known from just four of the highest mountain ranges in Minas Gerais. It typically grows in rocky, open campo or occasionally in forest patches. It has long been confused in the literature with *F. magellanica*, but *F. coccinea* is easily distinguished by its ovate, subsessile leaves with a conspicuous tuft of long hairs at the base of the lower surface. Its divergent or arching pedicels also differ markedly from the fully pendent flowers of the other species in the section.

Fuchsia regia subsp. *regia* is known to occur sympatrically with *F. coccinea* at the Pico do Itambé and near the summit of the Serra do Itacolomi,

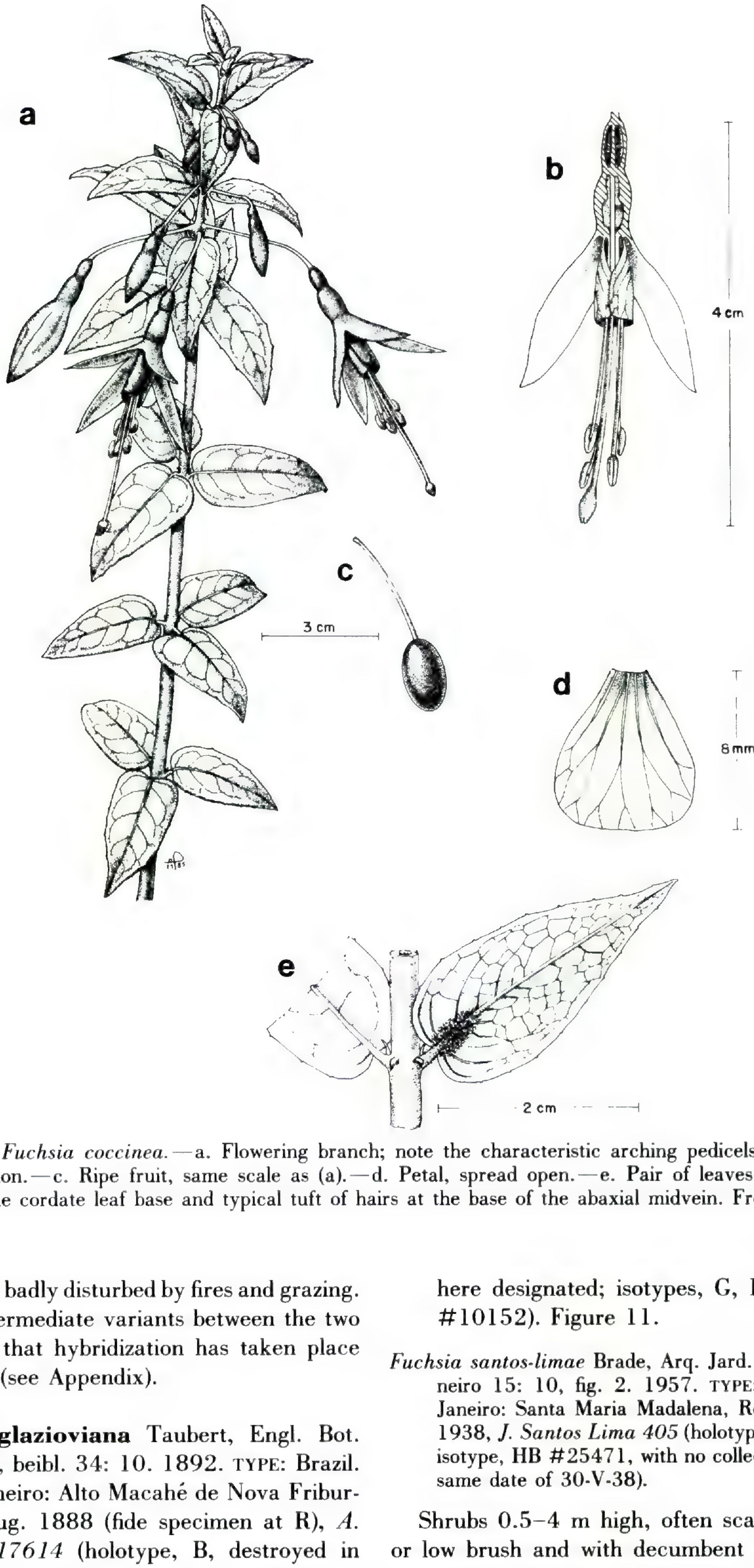

FIGURE 10. *Fuchsia coccinea*.—a. Flowering branch; note the characteristic arching pedicels.—b. Flower in longitudinal section.—c. Ripe fruit, same scale as (a).—d. Petal, spread open.—e. Pair of leaves from the lower stem, showing the cordate leaf base and typical tuft of hairs at the base of the abaxial midvein. From *Berry et al. 4558*.

which has been badly disturbed by fires and grazing. A series of intermediate variants between the two taxa indicates that hybridization has taken place in these areas (see Appendix).

6. Fuchsia glazioviana Taubert, Engl. Bot. Jahrb. 15, beibl. 34: 10. 1892. TYPE: Brazil. Rio de Janeiro: Alto Macahé de Nova Friburgo, 14 Aug. 1888 (fide specimen at R), *A. Glaziou 17614* (holotype, B, destroyed in World War II, photograph at F; lectotype, F, here designated; isotypes, G, LE, LY, P, R #10152). Figure 11.

Fuchsia santos-limae Brade, Arq. Jard. Bot. Rio de Janeiro 15: 10, fig. 2. 1957. TYPE: Brazil. Rio de Janeiro: Santa Maria Madalena, Rochela, 30 May 1938, *J. Santos Lima 405* (holotype, RB #37704; isotype, HB #25471, with no collector number but same date of 30-V-38).

Shrubs 0.5–4 m high, often scandent in trees or low brush and with decumbent branches to 6 m long. Branchlets subdivaricate and generally

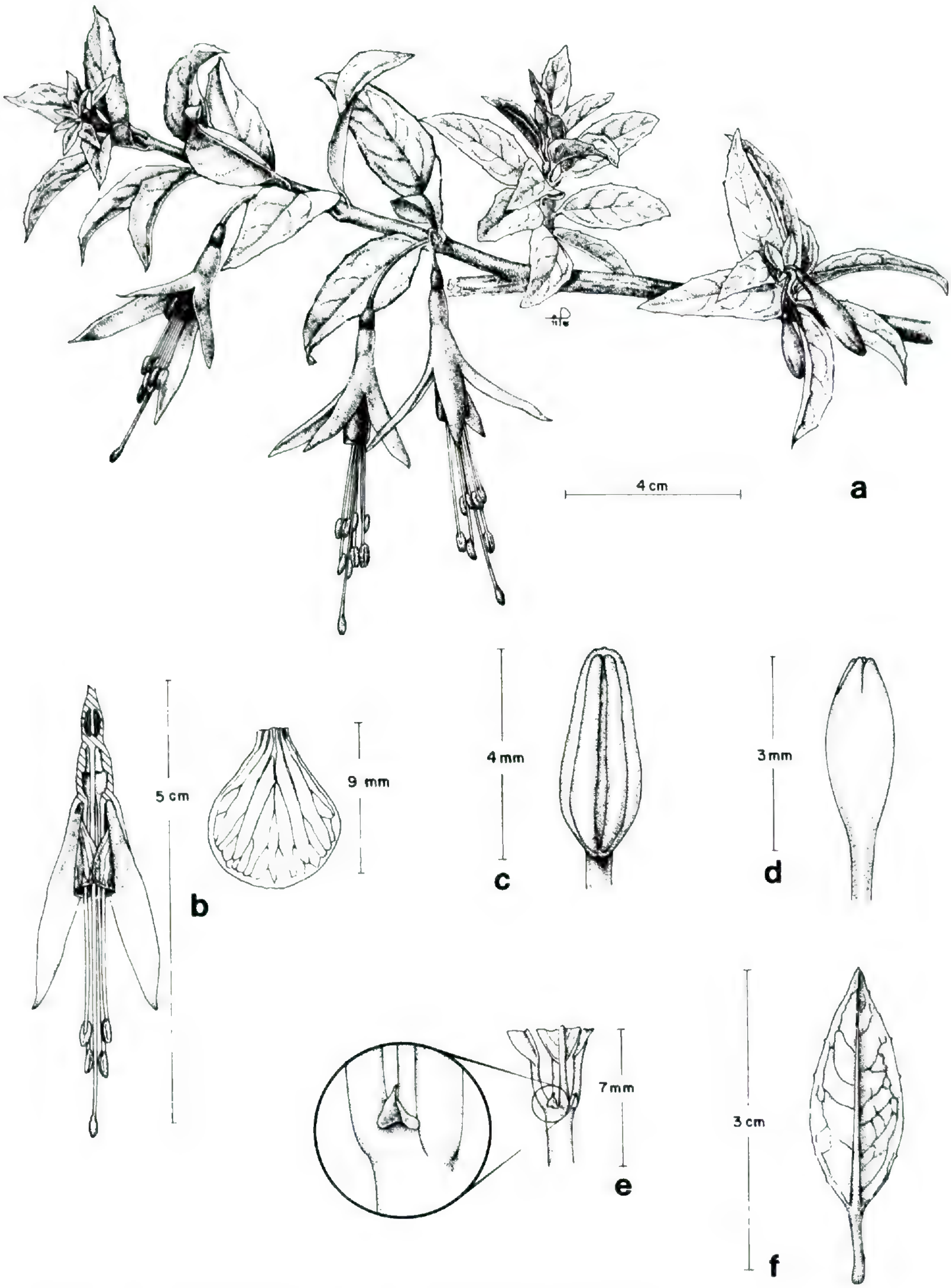

FIGURE 11. *Fuchsia glazioviana.*—a. Flowering branch.—b. Flower in longitudinal section and petal spread open.—c. Detail of anther.—d. Detail of stigma.—e. Detail of stipules.—f. Leaf underside. From *Berry et al. 4422.*

densely packed, minutely puberulent, dull purplish, readily exfoliating. Leaves opposite or ternate, firmly membranous to subcoriaceous, elliptic or lanceolate, 15–30(–40) mm long, 8–15 mm wide, acute at the base and apex, dark sublustrous green and glabrous above, paler and subglabrous below or sometimes pilose at the base of the midvein; margins remotely gland-denticulate, with 4–5(–6) secondary veins per side. Petioles 3–6 mm long, purplish and sparsely puberulent; internodes short, 3–12 mm long. Stipules broadly triangular, 0.6–1.2 mm long and wide, thick at the base, purplish, deciduous. Flowers solitary in the upper leaf axils; pedicels slender, sparsely puberulent, pendulous,

12–26 mm long. Ovary oblong, 4–5 mm long, 2–2.5 mm wide. Floral tube cylindrical, 5–7 mm long, 2.5–4 mm wide, subglabrous outside, glabrous inside; nectary smooth, 3–4 mm high. Sepals 17–22 mm long, narrowly lanceolate, connate at the base for 4–5 mm; free lobes 3–4 mm wide, acuminate at the apex, spreading at anthesis. Tube and sepals red or pink. Petals purple, obovate, 9–12 mm long, 6–9 mm wide, rounded at the apex. Filaments red-purple, 22–32 and 16–28 mm long; anthers oblong, 2.5–3.5 mm long, 1.1–1.6 mm wide. Style red, glabrous to puberulent; stigma clavate, 2–3 mm long and 1–1.4 mm wide, exserted 5–20 mm beyond the anthers. Berry shiny dark purple, subcylindrical, 10–16 mm long, 5–8 mm wide; seeds oblong, 2–4 mm long, 1–1.5 mm wide. Gametic chromosome number $n = 22$.

Distribution (Fig. 5). In open campo and in cloud forest on a few high mountains around the towns of Nova Friburgo and Santa Maria Madalena, in Rio de Janeiro state, from 1,500 to 2,100 m. Flowers throughout the year, mainly from November to March.

Additional specimens examined. BRAZIL. RIO DE JANEIRO: Nova Friburgo, Morro da Nova Caledônia, *Berry et al. 4420* (MO, RB), *4422*, *4423* (MO, RB; $n = 22$), *4426*, *4428*, *4431*, *4434* (MO, RB); *de Lima 530* (RB); *Martinelli et al. 2540* (RB); *Pabst 8134* (HB); Nova Friburgo au fond de la Bocaina do Conejo, *Glaziou 12667* (F, K, LE, LY, P); Nova Friburgo, Morro da torre de TV, *Vianna et al. 789* (MO); Santa Maria Magdalena, Pedra do Desengano, *Farney & Caruso 1190* (RB); *Santos Lima & Brade 13286* (RB, HB #25466, fragment).

Fuchsia glazioviana is distinguished by its small, tightly grouped, shiny, subcoriaceous leaves with short petioles. It is a local endemic known from only two mountains in the Serra do Mar of Rio de Janeiro, where it extends from upper cloud forest into open campo above treeline. On the Morro da Nova Caledônia, it is sympatric with *F. regia* subsp. *regia* in cloud forest habitats, and the two species hybridize locally (see Appendix).

7. Fuchsia hatschbachii P. Berry, sp. nov. TYPE: Brazil. Paraná: Serra São Luiz do Purunã, BR-277, Mun. Campo Largo, 25 Jan. 1985, *P. E. Berry, T. Plowman & F. Juarez 4458* (holotype, MO #3504627; isotype, MBM; $n = 22$). Figure 12.

Frutex erectus vel scandens 1–5 m altus. Folia plerumque opposita, anguste lanceolato-ovata, 3–11 cm longa, 0.8–3 cm lata, apice attenuata vel acuminata basi rotundata vel anguste subcordata, glabra; petiolis 2–6(–7) mm longis, interdum flexis ad basim laminae; stipulis parvis membranaceis 1–1.7 mm longis, 0.6–1.2 mm latis. Tubi florales cylindrici 10–15 mm longi, 3–5 mm lati. Sepala 18–26 mm longa, 3.5–5 mm lata, basi connata 2–6 mm. Petala late obovata 12–17 mm longa, 8–12 mm lata. Numerus gameticus chromosomatum $n = 22$.

Erect to scandent shrubs 1–3 m tall or climbers in trees to 5 m above ground. Branchlets glabrous, dull purple, older branches ascending on small shrubs or decumbent in large or climbing plants. Leaves mostly opposite, occasionally in whorls of 3–4, firmly membranous to subcoriaceous, narrowly lance-ovate, generally 3 times longer than wide, 3.0–7.5(–11.0) cm long, 0.8–2.5(–3.0) cm side, apex attenuate to acuminate, base rounded to narrowly subcordate, sublustrous dark green above, pale below and glabrous on both sides except for small tufts of hairs 0.8–1 mm long at the base of the lower midvein in some plants; margin remotely gland-denticulate, secondary veins 5–6(–7) per side. Petioles wine purple, (2–)3–6(–7) mm long, 1–2 mm thick, canaliculate above, at times making a marked angle at the junction with the midvein. Stipules narrowly triangular, 1–1.7 mm long, 0.6–1.2 mm wide, adjacent ones occasionally fused, semideciduous. Flowers glabrous and solitary in upper leaf axils; pedicels pendulous, (10–)20–30 mm long. Ovary cylindrical, 5–9 mm long, 2.5–3 mm wide. Floral tube cylindrical, 10–15 mm long, 3–5 mm wide; nectary 3–5 mm high. Sepals 18–26 mm long, connate at the base for 2–6 mm; free lobes 3.5–5 mm wide at the base, spreading at anthesis. Tube and sepals red. Petals violet, broadly obovate, 12–17 mm long, 8–12 mm wide. Filaments red, 40–45 mm and 32–40 mm long; anthers red-purple, 3–3.5 mm long, 1–1.5 mm wide. Style red, loosely pilose in lower half; stigma 2–3 mm long, 1–1.5 mm wide, exserted 15–20 mm beyond the anthers. Berry subcylindrical, ± 4-angled, 13–18 mm long, 7–10 mm thick, purple when ripe; seeds oblong-triangular, 1.4–1.8 mm long, 0.8–1.2 mm wide. Gametic chromosome number $n = 22$.

Distribution (Fig. 5). In low forests on limestone or sandstone outcrops, in the planalto north and west of Curitiba, Paraná, between 950 and 1,150 m. Flowers mainly from November to March.

Additional specimens examined. BRAZIL. PARANÁ: Serra São Luiz do Purunã, BR-277, Mun. Campo Largo, *Berry et al. 4459* (MBM, MO; $n = 22$), *4460*, (MBM, MO), *4461* (MBM, MO; $n = 22$), *4462*, *4463*, *4464*, *4465* (MBM, MO); *Brade 19494* (RB); *Frenzel in 28 Feb. 1951* (MBM #6372, MBM #75197); *Hatschbach 7541* (MBM); *Hatschbach & Oliveira 42962* (MBM); *Hatschbach et al. 42960*, *42964* (MBM); *Kummrow 1512*, *2217* (MBM); *Pereira 5193* (F, HB, MB, MO, RB); Sprea, Mun. Balsa Nova, *Hatschbach 42966* (MBM); Campinhos, Mun. Bocaiúva do Sul, *Hatschbach 1817* (MBM, PACA); Campina dos Tavares, Mun. Bocaiúva do

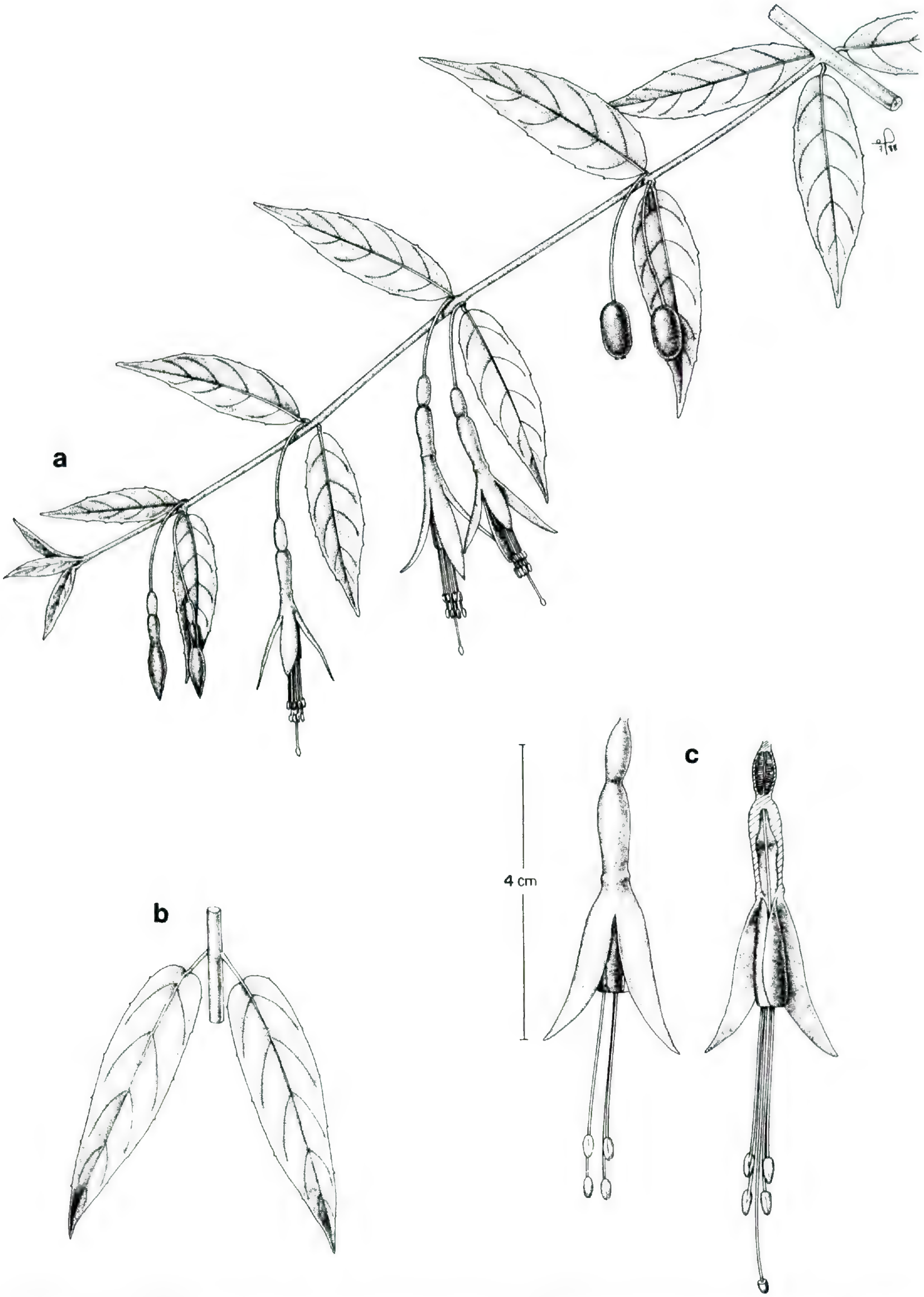

FIGURE 12. *Fuchsia hatschbachii*. —a. Flowering branch.—b. Details of leaves (upper surface).—c. Flowers. From *Berry et al. 4458*.

Sul, *Hatschbach 7776* (MBM): Bacaetava, near cave, Mun. Bocaiúva do Sul, *Kummrow 1022, 1418* (MBM), *Kummrow et al. 2998* (MBM; $n = 22$); Bateias, Mun. Campo Largo, *Hatschbach 40746* (MBM); Tigre, Mun. Cerro Azul, *Hatschbach 43632* (MBM); Colombo, *Falkenberg 2215* (FLOR); Manancial da Serra, *Braga 550* (RB, SP); Açungui, *Mattos & Labouriau in 1 Mar. 1948* (RB); Paredão, Mun. Jaguariaíva, *Hatschbach 31130* (MBM); Capão da India, *Hatschbach & Ramamoorthy 42972* (MBM, MO); Serra das Almas, Mun. Palmeira, *Hatschbach 13503* (MBM); Faz. Santa Rita, Mun. Palmeira, *Kummrow 2217* (MBM); *Landrum 3933* (MO); *Oliveira 299* (MBM); Curiola, Mun. Rio Branco do Sul, *Hatschbach 16155* (MBM); Madre, Mun. Rio Branco do Sul, *Hatschbach 7774* (MBM); Serra do Caete, *Hatschbach 40698* (MBM); Mun. Palmeira, BR-277, Rio Papagaio, *Hatschbach 50824* (MBM).

Fuchsia hatschbachii is most likely to be confused with *F. regia* but differs by having shorter petioles, narrow leaves with somewhat curved petioles, shortly connate sepals, and small stipules. It is tetraploid, whereas all examined populations of *F. regia* from Paraná are octoploid. *Fuchsia hatschbachii* grows within 20 km of populations of *F. regia* subsp. *serrae* and *F. brevilobis* but occurs in drier, more interior areas of the planalto and is unusual in its close association with limestone or sometimes sandstone outcrops. The species is dedicated to Gert Hatschbach, Director of the Museu Botânico Municipal de Curitiba, who has done more than any previous botanist to collect and study the flora of Paraná.

8. Fuchsia magellanica Lamarck, Encycl. 2: 565. 1788; Tabl. encycl. 1, Volume 2(1): pl. 282. 1792. *Fuchsia magellanica* var. *typica* Munz, Proc. Calif. Acad. Sci. IV. 25: 9. 1943. *Fuchsia coccinea* Dryander var. *robustior* Hooker, Bot. Antarc. Voy.: 269. 1847, pro parte. TYPE: Chile. Straits of Magellan, Jan. 1768, *Philibert Commerson* (holotype, P—Lamarck Herbarium, also on microfiche; isotypes, BM, P—Jussieu Herb., LINN). Figure 13.

Fuchsia macrostema Ruiz & Pavón, Fl. Peruv. Chil. 3: 88, pl. 324, fig. b. 1802. *Fuchsia macrostema* Ruiz & Pavón var. *grandiflora* Hooker, Bot. Misc. 3: 308. 1833. *Fuchsia gracilis* var. *macrostema* (Ruiz & Pavón) Lindley, Bot. Reg. 13: pl. 1052, 1827. *Fuchsia coccinea* Dryander var. *macrostema* (Ruiz & Pavón) Hooker, Bot. Antarc. Voy.: 270. 1847. *Fuchsia magellanica* var. *macrostema* (Ruiz & Pavón) Munz, Proc. Calif. Acad. Sci. IV. 25: 9. 1943. TYPE: Chile: VIII Región (Bío-Bío), Concepción, Quebrada de Carcamo, 1778–1788, *Hipólito Ruiz & José Pavón* (lectotype, MA, here designated).

Thilcum tinctorium Molina, Saggio Chili, 2nd edition: 146, 286. 1810. LECTOTYPE: plate 47 of *Thilco* Feuillée in J. Observ. Phys. Math. Bot. (Hist. Plantes Medicinales). 1725 here designated. (Feuillée described *Thilco* with five-merous flowers, which Molina thought worthy of generic recognition.)

Fuchsia gracilis Lindley, Bot. Reg. 10: pl. 847. 1824. *Fuchsia magellanica* var. *gracilis* (Lindley) Bailey, Cyclop. Amer. Hort., 614. 1900. TYPE: cultivated in Walton, England, *John Lindley in 1824* (holotype, CGE). First illustrated in Bot. Mag. 2507. 1824, where it was erroneously identified by Graham as *Fuchsia decussata* Ruiz & Pavón.

Fuchsia conica Lindley, Bot. Reg., t. 1062. 1827. *Fuchsia macrostemma* var. *conica* (Lindley) Sweet, Brit. Fl. Gard. 6: pl. 216. 1833. *Fuchsia magellanica* var. *conica* (Lindley) Bailey, Cyclop. Amer. Hort., 614. 1900. TYPE: cultivated in London, England in 1826, from seeds sent from Chile in 1824, *John Lindley* (not seen).

Fuchsia gracilis var. *multiflora* Lindley, Bot. Reg. 13: pl. 1052. 1827. TYPE: cultivated at the Horticultural Society, London, England, 1826, from Chilean seeds introduced in 1824, *John Lindley s.n.* (holotype, CGE; isotype, K).

Fuchsia discolor Lindley, Bot. Reg., pl. 1805. 1835. *Fuchsia magellanica* var. *discolor* (Lindley) Bailey, Cyclop. Amer. Hort., 614. 1900. TYPE: cultivated at the Horticultural Society, London, England, from plants growing in Port Famine in the Magellan Straits, *John Lindley s.n.* (holotype, CGE).

Fuchsia chonotica R. A. Philippi, Linnaea 28: 687. 1856. *Fuchsia coccinea* Solander var. *chonotica* (R. A. Philippi) Reiche, Anales Univ. Chile 98: 485. 1897. TYPE: Chile: X Región (Los Lagos), Chiloé, Archipiélago de Huaytecas, 6 Mar. 1857, *F. Fonk 153a* (lectotype, SGO #53136, here designated). The lectotype is mounted on the same sheet with *Fonk 153b*, collected on 8-III-1857 from Puerto Low, Chiloé.

Fuchsia araucana F. Philippi in R. A. Philippi. Bot. Zeit. 34: 577, t. 9, fig. 6. 1876. TYPE: Chile: IX Región (Araucanía), Prov. Cautín, Toltén, Feb. 1875, *F. Philippi s.n.* (holotype, SGO #53139).

Fuchsia magellanica var. *molinae* Espinosa, Bol. Mus. Nac. Chile 12: 102. 1929. TYPE: Chile, X Región (Los Lagos), Chiloé, quebrada de La Chacra, near Castro, 31 Jan. 1929, *Espinosa s.n.* (holotype, SGO #53152; isotype, SGO #53121).

Fuchsia magellanica var. *eburnea* Pisano, Ans. Inst. Pat. (Chile) 10: 155. 1979. TYPE: Chile: XII Región (Magallanes), Isla Englefield, Seno Otway, 53°05′S, 71°51′W, 26 Feb. 1979, *Edmundo Pisano & R. Cárdenas 4947* (holotype, HIP #6892; isotypes, MO, RNG, SGO #95030).

Erect to semiscandent shrubs 0.5–3(–5) m tall. Branchlets tan to reddish, glabrous or occasionally sparsely strigillose with appressed hairs 0.3–0.4 mm long; older stems with tan, flaky bark, up to 25 cm diam. at the base. Leaves opposite, ternate or occasionally quaternate, membranous, (narrowly) elliptic-ovate, 15–55(–70) mm long, 5–25(–40) mm wide, acute to acuminate at the apex, mostly obtuse at the base, glabrous to strigillose along veins on both sides, paler below and sometimes with reddish veins; margin serrulate or crenate-dentate,

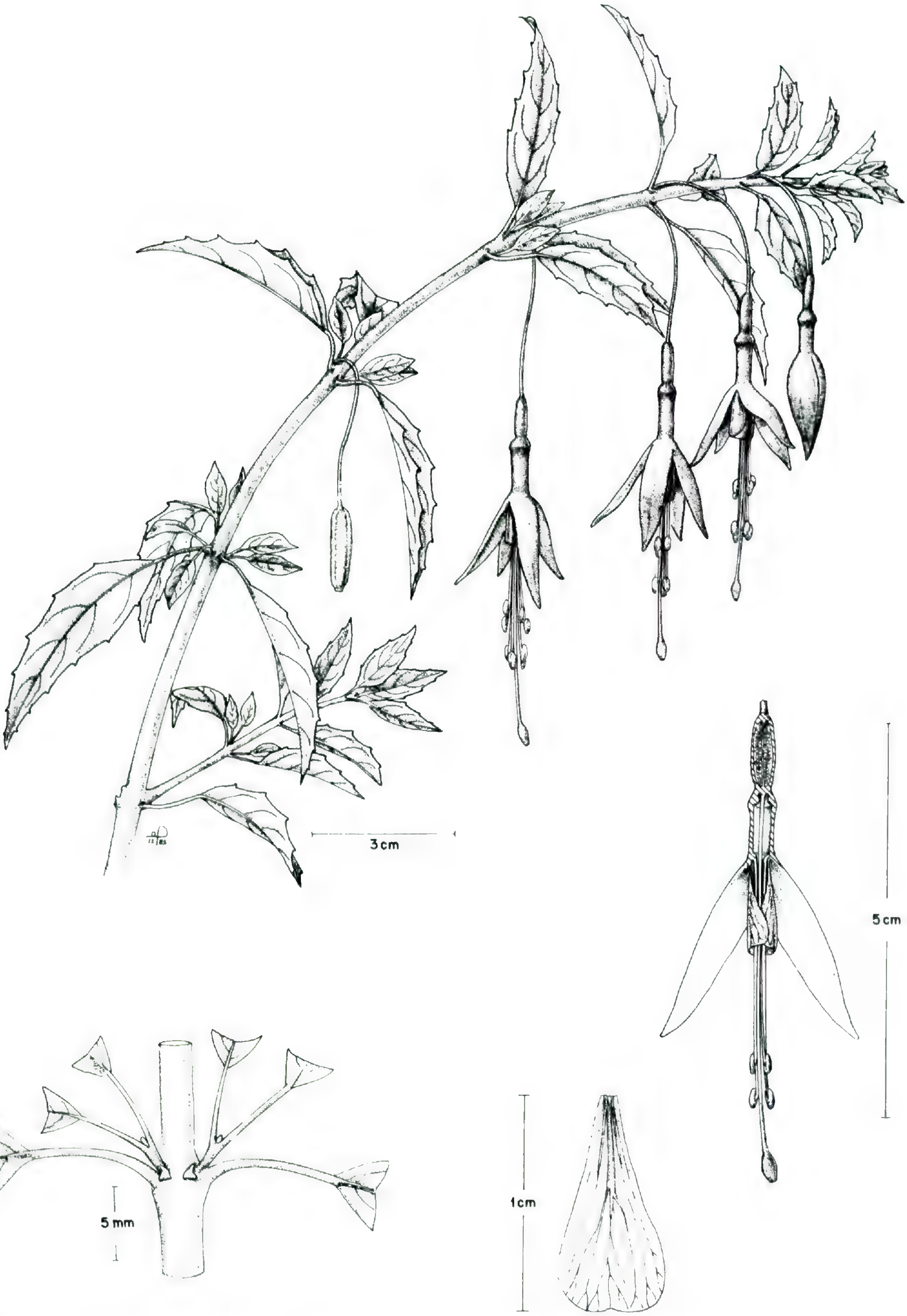

FIGURE 13. *Fuchsia magellanica*. Flowering branch, longitudinally split flower, individual petal spread open, and detail of stem with stipules and petioles. From *Solomon & Solomon 4599*.

veins; margin serrulate or crenate-dentate, often shallowly lobed between the teeth, secondary veins 4–7 per side. Petioles slender, 0.3–1 mm thick, 3–20 mm long. Stipules (narrowly) lanceolate, 0.7–1.3 mm long, 0.5–0.8 mm wide, deciduous. Flowers solitary or rarely in pairs in upper leaf axils; pedicels filiform, pendulous, (13–)20–55 mm long, glabrous to strigillose. Ovary (narrowly) oblong,

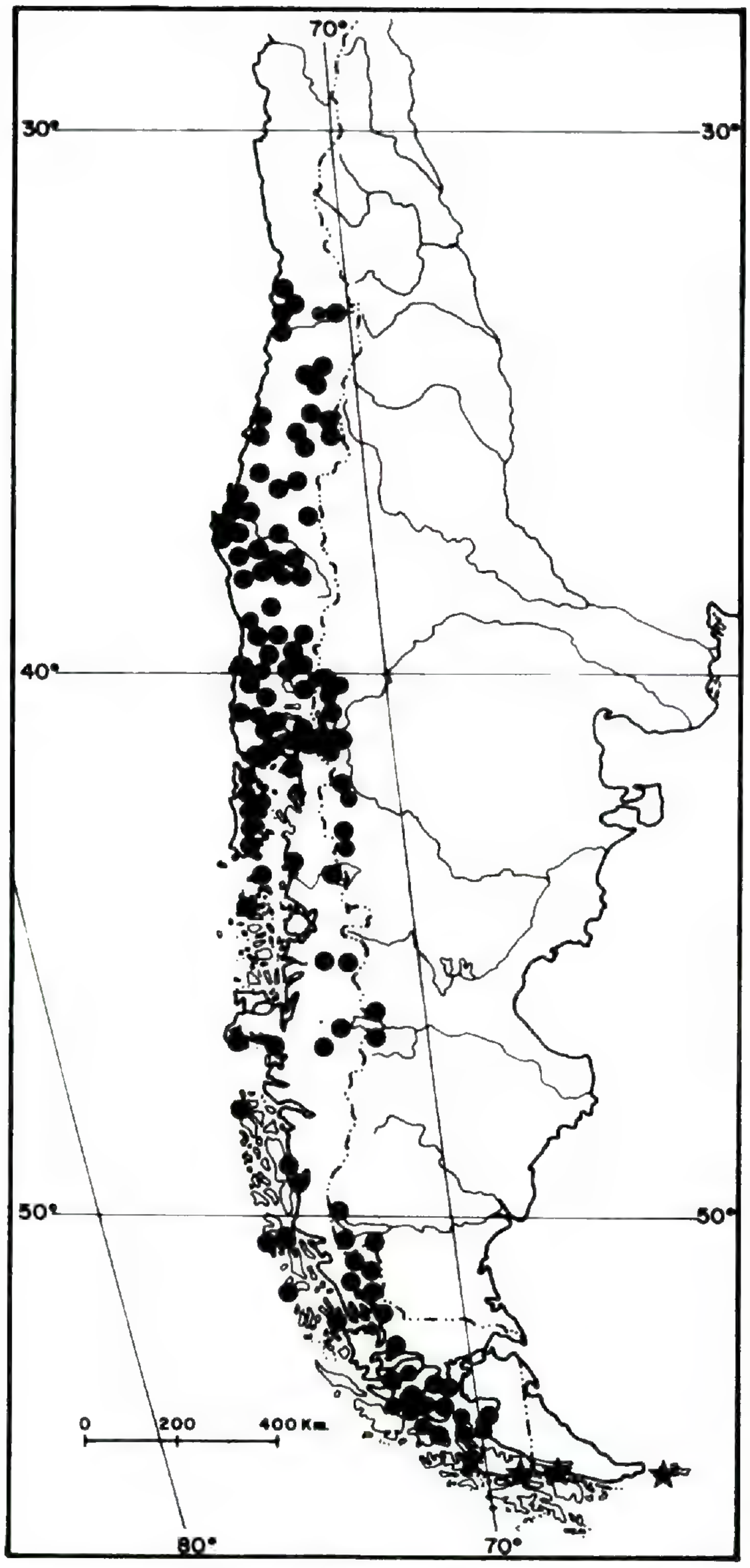

FIGURE 14. Native distribution of *Fuchsia magellanica*. Stars indicate collections made in the early 19th century from populations that have since been eliminated.

(5–)7–11(–14) mm long, 2–3 mm wide. Floral tube cylindrical to narrowly obconic, 7–15 mm long, 2–3.5 mm wide, glabrous to strigillose outside, pilulose inside; nectary 1.8–3 mm high, irregularly lobed. Sepals (15–)17–25(–30) mm long, narrowly lanceolate, connate at the base for 2–5 mm; free lobes (3–)4.5–7(–8) mm wide at base, acuminate at the apex, spreading at anthesis. Tube and sepals generally crimson, rarely pale whitish pink. Petals purple or rarely pale pink, narrowly obovate, (8–)11–20 mm long, 5–11 mm wide, apex rounded. Filaments red-purple, (18–)22–35 mm and (11–)19–31 mm long; anthers purplish, oblong, 2.5–3.5 mm long, 1–2 mm wide. Style purple-red, pubescent at the base; stigma clavate, purple-red, 2–3 mm long, 1–2 mm wide. Berry narrowly oblong, (10–)15–22 mm long, 4–7 mm thick; seeds irregularly oblong-triangular, 1.0–1.4 mm long, 0.7–0.9 mm wide. Gametic chromosome number $n = 22$.

Distribution (Fig. 14). In moist scrub and along forest margins or in clearings, usually near water. Throughout the central and southern Andes of Chile and Argentina and in coastal Chile; from Valparaíso, Chile (32°50′S) and Neuquén, Argentina (39°30′S) to southern Tierra del Fuego (55°S). From sea level (throughout the range) to 1,750 m in central Chile near Santiago. Flowering principally from December to March, occasionally as early as October and as late as April. Widely cultivated throughout the world and naturalized in parts of South America, east Africa, New Zealand, Ireland, and Hawaii.

Representative specimens examined. CHILE. V REGION (VALPARAÍSO). VALPARAÍSO: Viña del Mar, road to Concón, 23 Apr. 1939, *Behn s.n.* (NY); Concón, 14 Jan. 1950, *Boelcke 3920* (BAA, MO, SI); *Poeppig 124* (BM, MO, P); Valparaíso, 7 Dec. 1930, *Behn s.n.* (MO, UC); Oct. 1829, *Bertero 1008* (F, G, GH, MO); 1832, *Bridges 198* (LE, W), *s.n.* (G, K, W); *McRae in Feb. 1825* (LE); Las Docas, 26 Dec. 1949, *Boelcke 3838* (BAA, SI); Cerro Campana, Cajón Grande, Pozo de Coipo, 8 Oct. 1955, *Garaventa 6606* (CONC); Limache, Cajón Grande, 27 Dec. 1944, *Boelcke 427* (BAA); Curauma, 31 Jan. 1932, *Garaventa s.n.* (CONC); Fundo Pajonal, Valparaíso, 10 Oct. 1955, *Skottsberg s.n.* (S); N slope, Laguna Verde, 15 km S of Valparaíso, 29 Nov. 1935, *West 3980* (MO, UC). SAN ANTONIO: Playa Mirasol, ca. 36 km N of San Antonio, 1 Mar. 1982, *Landrum 4338* (NY). REGION METROPOLITANA (SANTIAGO): SANTIAGO: Peñalolen, Casa de Piedra, 1,500 m, 2 Jan. 1927, *Looser 148-H* (SI); Quebrada Peñalolen, E of Santiago, 33°29′S, 70°32′W, 1,600 m, 22 Feb. 1928, *Looser 2299* (POM), 28 Feb. 1928, *2300* (POM), 30 Dec. 1929, *Garaventa 828* (POM); Santiago, "ad rivulos frequens," *Gay 1234* (SGO); Santiago, 22 Sep. 1918, *Claude-Joseph 531* (NY, US). VI REGION (O'HIGGINS). CACHAPOAL: Montaña La Leona, 1828, *Bertero 280* (F, G, GH, LE, MO, NY, P, SGO, W); Rancagua, 1829, *Bertero 280* (F, GH, NY, P); San Vicente, 1925, *Pennell 12866* (SGO). COLCHAGUA: Talcaregue, 34°36′S, 70°53′W, 1870, without collector (SGO #41427); Ciruelos, Dep. de San Fernando, 15 Nov. 1943, *Aravena 38* (SGO); Hacienda Millahue de Apalta, 34°36′S, 71°16′W, 16 Feb. 1946, *Kausel 1821* (SGO). VII REGION (MAULE). CURICO: road Curicó to Argentina, beyond Los Queñes, along Arroyo Puerta, Andean foothills at 1,240 m, 13 Feb. 1936, *Mexia 7863* (BH, BM, F, G, GH, MO, NA, NY, S, U, UC, US); 19 km E of Los Queñes, 9 Mar. 1967, *Marticorena & Matthei 800* (BAB, CONC); Cordillera Peteroa–Planchón, Cañon Rio Claro, 950 m, 18 Feb. 1936, *Mexia 4406* (GH, MO, UC); Húmeda Puntilla, Norte Llico, 2 Feb. 1969, *Villagrán & Tapia s.n.* (SGO); Fundo La Morita, 20 Dec. 1968, *Mahu 2787* (BAB); Aquelame, near Laguna Vi-

chuquén, 16 Sep. 1963, *Barra s.n.* (CONC #28414); Vichuquén, Dec. 1861, without collector (SGO #53132). TALCA: Constitución, Feb. 1891, *Reiche s.n.* (SGO #60893). LINARES: La Mina, road to Melado, 17 Dec. 1953, *Ricardi 2793* (CONC); Quinamavida, 35°47′S, 71°26′W, 1912, *Husbando 840* (NA). VIII REGION (BÍO-BÍO). ÑUBLE: Termas de Chillán, 24 Dec. 1907, *Elwes s.n.* (K); Baños de Chillán, 1,400–1,500 m, 29–31 Jan. 1925, *Pennell 12473* (F, PH, SGO, US); *Reed s.n.* (K); Las Trancas, road to Chillán, 28 Feb. 1979, *Rodríguez 1107* (CONC); 25 km above Recinto, road to Termas de Chillán, 1,500 m, 17 Jan. 1979, *Solomon 4389* (MO); Guarilihue, 36°33′S, 72°41′W, 21 Feb. 1977, *Quezada 203* (CONC); Yungay, Fundo Baquedano–Sta. Lucía, 4–9 Feb. 1957, *Artigas 19587* (CONC). CONCEPCIÓN: Coronel, 1865, *Ochsenius s.n.* (MO); Rio Chivilingo, 4 km S of Coronel, 5 Jan. 1966, *Meyer 9777* (K, MO, NA, UC); *Walker 240* (GH, US); Puente La Araucana at Gualqui, 37°00′S, 72°55′W, 21 Jan. 1979, *Solomon 4418* (MO); 8 km E of San Rafael–Coelemu road, on road to San Ignacio, 300 m, 19 Jan. 1979, *Solomon 4397* (MO); hills back of Talcahuano, 22 Feb. 1917, *Skottsberg 1454* (NY, S); mouth of Rio Bío-Bío, 20 Dec. 1950, *Ricardi 11359* (CONC), 17 Oct. 1953, *Sparre 9989* (CONC); 5 km SE of Concepción along Rio Bío-Bío, 200 m, 17 Feb. 1967, *Skog 1033* (POM, US); Talcahuano, Parque Hualpén, 13 Dec. 1950, *Ricardi 11178* (CONC), 7 Jan. 1976, *Marticorena et al. 1814* (CONC), 6 Nov. 1969, *Carrasco 200* (CONC); 16 Sep. 1896, *Dusén s.n.* (S); Hualqui, Picacho, 13 Jan. 1937, *Junge 5934* (CONC); 1 km S of Ramuncho, base of W-facing coastal cliffs, W of Talcahuano, Punta Hualpén Peninsula, 31 Dec. 1951, *Hutchison 226* (K, UC, US); Talcahuano and Concepción, *Née? s.n.* (MA #183584); Isla Quiriquina, 15 Sep. 1942, *Junge 6879* (CONC); Quebrada Honda, Puentes Mellizos, 21 Apr. 1976, *Marticorena et al. 1075* (CONC); San Vicente, above beach, 3 Mar. 1925, *Pennell 12866* (GH, PH); Fundo Trinitarias, 29 Dec. 1934, *Pfister 1232* (CONC); Cerro Caracol, 14 Nov. 1937, *Pfister 6477* (CONC); Concepción, Predio Universitario, 26 Oct. 1950, *Ricardi s.n.* (CONC); Barrio Universitario, 13 Mar. 1980, *Riquelme s.n.* (MO; $2n = 44$); Las Canoas, road Concepción to Chaimávida, 12 Feb. 1980, *Riquelme s.n.* (MO; $2n = 44$); Concepción, 1855, *Germain s.n.* (BM, F, G); 1826–1830, *King & Andersson s.n.* (BM); Oct. 1825, *Macrae s.n.* (BR, G, K); *Née s.n.* (MA #183583). BÍO-BÍO: 4 km above dam on road to Laguna La Laja, 930 m, 23 Jan. 1979, *Solomon 4440* (MO); Antuco, *Reynolds s.n.* (GH); Cordillera Antuco, La Cueva, Feb. 1887, *Rahmer s.n.* (SGO); Laja, Salto del Trubunleo, 23 Jan. 1969, *Boelcke 6528* (BAA), *90359* (BAB); 23 Jan. 1969, *Ricardi & Marticorena 5802* (CONC); road from Bío-Bío to Copahue, 4 km E of Pitrillón, 13 Mar. 1976, *Marticorena et al. 990* (CONC); road Santa Bárbara to Río Huecuecura, 12 Mar. 1976, *Marticorena et al. 889* (CONC); road from Bío-Bío to Copahue, 3 km past Bío-Bío, 13 Mar. 1976, *Marticorena et al. 920* (CONC); road Bío-Bío to Santa Bárbara, 14 Mar. 1976, *Marticorena et al. 1010* (CONC). ARAUCO: Cordillera de Nahuelbuta, Contulmo tunnel, La Huina, 19 Feb. 1955, *Aravena 29* (BR, SI, UC); El Diamante, Cordillera de Nahuelbuta, 14 Mar. 1978, *Quezada 230* (CONC); Estación Lanalhue, 20 Feb. 1955, *Aravena 35* (UC); Laraquete, 37°10′S, 73°15′W, 20 m, 21 Jan. 1979, *Solomon 4413* (MO); Quebrada del Río Trongol, 13 Dec. 1974, *Rodríguez 634* (CONC); road Curanilahue to Cañete, 11 Jan. 1972, *Quezada et al. 18* (CONC); Trongol Bajo, 3 Mar. 1978, *Cuevas 3* (CONC); Isla La Mocha, Jan. 1959, *Behn 25364* (CONC); *Eights s.n.* (US); Fundo Sta. Sofía de Raqui, *Ricardi 9173* (CONC); cliffs on E side of Río Tubul, 20 Jan. 1979, *Solomon 4408* (MO). IX REGION (ARAUCANIA). MALLECO: Fundo Solano, Los Alpes, Cordillera de Nahuelbuta, 590 m, 12 Jan. 1958, *Eyerdam 10141* (NY, SGO, UC, US); Angol, 15 Nov. 1933, without collector (UC); 10 Feb. 1892, *Kuntze s.n.* (F); road Vegas Blancas–Angol, 22 Mar. 1973, *Rodríguez & Torres 155* (CONC); Ercilla, Feb. 1892, *Kuntze s.n.* (F, NY); between Manzanar & Malacahuello, 7 Jan. 1977, *Marticorena et al. 1226* (CONC); cuesta La Esperanza, 200 m, 3 Mar. 1980, *Marticorena & Quezada 1669* (CONC); Parque Nacional Nahuelbuta, 9 Jan. 1968, *Ricardi et al. 1969* (BAB, CONC); Collipulli to Curaco, 3 km before Curaco, 340 m, 3 Mar. 1980, *Marticorena & Quezada 1670* (CONC); Termas de Tolhuaca, 1,140–1,180 m, *Morrison & Wagenknecht 17499* (BH, F, G, GH, MO, NA, S, UC); Volcán de Tolguaca, 1,300–1,400 m, 24 Feb. 1925, *Pennell 12787* (PH); Reserva Forestal Malleco, Los Guindos, 38°03′S, 71°47′W, 7 Apr. 1978, *Rodríguez 128* (CONC); Río Blanco, 27 Dec. 1952, *Schwabe 13733* (CONC); 3 km below Vegas Blancas, 37°45′S, 72°58′W, 24 Jan. 1979, *Solomon 4469* (MO); Termas del Río Blanco, 2 Jan. 1948, *Pfister 7895* (CONC); Traiguén, Quecheregua, 600 m, 1 Dec. 1947, *Sparre 3327* (S); Pailahueque, Dec. 1929, *Pirión 201* (GH); Renaico Valley, 15 Jan. 1902, *Elwes s.n.* (K). CAUTÍN: Pucón, near Villarrica, 250 m, Jan. 1929, *Buchtien s.n.* (MO); Feb. 1935, *Pfister 1979* (CONC); Villarrica, Fundo Flor del Lago, 1 Jan. 1946, *Behn 26906* (CONC); Volcán Villarrica, 23 Apr. 1952, *Frödin 819* (BM); 3 km E of Puente Correntoso, 17 km E of Villarrica, 39°16′S, 72°00′W, 30 Jan. 1979, *Solomon 4535* (MO); Laguna Conguillío, Feb. 1963, *Gleisner 194* (CONC); 3 km from Laguna Captrén, Temuco, 20 Jan. 1976, *Marticorena et al. 830* (CONC); between Laguna Quililo and Melipeuco, 12 Jan. 1977, *Marticorena et al. 1475* (CONC); Lastarria, 39°13′S, 72°41′W, 3 Mar. 1980, *Marticorena & Quezada 1712* (MO; $2n = 44$); S of Lautaro, banks of Río Cautín, 7 Mar. 1980, *Marticorena & Quezada 1713* (MO; $2n = 44$); Río Cautín, Nov. 1919, *Hollermeyer s.n.* (G); Depto. Victoria, 12 Mar. 1939, *Morrison & Wagenknecht 17499* (K); Lago Caburgua, 6 Feb. 1969, *Navas 3419* (B); Toltén, Feb. 1875, *Philippi s.n.* (SGO #53139, SGO #41419); Termas de Palguín, 11 Jan. 1953, *Ricardi 2399* (CONC); Volcán Llaima, Parque Nac. Los Paraguas, 29 Jan. 1979, *Solomon 4511* (MO); entrance to Parque Nac. Villarrica, 30 Jan. 1979, *Solomon 4523* (MO); road to Curarrehue, 9 km E of Lago Caburga road, 30 Jan. 1979, *Solomon 4534* (MO); Cerro Nielol, 20 Nov. 1947, *Sparre 3209* (S); Río Imperial, Carahue, 4–5 Dec. 1947, *Sparre 3380* (S); Curilafquén, Río Allipén, 10 Dec. 1947, *Sparre 3509* (S); Puerto Saavedra, 18 Jan. 1951, *Garaventa 6333* (CONC); Cautín, 1914, *Calvert s.n.* (BAA). X REGION (LOS LAGOS). VALDIVIA: Calafquén, 21 Jan. 1927, *Comber 1031* (K); Depto. Panguipulli, 39°34′S, 72°04′W, 15 Jan. 1976, *Marticorena et al. 439* (CONC); Panguipulli, Mar. 1927, *Hollermayer 1364* (A, BM, CAS, F, G, GH, K, MO, NY, S, UC, US, Z); Pampa Pirihuín, Panguipulli, 17 Jan. 1976, *Marticorena et al. 609* (CONC); Purulón, 39°28′S, 72°41′W, 12 Jan. 1976 (CONC); Lago Riñihue, ribera Norte, Llascahue Chico, *Marticorena et al. 253* (CONC); desague del Lago Riñihue, 13 Jan. 1976, *Marticorena et al. 288* (CONC); Paso Carirriñe, Panguipulli, 18 Jan. 1976, *Marticorena*

et al. 646 (CONC); road to Choshuenco, Panguipulli, 16 Jan. 1976, *Marticorena et al. 536* (CONC); Coñaripe–Liquiñe road, 16 km E of Panguipulli road, 31 Jan. 1978, *Solomon 4544* (MO); road to camino del los Ríos Blanco and Rañintulelfu, 39°46′S, 71°45′W, 18 Jan. 1976, *Marticorena et al. 661* (CONC); W slopes of Cordillera Pelada, 9 km W of El Mirador on La Unión–Punta Hueicolla road, 18 Feb. 1976, *Crosby 12757* (MO); Bima district, W of La Unión, Cordillera de Alerce, 10 Feb. 1938, *Eyerdam 10669* (F, NY, UC, US); La Unión, Cerro Esmeralda, Feb. 1958, *Schlegel 1525* (CONC); Calle-Calle, 30 Oct. 1896, *Buchtien s.n.* (BREM, CGE, F, G, GH, OXF, S, US, WU, Z); La Unión, Llanacacura, 22–24 Dec. 1947, *Sparre 3612* (S); Quinchirica, 1 Mar. 1942, *Hollermayer 7* (UC); Curiñanco, 7 Mar. 1948, *Sparre 4683* (S); Niebla, 2 Nov. 1957, *Santos s.n.* (VALD); estero Puente Negro, 39°58′S, 73°05′W, *Marticorena & Quezada 1671* (MO; $2n = 44$); 2 km from Enco, 17 Jan. 1976, *Marticorena et al. 585* (CONC); S of Valdivia, 2 km past road to Los Guindos, 39°40′S, 73°02′W, *Marticorena & Quezada 1672* (MO; $2n = 44$); Rio Cruces, S of Lanco, 7 Mar. 1980, *Marticorena & Quezada 1711* (MO; $2n = 44$); 1 km SE of Puente Piedra Blanca, 8 km S of Valdivia, 29 Jan. 1979, *Solomon 4550* (MO); Trumao, Valdivia, Feb. 1865, *Philippi 633a* (SGO); Amargo, Valdivia, 18 Nov. 1956, *Schmitz 108* (VALD); Valdivia, 3 Nov. 1850, *Lechler 537* (CGE, G, O); Feb. 1852, *Philippi 35* (BM, CGE, G, O, P, S, TCD); Corral, Mar. 1938, *Pérez Moreau s.n.* (RSA), 12 Oct. 1929, *Gunckel 2* (BM, F), 3 Oct. 1930; Corral–La Aguada, 8 Dec. 1934, *Gunckel 3052* (CONC); Isla Manzeras, Corral, in the fort, 20 Sep. 1932, *Junge 2498* (CONC); Corral, near San Carlos, 31 Oct. 1932, *Junge 2525* (CONC); Arrigua, Nov. 1854, *Lechler s.n.* (GH); Cerro Llifén, 40°11′S, 72°15′W, 23 Feb. 1958, *Furet 55* (CONC). OSORNO: Puyehue, 15 Jan. 1947, *Wall s.n.* (S); Dec. 1939, *Sandeman 396* (OXF); 12 km above Aguas Calientes, Parque Nacional Puyehue, 4 Feb. 1979, *Solomon 4587* (MO); N shore Lago Llanquihue, 3 Dec. 1948, *Senn 4632* (GH, MO, RSA, US); Portezuelo Desolación, Volcán Osorno, *Rudolph 4713* (VALD); La Picada, Volcán Osorno, *Sparre s.n.* (S); Golgol, 40°34′S, 71°56′W, 6 Mar. 1948, *Rudolph 4726* (VALD); Pampa Alegre, sea shore, 14 Jan. 1948, *Sparre 3967* (S); Tres Esteros, 40°41′S, 72°53′W, 15 Dec. 1940, *Rudolph 4724* (VALD); Hueyusca, 40°55′S, 73°38′W, 16 Feb. 1950, *Rudolph 4711* (VALD); San Juan de la Costa, 40°31′S, 73°24′W, 10 Feb. 1950, *Rudolph 4710* (VALD); Osorno, 15 Jan. 1885, *Philipp & Borchers s.n.* (BM); Osorno, S of Puente Rahue, 40°41′S, 73°08′W, 4 Mar. 1980, *Marticornea & Quezada 1676* (MO; $2n = 44$); 10 mi. E of ocean, road to Termas Pucatrihue and Osorno, 29 Jan. 1958, *Eyerdam 10532* (F, NY, UC, US). LLANQUIHUE: Lago Llanquihue, 6 Mar. 1897, *Dusén s.n.* (G, O); Jan. 1909, *Hicken s.n.* (G); Llanquihue, Isla Loreley, 1913, *Hosseus 45* (CORD); Frutillar Bajo, shore of Lago Llanquihue, 4 Mar. 1980, *Marticorena & Quezada 1677* (MO; $2n = 44$); between Frutillar Bajo and Frutillar Alto, 4 Mar. 1980, *Marticorena & Quezada 1678* (MO; $2n = 44$); Ensenada, Lago Llanquihue, 8 Feb. 1939, *Eyerdam & Beetle 24621* (K); 2 km N of Llanquihue, 4 Mar. 1980, *Marticorena & Quezada 1679* (MO; $2n = 44$); Los Riscos, near Lago Llanquihue, 26 Feb. 1967, *Skog 1078* (POM, US); Santa Ida, between Puerto Varas and Ensenada, Lago Llanquihue, 6 Mar. 1980, *Marticorena & Quezada 1706* (CONC; $2n = 44$), *1707* (CONC; $2n = 44$); Puerto Varas, *Hicken 87* (SI); Llanquihue, 6 Feb. 1972, *Cantino 7* (GH); Parque Nacional Pérez Rosales, 41°09′S, 72°18′W, 8 Dec. 1971, *Marticorena et al. 1926* (CONC); Saltos del Río Petrohue, Parque Nac. Vicente Pérez Rosales, 6 Mar. 1980, *Marticorena & Quezada 1708* (MO; $2n = 44$); Puerto Varas, Punta Guano, 41°09′S, 72°18′W, 20 Sep. 1971, *Weldt 1248* (CONC); Puerto Varas, 4 Feb. 1945, *Hosseus 192* (CORD); Piedra Azul, 11 Feb. 1967, *Ricardi 5287* (CONC); foot of Cerro Hornohuinco, E side of Chamiza–Lago road, 20 Jan. 1946, *Pfister 6047* (CONC); Centinela, Jan. 1948, *Sparre 4398* (S); Lago Chapo, 235 m, 41°26′S, 72°35′W, 6 Mar. 1980, *Marticorena & Quezada 1704* (CONC; $2n = 44$); between Correntoso and Lago Chapo, 6 Mar. 1980, *Marticorena & Quezada 1703* (MO; $2n = 44$); Chamiza, 41°29′S, 72°51′W, 6 Mar. 1980, *Marticorena & Quezada 1699* (MO; $2n = 44$); between Puerto Montt and Pargua, El Avellanal, 41°45′S, 73°24′W, 4 Mar. 1980, *Marticorena & Quezada 1680, 1682* (MO; $2n = 44$); Puerto Montt, 1912, *Geisse s.n.* (Z); Isla Tengo, Puerto Montt, 20 Mar. 1969, *Plowman 2604* (GH, K, US); Peulla, 1922, *Weogelt s.n.* (G), 14 Feb. 1925, *Pennell 12675* (F, GH, NY, PH); Volcán Osorno, 11 km from Ensenada–Yerbas Buenas road to ski slopes, 6 Feb. 1979, *Solomon 4599* (MO); Ensenada, Volcán Osorno, 8 Feb. 1939, *Eyerdam & Beetle 24621* (GH, NA, UC); Petrohué, shores of Lago Todos Los Santos, 6 Mar. 1980, *Marticorena & Quezada 1709* (MO; $2n = 44$); Lago Todos Los Santos, 7 Feb. 1939, *Eyerdam et al. 24591* (BH, G, GH, K, MO, NA, UC); Casa Panque, between Nahuel Huapí and Laguna Todos Los Santos, Dec. 1926, *Edwards s.n.* (BM), 3 Jan. 1939, *Hunnewell 16069* (GH); Nahuel Huapí, 29 Dec. 1929, *Stuckert s.n.* (CORD). CHILOE: 1.5 km from Chacao to Ancud, 4 Mar. 1980, *Marticorena & Quezada 1683* (MO; $2n = 44$), 10 Jan. 1975, *Marticorena et al. 36* (CONC); near Ancud, 24–28 Jan. 1932, *Macmillan & Erlanson 36* (US); Isla Buta Chaques, Golfo de Ancud, 42°17′S, 73°10′W, 17 Nov. 1968, *McFarland & Barrett 35-14* (NA); Isla Chaullín, Golfo de Ancud, 43°03′S, 73°27′W, 18 Dec. 1965, *Schallenberger & Barrett 36-9* (NA); between Paranqui and Curamo, road Chacao–Ancud, 4 Mar. 1980, *Marticorena & Quezada 1684* (MO; $2n = 44$); road Ancud–Castro, 14 Jan. 1975, *Marticorena et al. 187* (CONC); road to Dalcahue, 42°20′S, 73°42′W, 5 Mar. 1980, *Marticorena & Quezada 1696* (MO; $2n = 44$); between Estero Mechaico and Río San Antonio, Ancud–Castro road, 5 Mar. 1980, *Marticorena & Quezada 1698* (MO; $2n = 44$); Castro, Tranque Río Gamba, 5 Feb. 1957, *Ricardi & Marticorena 4020* (CONC); Castro–Chonchi road, 12 Feb. 1967, *Ricardi 5290* (CONC); near Castro, 15 Mar. 1936, *Mexia 8009* (BH, BM, F, G, K, MO, NY, S, UC, US); 4 km S of Castro to Quellón, 5 Mar. 1980, *Marticorena & Quezada 1686* (MO; $2n = 44$); Río Mollueco, Castro to Quellón, 5 Mar. 1980, *Marticorena & Quezada 1692* (MO; $2n = 44$); 3 km past Coinco Alto, Castro to Quellón, 43°01′S, 73°38′W, 5 Mar. 1980, *Marticorena & Quezada 1693* (MO; $2n = 44$); near Río Trañic, Castro to Quellón, 5 Mar. 1980, *Marticorena & Quezada 1687* (MO); Lago Natri, E side, Castro to Quellón, 5 Mar. 1980, *Marticorena & Quezada 1689* (MO; $2n = 44$); 11 Jan. 1975, *Marticorena et al. 55* (CONC); Quellón, Punta lapa en Ñadi, 12 Jan. 1975, *Marticorena & Quezada 78* (CONC); Quellón, 5 Mar. 1980, *Marticorena & Quezada 1694* (MO; $2n = 44$); San Carlos, 8 Apr. 1872, *Blake s.n.* (GH); Cucao-Quilán, 1 Jan. 1932, *Junge 1483* (CONC); Valle del Río Manao, 41°52′S, 73°32′W, 16 Mar. 1947,

Rudolph 4714 (VALD); Piruquina-Ovejería, 6 Feb. 1932, *Junge 1777* (CONC); Isla Chiloé, 1871, *Reed 85* (BM, K), 1826–1830, *King (Andersson) s.n.* (BM, K, TCD); San Carlos de Chiloé, *Née s.n.* (MA). PALENA: Bahía Tictoc, Golfo Corcovado, 43°36′S, 72°54′W, 19 Nov. 1968, *Barrett 37-17* (NA); Rolecha, 41°55′S, 72°50′W, 5 Jan. 1951, *Pfister s.n.* (CONC); Mt. Leones, Río Palena, Nov. 1923, *Werdermann 61* (BM, CAS, F, G, GH, MO, SI, UC, Z); Puerto Low, 8 Mar. 1857, *Fonch 153G* (SGO). XI REGION (AISEN). AISEN: Islas Guaytecas, Melinka, 9 Feb. 1957, *Ricardi & Marticorena 4104* (CONC); Isla Johnson, 44°22′S, 74°19′W, 12 Nov. 1947, *Behn 65* (SGO); Puerto Aisén, 17 Feb. 1945, *Looser 5161* (US); road from Puerto Aisén to Coihaique, 13 Feb. 1943, *Maldonado 126* (F, GH, U); Puerto Barroso, Peninsula Tres Montes, Golfo Tres Montes, 46°49′S, 75°16′W, 22 Nov. 1968, *Norris & Barrett 39-17* (NA); Golfo San Estéban, Fiordo Kelley, 46°55′S, 74°05′W, 28 Nov. 1972, *Hoppe 14* (RNG); Peninsula Taitao, *Nordenskiold in 17 Dec. 1920* (GOT). COIHAIQUE: Laguna Fenchik, 45°33′S, 71°47′W, 13 Feb. 1959, *Schlegel 2246* (CONC); Parque Nacional Río Simpson, Mar. 1968, *Sanguiesa s.n.* (SGO). GENERAL CARRERA: Valle León, región Lago Buenos Aires, 11 Feb. 1939, *von Rentzell 6223* (GH, MO); Lago General Carrera, Mina Silva, 46°30′S, 72°20′W, 18 Dec. 1939, *Heim s.n.* (Z); Valle del Río Soler, slopes of Cerro Piña, 47°00′S, 73°15′W, 22 Dec. 1971, *Davison F-40* (HIP). CAPITÁN PRAT: Puerto Santa Barbara, 48°04′S, 75°29′W, 1826–1830, *King s.n.* (TCD). XII REGION (MAGALLANES). ULTIMA ESPERANZA: Puerto Edén, 49°1′S, 74°28′W, 23 Jan. 1968, *Anliot 6143* (SGO); 21 Mar. 1868, *Cunningham s.n.* (K, LE); Puerto Grappler, Promontorio Exmouth, 49°25′S, 74°19′W, 6 Feb. 1879, *Ibar s.n.* (SGO); Ring Dove Inlet, 49°44′S, 74°10′W, 24 Jan. 1879, without collector (SGO #53127); Ultima Esperanza, *Gusinde 295* (GOT); Portland Bay, Midpoint Channel, 50°15′S, 74°44′W, Jan. 1956, *Tillman 55* (BM); Isla Drummond Hay, Puerto Molyneux, 50°15′S, 74°55′W, 11 Dec. 1977, *Roig 144* (HIP); Bahía Corbeta Papudo, 50°22′S, 75°19′W, 25 Nov. 1968, *Barrett et al. 42-7* (NA); Cordillera de Paine, 50°54′S, 73°00′W, Jan. 1966, *Tsujii 784* (CONC); Andean foothills, ca. 51°00′S, 72°50′W, 1961, *Anderson 18* (HIP); Cerro Castillo, Lago Toro, La Península, 51°19′S, 72°46′W, 15 Dec. 1975, *Boelcke et al. 565* (HIP, RNG); Puerto Balmaceda, Costa E Río Serrano, 51°19′S, 73°07′W, 25 Jan. 1977, *Pisano 1993* (HIP, RNG); Puerto Toro, Río Serrano, 51°24′S, 73°05′W, 17 Jan. 1977, *Moore & Pisano 1762* (HIP, RNG); Península W of mouth of Río Serrano, 23 Jan. 1977, *Moore & Pisano 1915* (HIP, RNG); Isla Diego de Almagro, 51°26′S, 75°04′W, 28 Mar. 1945, *Biese 1486* (SGO); Puerto Bellavista, 51°31′S, 73°16′W, 11 Jan. 1977, *Moore & Pisano 1628* (CONC, HIP, RNG); near Ultima Esperanza, 51°30′S, 73°00′W, *Borge 339* (GH, K, NY, S, US); Seno Ultima Esperanza, *Hicken 87* (SI); Isla Virtudes, Canal Elías, Puerto Virtudes, 51°33′S, 74°54′W, 9 Feb. 1976, *Dollenz et al. 1444* (HIP, RNG); Península Roca, Seno Resi, 51°51′S, 73°02′W, 24 Jan. 1978, *Pisano 2877* (HIP, RNG); Seno Unión, Ancón, 52°09′S, 73°02′W, 12 Jan. 1976, *Dollenz et al. 984* (HIP, RNG); Isla Long, 52°18′S, 73°38′W, 1 Feb. 1879, *Guero s.n.* (SGO); Smith Channel, Long Island, 1921, *Asplund 126* (S); Cueva del Milodón, 13 Jan. 1952, *Pfister & Ricardi 12065* (CONC); Eberhardt, 13 Apr. 1899, *Borge 344* (GH, MO, NY, S, US), *Donat 384* (BM, CAS, F, GH, K, MO, NY, Z). MAGALLANES: Isla Riesco, Mina Elena, 53°02′S, 72°45′W, 30 Apr. 1940, *Santesson 751* (K); Estancia Cerro Pinto, N side of Skyring Water, 16 Dec. 1968, *Goodall 1938* (NA, RNG); Skyring, 1 and 2 Feb. 1879, without collector (SGO #53128); Seno Otway, Punta Prat, *Seibert 2255* (M); Seno Otway, Punto Otway, 9 Feb. 1888, *Lee s.n.* (US); Río Caleta, Seno Otway, 53°09′S, 71°32′W, 5 Jan. 1979, *Cárdenas 17* (HIP, MO); Isla Engelfield, Seno Otway, 53°05′S, 71°51′W, 24 Feb. 1979, *Pisano & Cárdenas 4926* (HIP, MO, RNG, SGO); Seno Otway to Punta Arenas, 1 Mar. 1945, *Biese 1250* (F, GH); Fiordo Silva Palma, Angostura Titus, 53°26′S, 71°44′W, 9 Jan. 1973, *Pisano 3825* (HIP, MO, RNG); Borja Bay, Straits of Magellan, 53°32′S, 72°29′W, Feb. 1882, *Coppinger s.n.* (K); Ballena Cove, S point of Isla Carlos III, 53°35′S, 72°22′W, 18 May 1973, *Goodall 5* (NA); Península Brunswick, Bahía del Aguila, 53°47′S, 71°01′W, Nov. 1975, *Samsing s.n.* (HIP); Bahía del Indio, Lote San Isidro, Río Yumbel, 53°48′S, 71°00′W, 1 Mar. 1973, *Pisano 4024* (HIP, MO, RNG); Puerto San Antonio, 53°53′S, 70°54′W, 1826–1830, *Anderson et al. s.n.* (W), *King s.n.* (TCD); Fuerte Bulnes, 53°35′S, 70°56′W, 13 Mar. 1970, *Pisano 2501* (CONC, HIP, MO, NA), 25 Apr. 1951, *Pisano s.n.* (MO; $2n = 44$); junction roads to Puerto Hambre and Fuerte Bulnes, 53°40′S, 70°55′W, 9 Mar. 1979, *Solomon & Solomon 4691* (HIP, MO); Puerto Edén, *Anliot 6143* (SGO); Port Gallant, 1838–1840, *Hombron s.n.* (P); 1838, *d'Urville s.n.* (TCD), 11 Feb. 1877, *Savatier 134* (K, P, RSA); Port Famine, 1826–1830, *King 75* (BM, CGE, K, TCD), 1834, *s.n.* (U, W); 1838–1840, *le Guillou 41* (P, TCD); Shipton Glacier, Bay of Mountains, 53°55′S, 72°01′W, 13 Feb. 1976, *Barclay 6* (US); Isla Dawson, 54°00′S, 70°45′W, 12 Mar. 1896, *Dusén s.n.* (P), 12 Mar. 1896, *Nordenskjold 657* (O); Isla Dawson, Harris Bay, 25 Feb. 1908, *Skottsberg 174* (S); Islote Offing, Isla Dawson, *Pastore in 7 Feb. 1921* (SI #4842); Isla Capitán Aracena, Bahía Morris, 54°14′S, 71°01′W, 8–9 Dec. 1971, *Moore 2745* (BAB, NA, RNG); Magellan Straits, 1852, *Andersson 330* (MO), *Handisyd in July 1690* (BM, Sloane Herb.), 1826–1830, *King s.n.* (BM, F). TIERRA DEL FUEGO: Río Santa María, 60 km by Camino Sur, 53°43′S, 69°58′W, 10 Feb. 1972, *Pisano 3517* (HIP, MO); Canal Whiteside, Puerto Yartou, 53°50′S, 70°18′W, 12 Nov. 1941, *Santesson 1697* (K); S side of Bahía Inútil, 2 km E of Puerto Yartou, 53°52′S, 70°07′W, 13 Nov. 1971, *Moore 2439* (K, RNG); Bahía Inútil, 1905, *Crawshay s.n.* (BM); Isle Grawe, *Skottsberg 195* (W); N. Esperanza, *Goteborg 298* (LE, M, W). ARGENTINA. NEUQUEN: Hua-Hum at Lago Lacar, *Dawson & Schwabe 2359* (BAA, BAB, MO); San Martín de Los Andes, Dep. Lacar, 10 Feb. 1957, *Hunziker 6909* (BAB); Cascada Maipú, San Martín de Los Andes, 12 Dec. 1946, *Dawson 1358* (BAA, BAB); cerros N of San Martín de Los Andes, 10 Dec. 1946, *Dawson 1257* (BAA, BAB); Lago Lolog, 12 Mar. 1926, *Comber 813* (K), 2 Feb. 1947; Lago Espejo, 7 Feb. 1940, *Cabrera 5976* (NY); Pichi Freful, 17 Feb. 1968, *Cabrera & Crisci 19206* (CONC); Puerto Correntoso, 5 Feb. 1934, *Parodi 11679* (BAA); road Bariloche–Correntoso, 20 Mar. 1939, *Cabrera 5044* (F, GH, NY); Isla Victoria, Parque Nac. Nahuel Huapi, 9 Jan. 1946, *Boelcke 1781* (BAA); Isla Victoria, Zoological Station, 31 Mar. 1946, *de Barba 1122* (LIL); Lago Epilaufquén, 4 Feb. 1948, *Dawson & Schwabe 2392* (BAA); Lago Paimún, 5 Feb. 1948, *Dawson & Schwabe 2507* (BAA); Quetrihue, 14 Jan. 1951, *Diem 1774* (BAA, BAB, SI); Villa La Angostura, 30 Mar. 1980, *Diem 3615* (MO; $2n = 44$); Lago Tromén, 19 Feb. 1941, *Pérez Moreau s.n.*

(RSA); Laguna Currilafquén, Feb. 1942, *Pérez Moreau s.n.* (RSA); Lago Epulafquén, Feb. 1942, *Pérez Moreau s.n.* (LIL, RSA); Lago Espejo Grande, 2 Mar. 1941, *Pérez Moreau s.n.* (RSA); NE of Lago Quillén, 30 Jan. 1963, *Valla et al. 3121* (BAA, MO); Lago Nahuel Huapi, 14 Feb. 1980, *Ajioka & Vicksy s.n.* (MO); Villa Puerto Manzano, 16 Jan. 1966, *Walter & Walter 708* (B); Brazo Huemul, Lago Nahuel Huapi, 20 Feb. 1979, *Solomon & Solomon 4622* (MO); valley Río Machete, Lago Nahuel Huapi, Feb. 1940, *Pérez Moreau s.n.* (RSA); Bariloche, Isla Victoria, Puerto Pampa, 800 m, 12 Mar. 1934, *Spegazzini s.n.* (BAB, MO). RÍO NEGRO: Puerto Blest to Los Cántaros, 21 Dec. 1944, *Meyer 7431* (DS, MO, NY, S); Puerto Blest, 21 Dec. 1944, *Meyer 7430* (CAS, LIL, MO, NY, S); Puerto Blest, paso de Los Raulies, 20 Jan. 1940, *Pérez Moreau s.n.* (RSA); 5 km below Puerto Blest, 8 Mar. 1914, *Hosseus 1071* (CORD); Puerto Blest, 25 Jan. 1930, *Offermann s.n.* (BAA); Cerro Tronador, 1,200 m, 21 Feb. 1979, *Solomon & Solomon 4639* (MO); road to Tronador, *Castagnet 84* (LP); Lago Mascardí, 8 Feb. 1940, *Pérez Moreau s.n.* (RSA); between Llao-Llao and Bahía López, 23 Mar. 1955, *Fabris 1134* (F); Llao-Llao, *Crespo 161* (SI); Feb. 1940, Bahía López, *Castagnet 54* (LP); Lago Moreno Este, 10 Feb. 1914, *Hosseus 105* (CORD); Laguna Frías, 20 Dec. 1944, *Meyer 7384* (LIL); Lago Frías, Puerto Alegre, 4 Mar. 1941, *Pérez Moreau s.n.* (RSA #45319); Lago Frías, road to Ventisquero Frías, 16 Jan. 1940, *Pérez Moreau s.n.* (RSA); valley of Río Frías, 5 Jan. 1946, *Boelcke 2063* (BAA); Lago Guillermo, 11 Jan. 1945, *Meyer 7789* (UC); Lago Hess, 10 Jan. 1945, *Meyer 8120* (LIL); Península Los Luizos, Dep. Bariloche, 4 Feb. 1914, *Muriey & Rothkugel 73* (BAB); bank of Lago Gutiérrez, Jan. 1957, *Nicora 6450* (BAA); Pampa Linda, 16 Jan. 1943, *Pérez Moreau s.n.* (RSA); Lago Philippi, 14 Feb. 1943, *Pérez Moreau s.n.* (RSA); Lago Martín, 28 Feb. 1941, *Pérez Moreau s.n.* (RSA); Paso Pérez Rosales, Nov. 1941, *Rodríguez s.n.* (RSA); Lago Nahuel Huapí, road to Cerro V. López, 19 Feb. 1979, *Solomon & Solomon 4610* (MO); Puerto Nuevo, Lago Nahuel Huapí, 29 Mar. 1934, *Ljungner 964* (NY); Cascada de Los Alerces, 13 Feb. 1965, *Vuilleumier 202* (GH); El Bolsón, Feb. 1945, *Corvetto 3248* (BAB); near Bariloche, 1 Dec. 1965, *Walter & Walter 479* (B); Bariloche, Colonia Suiza, 12 Mar. 1945, *de Barba 354* (A, NY, SI, UC); region of San Carlos de Bariloche, 1963, *de Lesse 7* (P); Parque Nacional Nahuel Huapi, 5 Jan. 1946, *Boelcke 2063* (K). CHUBUT: Epuyén, Feb. 1937, *Lahitte s.n.* (BAB); Futaleufú, 7 Dec. 1967, *Constance et al. 4157* (BAA); Los Rápidos, Río Futaleufú, 21 Jan. 1945, *Castellanos s.n.* (F, LIL); Colonia 16 de Octubre, Futaleufú, Jan. 1948, *Tschudi s.n.* (LIL); Parque Nacional de Los Alerces, Lago Futalaufquén, 6 Feb. 1955, *Burkart 19851* (MO); Lago Cisne, 10 Feb. 1944, *Pérez Moreau s.n.* (RSA); Valle de las Plumas, Lago General Paz, 2 Mar. 1903, *Gerling 102* (Z); Lago Menéndez, P.N. Los Alerces, Feb. 1944, *Pérez Moreau s.n.* (RSA); Puelo, Dep. Cushamen, Jan. 1939, *Lahitte s.n.* (BAB); Lago Puelo, 14 Feb. 1940, *Pérez Moreau s.n.* (RSA); Anexo Pueblo, 15 Feb. 1961, *Lourteig & Buchinger 194* (P); Cordillera, Jan. 1901, *Burmeister s.n.* (BAB); cerros N of La Comisaría, Feb. 1942, *Pérez Moreau s.n.* (RSA); Los Alerces, 9 Jan. 1948, *Soriano 2885* (BAA). SANTA CRUZ: Glaciar Spegazzini, 50°15′S, 73°15′W, 19 Mar. 1968, *Anliot 6016* (SGO), 19 Jan. 1967, *Boelcke et al. 12612* (BAA, BAB, CONC, P, SI); Santa Cruz, 14 Nov. 1975, *Boelcke 16403* (BAA); S shore of Lago Argentino, 1907–1908, *Furlong 98* (GH, NY, US); Cerro Buenos Aires, near Moreno Glacier, 5 Jan. 1959, *James 669* (BM, DS); Valle León, region of Lago Buenos Aires, 11 Feb. 1939, *von Rentzell 6223* (SI); Mayo Glacier, Cerro Mayo, 14 Feb. 1959, *James 2272* (BM, DS, SI); Punta Bandera, Lago Argentino, 1900–1901, *Prichard s.n.* (BM, K, NY); in front of Ventisquero Moreno, 220 m, 18 Dec. 1950, *Sleumer 1151* (US); Lago Argentino, Glaciar Ameghino, 28 Mar. 1953, *Vervoorst 4785* (MO). TIERRA DEL FUEGO: Río Grande, *Cordini s.n.* (RSA); Isla de Los Estados, 64°00′W, 54°45′S, *Webster s.n.* (G); Estancia Harberton, cultivated from bush said to have been brought from the western Beagle Channel by Thomas Bridges, 25 Mar. 1968, *Goodall 1677* (NA, RNG, UC, US), 8 Nov. 1968, *1836* (NA, RNG, UC, US); Harberton Garden (cultivated), 24 Jan. 1966, *Goodall 298* (LP, RNG).

Representative naturalized specimens. ARGENTINA: San Javier to Villa Nougues, Tucumán, 12 June 1945, *Ortiz s.n.* (NY); road Santa Lucía–Tafí del Valle, 20 Sep. 1944, *Torrent s.n.* (NY). BOLIVIA: Unduavi, La Paz, 8 Apr. 1946, *Llanos 239* (BAB); Chapare, Cochabamba, June 1966, *Cárdenas 6279* (LIL), Apr. 1961, *3969* (LIL); Incachaca, Apr. 1938, *Cárdenas 688* (LIL), Mar. 1941, *2248* (LIL); Toralapa, 18 Dec. 1973, *Cárdenas 3753* (LIL); Ayopaya, Dec. 1935, *Cárdenas 3369* (LIL); Carrasco, Sehuenka, 1964, *Cárdenas 6153* (LIL). COLOMBIA: Macizo de Bogotá, 10 Apr. 1946, *Schultes 7275a* (COL). KENYA: Mt. Kenya forest, 5 Jan. 1967, *Perdue & Kibuwa 8416* (K); Nyeri, 16 Apr. 1971, *Wandumbi School 757* (K). MEXICO: Orizaba, Veracruz, July 1855, *Botteri 1047* (K). MALAYA: Cameron Highlands, 1 Apr. 1976, *T. & P. 612* (K). RWANDA: Kinigi, 5 Aug. 1977, *Runyinga 724* (LG). TANZANIA: Jaegstal, 21 Apr. 1971, *Mshana 170* (K); 2 km E of Lushoto, 26 Dec. 1966, *Semsei 4176* (K). U.S.A. HAWAII: Hawaii, Upper Waiakea Forest Preserve, 580 m, 26 July 1983, *Wagner et al. 4847* (BISH); Hawaii National Park, *Fagerlund & Mitchell 87* (BISH); Volcanoes National Park, Crater Rim Drive, 16 Apr. 1978, *Fosberg 57479* (BISH); near Kilauea Crater, *Degener 1588* (BISH); near Volcano House, 3,900 ft., 1 Sep. 1937, *Neal 946* (BISH); Kauai, Kokee State Park, 3,500 ft., 24 Apr. 1968, *Herbst 1075* (BISH).

Fuchsia magellanica is separated from the Brazilian members of section *Quelusia* by 1,000–1,500 km. Yet it is remarkably similar to those species morphologically and can be best distinguished by its elongated ovary and fruit, relatively long petioles (usually over ¼ the length of the blade), and more dentate leaf margins, which are sometimes shallowly lobed between the teeth. *Fuchsia magellanica* lacks the long, drooping branches of some of the lianoid species from Brazil, and it generally grows as an upright shrub. In cultivation it can also reach treelike proportions and is considered the hardiest (most frost-resistant) of all *Fuchsia* species.

A number of different species and varieties have been recognized by others for what is considered here to be a monotypic species. Two different color varieties have been named for plants that lack the typical red coloration of the floral tube, sepals, leaf

veins, and petioles. One, *F. magellanica* var. *molinae*, comes from the island of Chiloé; the other, *F. magellanica* var. *eburnea*, is from the southern Magallanes Region of Chile. Similarly pale-colored plants are also known from Corral, Prov. Valdivia, Chile (*Gunkel 2133*, GH). All of these plants occur sympatrically with red-flowered populations of *F. magellanica* and probably result from minor recurring mutations on pigmentation.

Munz (1943: 9) thought that plants from the southern part of the range, which he called *F. magellanica* var. *typica*, had consistently smaller leaves and flowers than those from the north, but this is clearly not the case. Large-leaved plants occur throughout the range of the species. James Solomon (pers. comm.) examined many local populations in Chile and Argentina and found that individuals growing in the sun usually have smaller leaves and flowers than those nearby in shadier sites. Similarly, clines in leaf size and texture occur along climatic gradients, such as that along the shores of Lago Nahuel Haupi in Argentina. The vegetation in that area becomes increasingly xeric from west to east, and plants of *F. magellanica* respond to this gradient by developing lower, more compact plants with smaller, thicker leaves.

Populations of plants with small, densely packed leaves are common on the island of Chiloé, where high levels of humidity predominate throughout the year. Larger-leaved individuals also occur together with these variants. Some of the phenotypic variants of *F. magellanica* may also be genetically determined, as they are known to maintain their distinctive characteristics under uniform growing conditions. In horticultural circles, there has been a strong tendency to assign varietal names to some of these strains.

In this treatment, I am not recognizing any varietal or subspecific taxa under *F. magellanica*, because it is apparent that a great deal of local variation exists over the broad geographical range of the species, without any clear geographical correlations. The species is cytologically uniform, with over 40 populations counted with $2n = 44$. Since most of the present range of the species, south of 44°S latitude, was completely glaciated during the major glacial advances of the Pleistocene (Vuilleumier, 1971), there has probably been very little time for populations to diverge in the southern part of the range.

In his *Flora of Tierra del Fuego*, Moore (1983) cited localities of *F. magellanica* from as far south as the Beagle Channel at 55°S, and west to Staten Island, at 64°W. Collections from these areas were made in the past century, however, and it is unlikely that the species occurs there naturally today. According to D. Moore (pers. comm.), the introduction of goats on Staten Island early in the last century and the activities of Europeans in the vicinity of the Beagle Channel during the past 100 years have badly deteriorated the woody vegetation of these areas.

On the drier, Argentinian side of the Andean Cordillera, *F. magellanica* occurs natively as far north as the Lago Quillén, at 39°30′S. Northwards, the mountains become increasingly arid. On the Pacific side of the Andes, native populations are found as far north as Concón (32°50′S), just north of Valparaíso. These populations grow close to the coast, along streams in wooded ravines. Looser (1928) found native populations of *F. magellanica* east of Santiago (33°30′S), in the Quebrada de Peñalolén, between 1,450 and 1,750 m, and Navas (1976) reported the species from the nearby Quebrada de Macul.

The northernmost extension of *Fuchsia magellanica* barely overlaps with the southernmost populations of the xeromorphic *F. lycioides* (sect. *Kierschlegeria*) in the vicinity of Concón, north of Valparaíso, Chile. A number of specimens collected in this area during the last century are morphologically intermediate between the two species and may represent interspecific hybrids (see Appendix).

9. Fuchsia regia (Vellozo) Munz, Proc. Calif. Acad. Sci. IV. 25: 13, pl. 1, fig. 5, 1943. *Quelusia regia* Vellozo, Fl. Flum. 149. 1829; Icon. 4: tab. 6. 1831. LECTOTYPE: The illustration in Tab. 6, Volume 4 of the *Icones* of *Flora Fluminensis*. Vellozo stated for the type locality: "in the Pharmacopolitan Alps on the way to the town of Cunha," which is located between Paraty and Cunha, in the Serra da Bocaina, near the São Paulo–Rio de Janeiro border, Brazil. According to Borgmeier (1937), Vellozo collected in this area between 1779 and 1787, and the original illustrations were made in the field from live plants.

Erect to generally scandent or climbing shrubs 0.5–5 m tall, or lianas up to 15 m high in trees. Branchlets wine purple, glabrous to puberulent, rarely densely pilose; main branches ascending in small plants, decumbent to drooping and 1–6 m long in large ones. Leaves opposite, or in whorls of 3, 4, or rarely 5, firmly membranous to coriaceous, (narrowly) elliptic-ovate to ovate, 20–140 mm long, 8–70 mm wide, apex acute to acuminate, base acute to rounded, glabrous to pilose on both

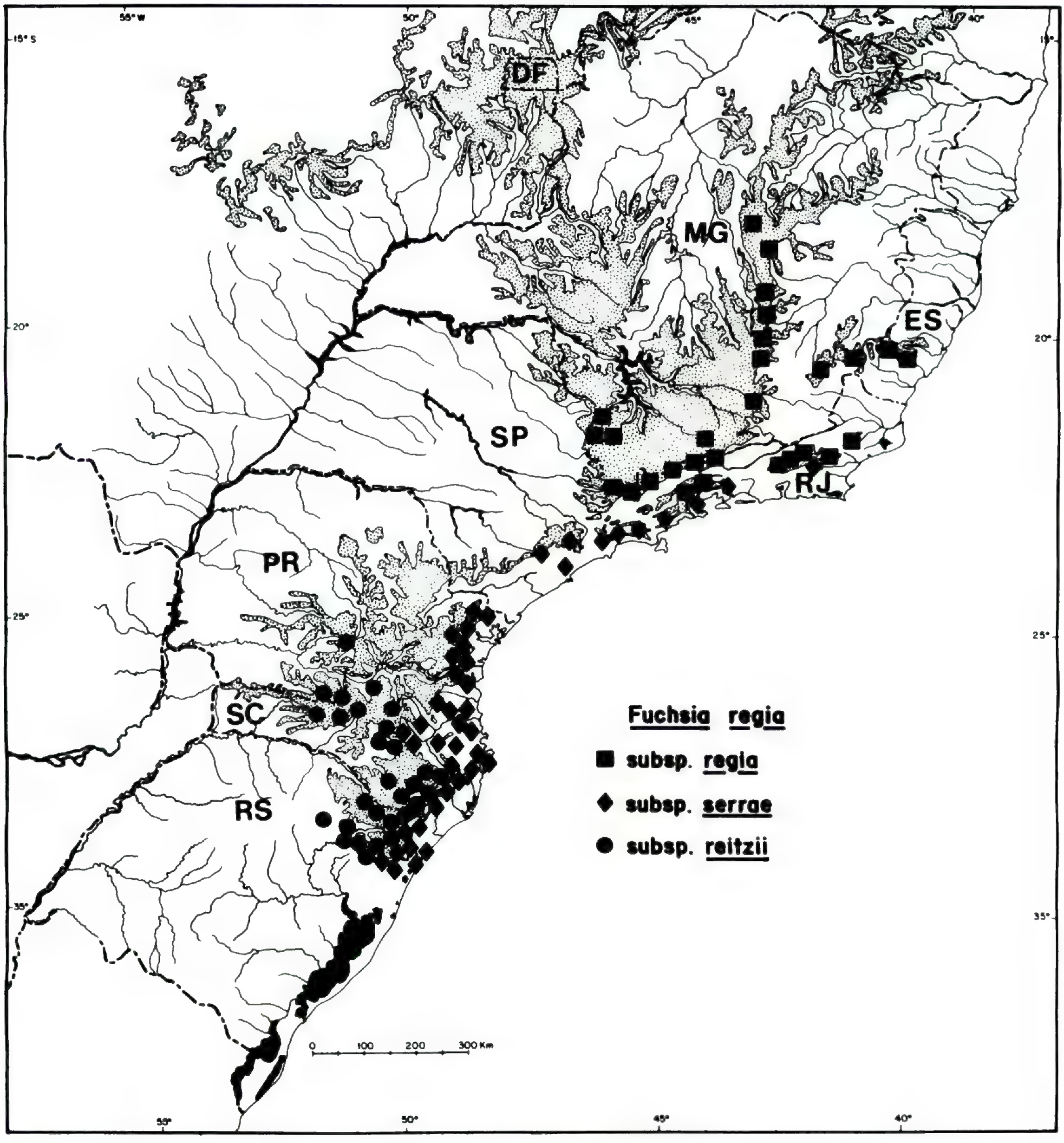

FIGURE 15. Native distributions of the three subspecies of *Fuchsia regia*. Contours higher than 800 m are indicated by the stippled areas. Capital letters are Brazilian state abbreviations. (See caption of Fig. 5.)

surfaces; margin entire to gland-serrate, secondary veins 4–10 per side. Petioles 1–3 mm thick, 3–35 mm long. Stipules triangular, membranous to thick-stubby, 0.8–3 mm long, 0.4–3 mm wide, adjacent ones sometimes fused, usually recurved with age, ephemeral to persistent. Flowers solitary or rarely in pairs in upper leaf axils; pedicels pendulous, 10–55 mm long, usually wine red. Ovary oblong, 5–12 mm long, 2–4 mm wide. Floral tube cylindrical-fusiform, 5–16 mm long, 3–7 mm wide, glabrous to puberulent or pilose outside; nectary smooth or lightly ridged, 2.5–8 mm high. Sepals 15–45 mm long, connate at the base for 3–14 mm; free lobes 3–9 mm wide at base, spreading to recurved or reflexed at anthesis. Tube and sepals red or rose. Petals purple, obovate to spathulate, 10–25 mm long, 8–16 mm wide. Filaments red-purple, 25–45 mm and 20–38 mm long; anthers oblong, purplish, 2–5 mm long, 1–2 mm wide. Style glabrous to pubescent in lower ½; stigma clavate, 2–6 mm long, 1–2 mm wide, exserted 8–25 mm beyond the anthers. Berry oblong, ellipsoid or globose, 10–27 mm long, 9–13 mm thick, dark purple when ripe; seeds tan, oblong to narrowly

triangular, laterally compressed, 1.6–2.5 mm long, 1–1.6 mm wide. Gametic chromosome numbers $n = 22, 44$.

Distribution (Fig. 15). This is the most widely distributed species of *Fuchsia* in Brazil, occurring in the states of Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul from 18°20′S to 29°30′S. Most common between 700 and 2,000 m, on the upper, wettest slopes of ranges such as the Serra do Mar, Serra Geral, Serra da Mantiqueira, and Serra do Espinhaço. *Fuchsia regia* subsp. *reitzii* is associated with the *Araucaria* forests of the southern planalto from Paraná to Rio Grande do Sul. Plants occasionally occur as high as 2,400 m on Mt. Itatiaia and at sea level in coastal restingas of Santa Catarina and Rio Grande do Sul. Flowers mainly from October to April.

This is the most variable of the Brazilian species of sect. *Quelusia*. Three distinct and largely allopatric series of populations can be recognized based on differences in several floral and vegetative characters. They intergrade in areas where their ranges overlap, and the presence of octoploid populations in some or all of the populations sampled in each series is unique in the genus. For these reasons, the different series are treated here as subspecies of *F. regia*.

KEY TO THE SUBSPECIES OF *FUCHSIA REGIA*

1a. Sepals strongly connate above the point of insertion of petals and stamens, joined for more than ⅓ of their total length, the free lobes generally recurved; stipules crassate and persistent, giving a nodose appearance to young stems ..... 9b. subsp. *serrae*

1b. Sepals slightly connate at the base, joined for less than ¼ of their total length, the free lobes spreading; stipules membranous or thickened only at the base and young stems not apparently nodose.

2a. Leaves in whorls of 3–5, membranous, tertiary venation conspicuous; margins gland-serrulate and petioles mostly shorter than 10 mm; floral tubes 5–10 mm long, sepals 17–28 mm long ..... 9c. subsp. *reitzii*

2b. Leaves mostly opposite or ternate, subcoriaceous, tertiary venation not conspicuous; margins entire or gland-denticulate and petioles mostly longer than 10 mm; floral tubes 10–16 mm long, sepals 24–45 mm long ..... 9a. subsp. *regia*

9a. Fuchsia regia (Vellozo) Munz subspecies **regia.** *Fuchsia regia* (Vandelli) Munz var. *typica* Munz, Proc. Calif. Acad. Sci. IV. 25: 13. 1943. Vellozo's type illustration shows a plant with narrowly ovate-lanceolate leaves in pairs and threes, and flowers with very shortly connate, long sepals. These characters correspond to the northernmost subspecies, which reaches as far south as the type locality in northern São Paulo state. Figure 16.

Fuchsia integrifolia Cambessèdes in St. Hilaire, Fl. Bras. Merid. 2(17): 273. 1830. TYPE: Brazil. Minas Gerais: "Serra da Caraça, near city of Villa Rica (Ouro Preto) and near São Gabriel," 1819, *Auguste de Saint Hilaire C¹80* (holotype, P, with two different branches, the one to the left the type and tagged as C¹ 80, the one to the right with a tag stating "Serra da Caraça," photograph at F; isotypes, P—again with two different branches, the one to the left numbered C¹ 80, F #1008268 "ex P," RB).

Fuchsia pyrifolia K. Presl, Symbol. Bot. 2: 19, tab. 65. 1834. TYPE: Brazil, "ad Rio Janeiro," *Presl?* (holotype, PRC—445/a).

Shrubs 0.5–5 m tall, occasionally erect but usually scandent, or lianas to 15 m high in trees. Branchlets generally glaucous and wine purple, occasionally loosely to densely pilose, older plants with long hanging branches to 5 m long. Leaves opposite, or in whorls of 3 and 4, subcoriaceous, elliptic to lance-elliptic or ovate, 40–140 mm long, 10–50(–70) mm wide, apex acute to acuminate, base acute to cuneate or rounded, sublustrous green and glabrous to pubescent above, veins often reddish-tinged, paler green and glabrous to pilose below, sometimes with tufts of pilose hairs at the base of the lower midvein; margin subentire to remotely gland-denticulate, secondary veins 6–9(–10) per side. Petioles stout, 2–3 mm thick, canaliculate above, (6–)10–28 mm long, wine purple. Stipules triangular, membranous or thickened at the base, ± recurved, 0.9–2(–3) mm long, 0.5–1.8 mm wide, adjacent ones sometimes fused, the base usually persistent but the tip deciduous. Flowers solitary in upper leaf axils; pedicels 22–55 mm long, pendulous. Ovary cylindrical, 6–11 mm long, 3–4 mm thick. Floral tube narrowly to broadly cylindrical-fusiform, 10–16 mm long, 4–6 mm wide, glabrous to subpilose outside; nectary smooth to ridged, 5–8 mm high. Sepals 24–45 mm long, narrowly lanceolate, connate at the base for 3–7 mm; free lobes 4–9 mm wide at base, spreading at anthesis. Tube and sepals red to rose. Petals violet, obovate, 13–22 mm long, 10–16 mm wide. Filaments red-purple, 25–44 mm and 23–38 mm long; anthers oblong, 3–5 mm long, 1.5–2 mm wide. Style glabrous to pilose in lower half; stigma red, narrowly clavate, 3.5–6 mm long, 1.2–1.6 mm thick, exserted 10–27 mm beyond the anthers when fully extended. Berry oblong-ellipsoid, purple when ripe, 20–25 mm long, 9–12 mm thick; seeds

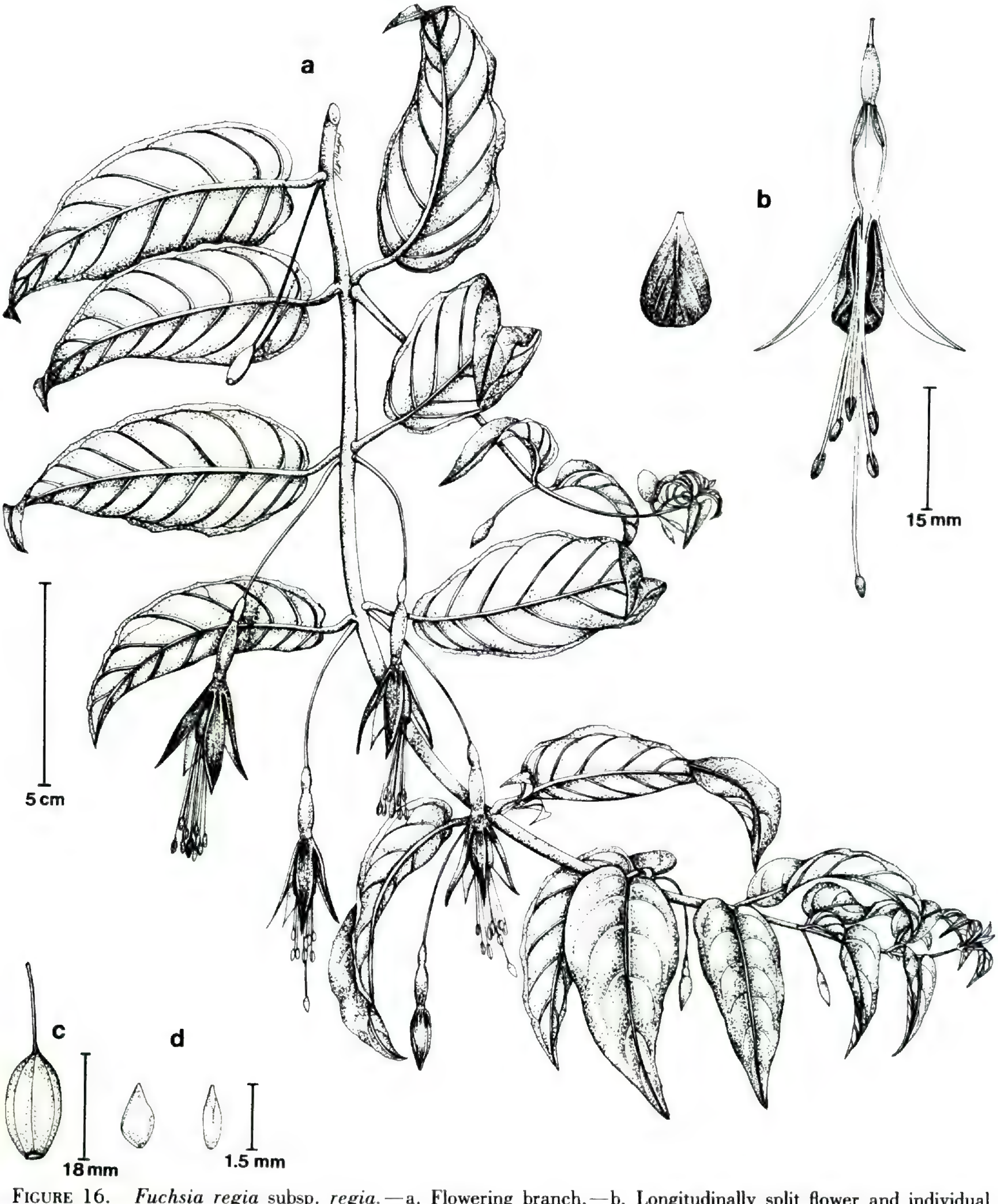

FIGURE 16. *Fuchsia regia* subsp. *regia*.—a. Flowering branch.—b. Longitudinally split flower and individual petal.—c. Slightly immature berry.—d. Seed from (c) in two lateral views. From *Ramamoorthy 683-2*.

1.8–2.8 mm long, 1.2–1.8 mm wide. Gametic chromosome numbers $n = 22, 44$.

Distribution (Fig. 15). In montane cloud forests of the Serra do Mar, Serra do Caparaó, Serra do Espinhaço, Serra da Caraça, Serra da Mantiqueira, Serra da Bocaina, and other subsidiary mountain ranges in Espírito Santo, Minas Gerais, Rio de Janeiro, and northern São Paulo states, 1,000–2,400 m. Flowering mainly from October to April.

Additional specimens examined. BRAZIL. ESPÍRITO SANTO: Pico de Forno Grande, Mun. Castelo, *Brade 19275* (M, RB); km 1 of Domingos–Gerhardt road, Pedra Azul to Domingo Martins, 1,000 m, *Pereira 450* (UEC). MINAS GERAIS: Carangola, Serra da Gramma, *Chase 9579* (US); *Kuhlmann 137* (RB); *Mexia 4278* (A, BM, F, G, GH, MO, NY, UC, US); Serra da Gramma, trail to Araponga,

Mexia 4326 (A, BH, BM, F, G, K, MICH, MO, NY, P, PG, S, U, UC, US, Z); Araponga, *Kuhlmann 33934* (RB); Alto Caparaó, Tronquieras to Vale Verde, *Souza & Marcia 85* (HBR, RB, US); Tronquieras, Alto Caparaó, *Berry et al. 4543* (MO, RB; $n = 22$); Vale Verde, Caparaó, *Hatschbach & Ahumada 31445* (MBM); Pico da Bandeira, close to Caparaó, 1,500–1,600 m, *Shepherd et al. 5769* (MBM); Macieiras to Fazendinha, Serra Caparaó, *Lanna 32* (MO); Serra de Macieiras, Caparaó, *Moreira 47* (R); Rancho das Três Barras, Serra Caparaó, *Santos & Campo in 26 June 1950* (RB); Caparaó Velho, *Torgo 30* (HB); Serra da Caraça, *Mello Barreto 7157* (F); *Gounelle in Feb. 1889* (P); Caraça, Tanquinhos, *Grandi & Tales 165* (BHCB); Ouro Preto, *Berry et al. 4551, 4552* (MO, RB); *Cochran 29191* (R, US); *Claussen s.n.* (P); *Macedo 3078* (MO, US); Morro do Baú, Ouro Preto, *Badini 25103* (OUPR); Campo Grande, Mun. Ouro Preto, *Badini 20113* (OUPR); Morro da Queimada, Ouro Preto, *de Lima et al. 1369* (MO); Camarinhas, *Godoy #106 Esc. Pharmacia* (OUPR); Fonte dos Amores, Mun. Poços de Caldas, *Mello Barreto 11078* (BHCB); Poços de Caldas, *Barros 667* (SP); *Hoehne 2703* (SP); Poços de Caldas, Caixa d'Agua, *Santos 5734* (DS); road Botelho–Poços de Caldas, *Pabst 9500* (HB, MBM); Caldas, *Araujo s.n.* (R #41685); *Lindberg 346, 347* (S); *Mosén 472* (MO, P, S), *473, 4509* (S); *Regnell 148* (R), *Regnell in 1862* (BR, K, M, NY), *in 1864–1865* (LE, O, R), *in 1846* (P, W), *in 1867, in 1871* (S); Caldas, Ribeirão dos Bugres, *Mosén 474* (S); Serra do Cipó, *Irwin et al. 20542* (F, K, NY, US); Serra do Cipó, road to Conceição, *Mello Barreto 8855* (NY, R), *9204* (BHCB), *9254* (F); São João da Chapada, *Irwin et al. 28499* (MO, NY, US); Pico do Itambé, E slopes, *Anderson et al. 35830* (MO, NY, RB, US); Serra de Itabira, *Sello s.n.* (LE, S); Rio Acima, Fazenda Gandarela, *Duarte 926* (HB); Oiro Branco, *Weddell 1553* (P); Morros do Lobo, no coll. *647* (M); Passa Quatro, Itaguaré, *Brade & Araujo 1981* (MO); *Vidal 2120* (R); Fazenda dos Campos, Passa Quatro, *Vidal 1789* (R); Cidade Azul, Serra da Mantiqueira, Sapuçai-Mirim, *Kuhlmann 2915* (SP); Delfim Moreira, 7 km from Isópolis, *Mattos 15397* (SP); São Francisco dos Campos, Alto do Morro do Cabrito, divisória SP-MG, Mun. Delfim Moreira, *Kuhlmann 2466* (SP); Aguas de Prata, 3 km NW of Cascata, road to São Roque da Fatura, *Mattos & Mattos 14192* (SP); Aiuruoca, Serra do Papagaio, *Silveira in Nov. 1897* (R #102490); Serra do Picú, *Schwacke in 10 Dec. 1886* (R); Fazenda Santa Alda, Teixeira Soares, *Sampaio in 1944* (R #41684); Fazenda São Benito, Serra da Mantiqueira, *Vidal in Apr. 1949* (R #41684); Hermilio Alves, Cacholina, *Duarte 2384* (MO); Serra do Itacolomi, Mun. Ouro Preto, *Badini 23131, 25273* (OUPR); *Barbosa 1058* (R); *Berry et al. 4544* (MO, RB; $n = 22$), *4545* (MO, RB); *Claussen 7* (F, LE, P, RSA); *de Lima 1307* (MO, RB); *Macedo 2774* (MO, NY, S); *Magalhaes Gomes 1744* (OUPR); no locality, *Ackermann s.n.* (BR); *Claussen in June 1840* (BM, BR, F, G, GH, OXF); *Miers 2433* (US); *Langsdorff s.n.* (LE); *Regnell in 1842* (P, U); *Riedel 62* (P); *St. Hilaire B*[1] *200* (P); *Velho 4555* (BM, K); *Widgren in 1845* (BR, US). RIO DE JANEIRO: Monte Estrela, *Mieire 553, s.n.* (LE); Serra da Estrela, Petrópolis, *Goés 75* (RB); Serra da Estrela, near Cachoeira de Véu da Noiva, Correias, Fazenda do Sampaio, *Pabst in 5 Jan. 1964* (HB); Petrópolis, Correias, Serra dos Órgãos, Fazenda Bom Fim, *Carauta 693* (MO); Serra de Petrópolis, *Duarte 1163* (RB); *Duarte & Pereira 4669* (RB); Vale das Videiras, Mun. Petrópolis, *Martinelli & Gurken 508* (RB); *Martinelli et al. 169* (MO); Vale das Videiras, Morro da Cuca, *Jouvin 3* (RB); Petrópolis, road to Fazenda Inglesa, *Rocha & Silva 14* (R, US); Itaipava, Vale de Cuiaba, Mun. Petrópolis, *Martinelli et al. 1641* (RB); 26 km from Itaipava, road to Teresópolis, *Berry et al. 4419* (MO, RB; $n = 44$); Petrópolis–Teresópolis, *Lutz 1734* (R); Petrópolis–Quitandinha, *Lutz 1356, 1577* (R); Petrópolis, Araras, Morro Bolo de Milho, *Sucre & Braga 2808* (RB), Petrópolis–Itamaraty, *Glaziou 8676* (R); Pati do Alferes, Mun. Petrópolis, *Plowman & Martinelli 10125* (F); Petrópolis, *Glaziou 8676* (P); Alto do Imperador, Petrópolis, *Preston s.n.* (K); Serra dos Orgãos, Mun. Petrópolis, *Martinelli et al. 1749* (RB); Represa dos Guinle, Mun. Teresópolis, *Gentry & Peixoto 907* (MO, RB); Teresópolis, Parque Nacional Serra dos Órgãos, *Carauta 1343* (MO); *Frasão 15265* (RB); *Fromm et al. 181* (B); *Lanna 133* (MO); *Lem in 19 Mar. 1964* (NY); *Lott 12* (MO, RB); *Rodrigues 53* (R); *Sampaio 1622* (R); *Santos et al. 202* (R), *1208* (PEL, R); *Vidal 11.147, 11.654, 11.6489* (R); *Wawia 334* (W); Campo dos Antas, Serra dos Órgãos, *Caris in 22 May 1948* (RB); *Emygdio et al. in Mar. 1942* (R); *Pereira 1917* (RB), *25 July 1949* (HB, MBM); *Santos & Pessoa in 25 Feb. 1942* (R); *Vianna 429* (R); Serra dos Órgãos, *Araujo 148* (MO, RB); *Badini 22136, 22263* (OUPR); *Brade 16355* (RB); *Burchell 2327* (BR, K), *2196* (GH, K); *Fromm et al. 180* (HB); *Gardner 375* (BM, CGE, F, G—2 sheets, GH, K—2 sheets, NY, OXF, P, TCD, W); *Glaziou & Simart 3733* (P); *Lusihnath 835* (LE); *Miers 3473* (TCD), *4453* (US), *in Feb. 1938* (BM—mixed collection); *Peckolt s.n.* (W); *Wilkes s.n.* (NY, US); Serra dos Órgãos, Castelo, *Brade 10945* (R); Morro Assú, Serra dos Órgãos, *Vianna 654* (R); *Brade 9918* (R); Teresópolis, *Bailey & Bailey 1296* (BH); Teresópolis to Pedra da Baleia, *Cardoso 145* (R); Morro da Nova Caledônia, Nova Friburgo, *Berry et al. 4421, 4425* ($n = 22$), *4432, 4433* ($n = 22$) (all MO, RB); Pico de Frade, Mun. Macaé, *Brade 15876* (B, RB); *Farney et al. 621* (RB); Corrisas, *Brade & Aparicio 18703* (RB); Alto Soberbo, *Gentry & Peixoto 937* (MO, RB); Itatiaia, Serra da Mantiqueira, including Maceiras and Planalto, *Altamirano & Watter 71* (M, RB); *Altamiro in 11 Oct. 1945* (PACA), *Aparicio & Edmundo 829* (RB); *Barth 1136* (US); *Brade 17515* (PACA, RB); *Campos Porto 2773* (B, NY, PACA, RB); *Carauta 528* (MO); *Dusén 81* (GH, MO, R, S, W), *650* (S), *in 25 May 1902* (S); *Eiten & Eiten 6662, 6674* (SP, US); *Emmerich 53* (R); *Ferreira & Briolando 184* (RB); *Fromm 17* (R); *Fromm et al. 164* (R); *Ginzberger 142, 143* (F, W); *Hunt 6418* (K); *Kuhlmann 26436* (RB); *Lanna 54* (MO); *Lanstyak 253* (MO); *Lindeman & Haas 5203* (U); *Lutz in Jan. 1957* (R); *Markgraf & Brade 3651* (RB); *Occhioni 16483* (RB); *Ramamoorthy 103, 116, 815–823* (MO); *Sampaio 4784* (R); *Scheinvar 78* (R); *Ule 148* (R); Abrigo Rebouças, Itatiaia, *Berry et al. 4437, 4439* (MO, RB; $n = 44$); *Oliveira 413* (RB); *Pereira & Pabst 8222* (HB), *5178* (GH, RB); *Santos 5034* (US); *Smith 1476* (GH); *Sucre & Plowman 5178* (GH, RB); *Walter 71* (RB); no locality, *St. Hilaire D 22* (F, P), *800* (P); *Luschnatte s.n.* (OXF). SÃO PAULO: Serra da Mantiqueira, between Itajuba and Guaratinguetá, *Castellanos 23371* (MO); Pico Itapeva, Campos do Jordão, *Vital & Ramamoorthy 4860* (MBM); Parque Estadual, Campos do Jordão, *Mattos 15956-a* (SP); Umuarama, Campos do Jordão, *Kuhlmann 32492* (SP); Campos do Jordão, *Bailey & Bailey 811* (BH); *Campos Porto 313* (B, RB), *2991, 2992* (RB), *3233* (MO); *Davis et al. 3006* (RB, SP, UEC); *de Lima 1131* (MO; *Emmerich*

15 (HB); *Gonçalves & Kuhlmann 2169* (SP); *Friedrichs in Jan. 1944* (PACA); *Hashimoto 313* (SP); *Lanstyack 33105* (B, RB); *Leite in 1945* (A); *Lutz & Lutz 1614* (R); *Mattos & Mattos 14467* (SP); *Pabst 4212* (F, HB, MBM, RB); *Ramamoorthy & Vital 673* (MO; $n = 44$), *674* (MBM, MO), *675* (MO), *676* ($n = 44$), *677*, *680* ($n = 44$), *682*, *684* (MO), *817* (MB), *Sakane 206*, *211* (SP); Serra da Bocaina, *Gibbs et al. 4573* (F); *Duarte 7689* (HB, MO); *Handro 808* (SP); *Ramamoorthy & de Lima 1172*, *1174* (MO); *Vianna 2949* (R, US); *Vianna et al. 286* (R, US); Serra da Bocaina, Mun. São José do Barreiro, km 16 near Silveiras, *Shepherd & Shepherd 12858* (SP, UEC); Serra da Bocaina, road to Mambucaba, *Lutz in Apr. 1951* (R #116696); Serra da Bocaina, Sertão da Bocaina, margins Rio Pintado, *Pabst 4744* (HB, MO); Bananal, Sertão do Rio Vermelho, Serra da Bocaina, *Brade 15268* (RB); *Brade & Duarte 20129* (MO). Cultivated in the city of São Paulo: Horto Botânico Cantareira, *Puttemans 204* (P, SP); Agua Funda, Jardin Botânico do Estado, *Teixeira 241* (SP); Ypiranga, Jardim Museu Paulista, *Luederwaldt s.n.* (SP); Chácara dos Morrinhos, *Pickel 4447* (SP).

Fuchsia regia subsp. *regia* is the most widespread of the Brazilian fuchsias, occurring in four different states, centered in Rio de Janeiro and Minas Gerais. As a result of its fragmented distribution, with populations in a number of discrete mountain ranges, considerable morphological differentiation has taken place throughout the range of this subspecies. It is also cytologically heterogeneous, with tetraploid and octoploid populations. All counts made from Minas Gerais and northern Rio de Janeiro have been tetraploid, whereas octoploid and tetraploid individuals occur together in northern São Paulo and south-central Rio de Janeiro states, in areas such as Itatiaia, Serra da Bocaina, and Serra dos Órgãos (see fig. 9 in Hoshino & Berry, 1989). The different cytotypes cannot be distinguished morphologically, however, and their relationships are not well understood.

Fuchsia regia subsp. *regia* can be distinguished from other taxa of sect. *Quelusia* by having large flowers with spreading sepals and only slight sepal connation, large leaves with petioles generally longer than 10 mm, and mostly glabrous stems and foliage.

This subspecies has a particularly broad ecological tolerance, extending from tall cloud forest at 1,000 m to open campos as high as 2,400 m. When it occurs inside the forest, *F. regia* subsp. *regia* grows as a liana, flowering when its branches reach sufficient light in the tree canopies. As the vegetation decreases in height with greater elevation, it grows as a scandent shrub, and as a short, erect shrub when found on the edges of the open campos. This gradual transition in the habit of subsp. *regia* has been observed in several localities, such as the Serra dos Órgãos and the Morro da Nova Caledônia in Rio de Janeiro, and the Serra do Itacolomi and Serra do Itambé in Minas Gerais.

As a result of its broad altitudinal and geographical distribution, *F. regia* subsp. *regia* occurs sympatrically with four other species from sect. *Quelusia*. In each case, morphologically intermediate individuals have been found that indicate the occurrence of interspecific hybridization (see Appendix). It also occurs sympatrically with *F. regia* subsp. *serrae* in northern São Paulo along the eastern slopes of the Serra da Bocaina, where it forms hybrid populations, with further intergradation southwards along the Serra do Mar as far as Caraguatatuba. These populations are discussed in the Appendix.

Several collections of *F. regia* subsp. *regia* from widely distant localities are unusually pubescent yet do not appear to be the result of hybridization or introgression with pubescent species growing nearby, such as *F. alpestris* or *F. coccinea*. The specimen *Campos Porto 3421* (RB, from Campos do Jordão, São Paulo, 1,600 m) is similar in all morphological features to nearby glabrous populations of *F. regia*, but the entire plant is covered by a dense, pilose indumentum. Three collections from Minas Gerais are similarly pubescent: *Gardner 4555* (K), *Claussen 88* (G), and *Brade 16953* (RB, US, from the Serra do Caparaó). *Martinelli et al. 169* (RB, Vale das Videiras, Petrópolis, Rio de Janeiro) is covered by short, fine pubescence, which is unusual among the populations of *F. regia* from Rio de Janeiro. These pubescent variants are apparently quite rare, and none were found during my fieldwork in Brazil.

9b. Fuchsia regia subsp. **serrae** P. Berry, subsp. nov. TYPE: Brazil. Paraná: Mun. Morretes, Recanto Engº Lacerda, Estrada da Graciosa, 850 m, 28 Jan. 1985, *P. E. Berry, T. Plowman & F. Juarez 4493* (holotype, MO; isotype, MBM; $n = 44$). Figure 17.

Fuchsia affinis Cambessèdes, Fl. Bras. Merid. 2(17): 274. 1830. TYPE: Brazil. Paraná: "in forest near Ferraria, district of Curitiba," May 1820, *Auguste de Saint Hilaire C² 1622* (lectotype, P, here designated; isolectotype, P, with no number). The lectotype sheet contains two different specimens, but the branch corresponding to *St. Hilaire 1622* is clearly marked on the left side; it was annotated, possibly by St. Hilaire, and labeled as the type collection of *F. affinis*.

Fuchsia radicans Miers in Lindley, Bot. Reg. 27: pl. 66. 1841. TYPE: Brazil. Rio de Janeiro: Organ Mts., *John Miers in Feb. 1838* (holotype, BM; isotype, K). There are two sheets of Miers collections labeled as *F. radicans* at BM; one sheet contains three different plants, but the holotype has only one specimen on its sheet, with a pasted blue slip stating

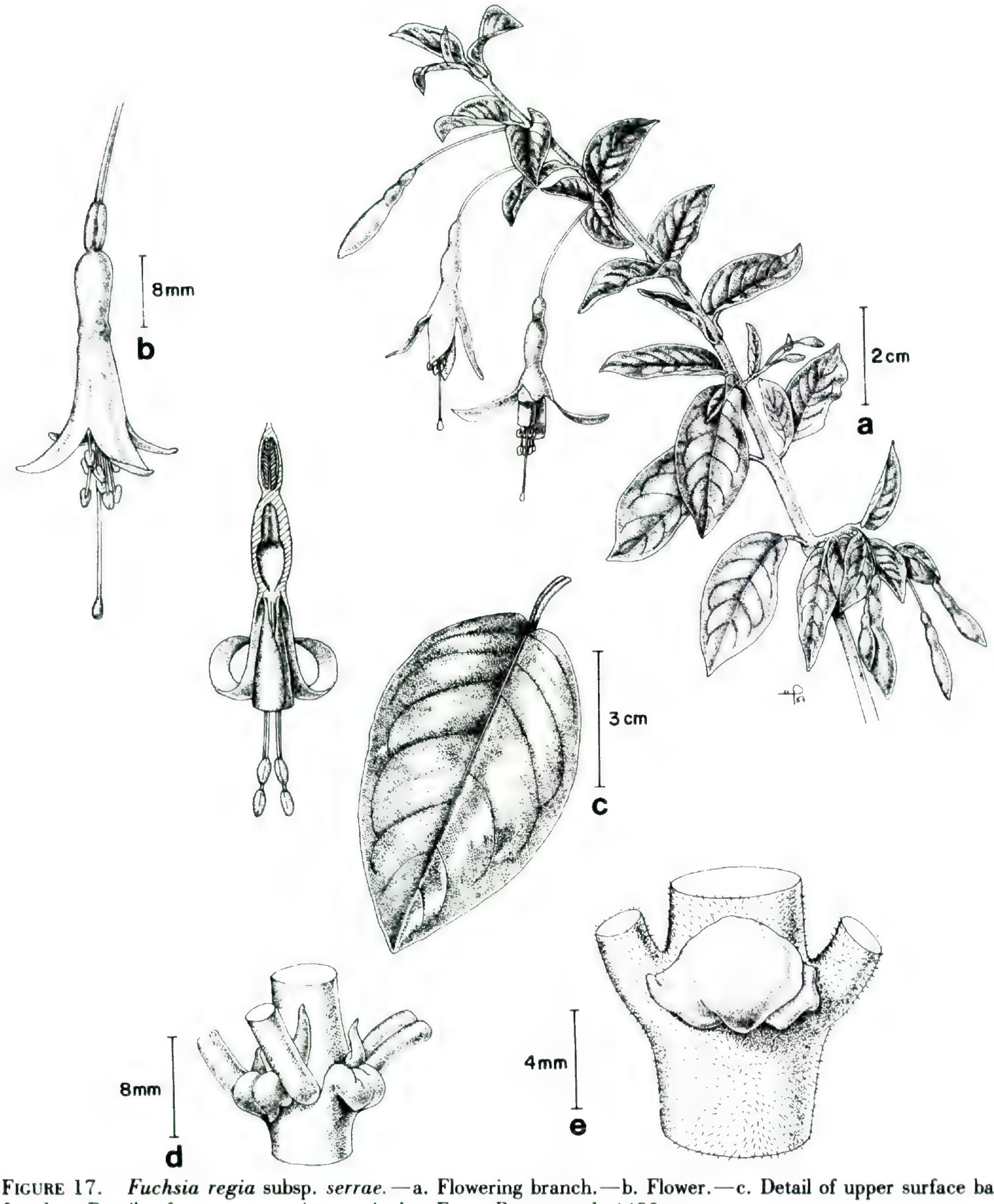

FIGURE 17. *Fuchsia regia* subsp. *serrae*.—a. Flowering branch.—b. Flower.—c. Detail of upper surface basal leaf.—d, e. Details of crassate, persistent stipules. From *Berry et al. 4492*.

"*Fuchsia radicans* Nob., Organ Mts., Feb., 1838" and a small typeset label of "Herb. John Miers."

Frutex 1–4 metralis aliquando in arboribus scandens usque ad 15 m, ramulis plerumque subtiliter puberulentibus interdum dense pilosis, lateralibus saepe brevibus divaricatisque. Folia opposita vel 3–4 verticillata, coriacea, (anguste) ovata ellipticave, margine subintegro, petiolis 1.5–3 mm crassis (7–)10–35 mm longis, stipulis prominentibus incrassatis recurvatis 2–3 mm longis latisque, ca. 0.5 mm crassis, contiguis interdum connatis, facie nodosis. Tubi florales cylindrico-fusiformes (6–)7–15 mm longi, sepalis (15–)19–34 mm longis, (4–)5–7 mm latis, basi (5–)8–14 mm connatis, lobis patentibus saepe recurvatis vel raro reflexis. Bacca oblonga 16–26 mm longa, 9–13 mm crassa, seminibus 2–2.5 mm longis, 1–1.5 mm latis. Numerus gameticus chromosomatum $n = 44$.

Scandent to climbing shrubs 1–4 m tall, or lianas to 15 m high in trees. Branchlets generally finely puberulent, sometimes subglabrous or densely short-pilose, the lateral ones often short and divaricate; older branches on large plants hanging, to 6 m long, with basal stems to 6 cm diam. Leaves op-

posite or in whorls of 3–4, coriaceous, (narrowly) ovate to elliptic, (35–)60–110 mm long, (15–)25–45 mm wide, apex acute to acuminate, base rounded to acute and sometimes ± uneven, smooth and lustrous dark green above, pale below, glabrous to lightly pubescent on both surfaces; margin subentire, secondary veins 5–8(–10) per side. Petioles 1.5–3 mm thick, usually dull purple, canaliculate above, (7–)10–24(–35) mm long. Stipules prominent, crassate, 2–3 mm wide, 2–3 mm long, ca. 0.5 mm thick, recurved, persistent, adjacent ones sometimes fused, drying tan-colored and giving a nodose appearance to the stems. Flowers solitary in upper leaf axils; pedicels 20–45 mm long, pendulous. Ovary cylindrical, 6–12 mm long, 2–4 mm wide. Floral tube cylindrical-fusiform, (6–)7–15 mm long, 3–7 mm wide, glabrous to puberulent outside; nectary ± smooth, 5–8 mm high. Sepals (15–)19–34 mm long, connate at the base for (5–)8–10(–14) mm and forming a long, usually 4-ridged sepal tube, the free lobes (4–)5–7 mm wide at base and spreading to most often recurved or rarely reflexed at anthesis. Tube and petals bright red. Petals violet, obovate to spathulate, 11–20 mm long, 8–15 mm wide. Filaments red, 22–48 and 20–40 mm long; anthers red-purple, 3–4 mm long, 1.5–2 mm wide. Style red, glabrous to pilose near base; stigma red, clavate, 2–4 mm long, 1–2 mm wide, exserted 15–23 mm beyond the anthers. Berry oblong, 16–26 mm long, 9–13 mm thick, purple when ripe; seeds 2–2.5 mm long, 1–1.5 mm wide. Gametic chromosome number $n = 44$.

Distribution (Fig. 15). Typical of dense cloud forests on the crest and wet, coastal escarpments of the Serra do Mar and Serra Geral, in Rio Grande do Sul, Santa Catarina, Paraná, São Paulo and southern Rio de Janeiro states, from 500 to 1,450 m. Also found at lower elevations on the top of isolated "morros" in the Atlantic coastal forest of Santa Catarina, or rarely occurring near sea level in coastal restingas in northern Rio Grande do Sul and southern Santa Catarina. Flowering mainly from November to March, occasionally in other months.

Additional specimens examined. BRAZIL. RIO DE JANEIRO: Cachoeira de Macacú, road to Nova Friburgo, *Sucre & Soderstrom 9044* (MO, RB); Angra dos Reis, Alto da Serra, 600 m, *Sucre et al. 4908* (MO); RJ-16, Rio Claro, first tunnel, 550 m, *de Lima 270* (RB); Organ Mountains, *Gardner in Mar. 1841* (BM), *Ramamoorthy & de Lima 1181* (MO); Province of Rio de Janeiro, *St. Hilaire B 2475*[ter] (P). SÃO PAULO: Alto da Serra, above Caraguatatuba, *Ramamoorthy & Vital 685, 686* (MO), *688* (MO; $n = 44$); Parque Estadual de Caraguatatuba, *Gentry & Zardini 49376* (MO); Alto da Serra de Paranapiacaba, *Emygdio 1520* (R); Serra de Cubatão, *Guillemin 470 in 1839* (P); Alto de Serra, São Paulo to Santos, *Pabst & Pereira 5750* (HB, MBM); *Vidal in Apr. 1937* (R #35043); Alto da Serra, *Hoehne 7617* (A); *Mattos 11714* (MBM); *Munz 15415* (F, G, GH, NY, POM, US); *Sandeman 2012* (K, OXF); *Smith 1900* (F, GH, S): *Wettstein & Schiffner in May 1901* (W); Santos, *King s.n.* (G); Sallesópolis, *Travassos 314* (MO, RB); Est. Campo Grande, *Hoehne 11894* (POM); Borraceia Exper. Station, *Nascimento in 4 Feb. 1943* (UC); road to Atibain, *Monteiro et al. 4894* (F); near San Bernardo, *Wettstein & Schiffner in July 1901* (W); Cantareira, *Hoehne 1477* (SP); Rio Grande, estrada do Mar, *Hauff 120* (SP); Serra do Mar, between Mogi das Cruzes and Bertioga, *Kirizawa et al. 552, 1015, 1038* (SP); km 74 of SP-98 from Mogi to Bertioga, Mun. Biritiba-Uçu, *Pirani & Yano 730* (SP); Miracatu, Sítio Urupuã, km 348.5 of BR-116, *Martuscelli 4* (SP); Reserva Capão Bonito, 70 km from Itapetininga, SP-139, *Sakane 543* (SP); Reserva Carlos Botelho, between São Miguel Arcanjos & Sete Barras, *Prance et al. 6871* (MBM), *6896* (F); no locality, *Burchell 3742* (BR, K); *Kuhlmann s.n.* (RB). PARANÁ: Santa Ana, Mun. Bocaiúva do Sul, *Hatschbach & Guimarães 23408* (M, MBM, MO); Jaguatirica, Mun. Bocaiúva do Sul, *Ramamoorthy & Vital 124* (MO); Serro, Mun. Bocaiúva do Sul, *Hatschbach 42976* (MBM); Serra Capivari, Mun. Campina Grande do Sul, *Oliveira & Oliveira 867* (MBM); 7–12 km W of Sesmaria and Rio Capivari, *Berry et al. 4446, 4447, 4449, 4450* ($n = 44$) (all MBM, MO); Sítio do Belizário, Mun. Campina Grande do Sul, *Hatschbach 16426* (MBM); Papanduva, Mun. Campina Grande do Sul, *Hatschbach 7091* (MBM); Curitiba, *Hoehne 23109* (POM); *Dusén in 12 Jan. 1914* (F, GH, MO, NY, SP, US), *in 20 Oct. 1928* (SP); Parque Nova Iguaçu, Mun. Curitiba, *Berry et al. 4455, 4456* (MBM, MO); *Kummrow 1294* (MBM); 10 km E of Curitiba, *Lindeman & Haas 2539* (MBM); km 34 road Curitiba–Paranaguá, *Fromm et al. 304* (R); *Pabst et al. 5876* (HB, MBM); Rio da Santa, Curitiba to Joinville, *Conrad & Dietrich 2055, 2056* (MO); Rio Taquary, Mun. Quatro Barras, *Berry et al. 4492* (MBM, MO; $n = 44$); *Hatschbach 19942* (MBM); *Oliveira 577* (MBM); Serra de Araçatuba, Mun. Guaratuba, *Hatschbach 7082* (MBM); Alto da Serra, Mun. Guaratuba, *Kummrow 1914* (MBM); Pico Abrolhos, Mun. Morretes, *Curiel in 14 Apr. 1947* (MBM #39718); *Hatschbach 751* (PACA); Mun. Morretes, *Ramamoorthy & Hatschbach 828* (MBM), *829* (MO; $n = 44$, $2n = 88$), *830* (MO; $n = 44$); Pilão de Pedras, Mun. Morretes, *Kummrow 1917* (MBM); Piraquara, *Hatschbach 188* (PACA); Serra do Emboque, Mun. Piraquara, *Hatschbach 24946* (MBM, UC); Rio Pequeno, Mun. São José dos Pinhais, *Hatschbach 8019* (HB, U); São José-Colônia Murici, Mun. São José dos Pinhais, *Saito 404* (A); Malhada, Mun. São José dos Pinhais, *Hatschbach 39764* (MBM, NA); Colônia Roseira, Mun. São José dos Pinhais, *Hatschbach 17657* (MBM, UC); Guaricana, Mun. São José dos Pinhais, *Oliveira 518* (MBM, MO); *Hatschbach 34905* (MBM); Zinco, Mun. São José dos Pinhais, *Oliveira 534* (MBM); Barro Preto, Mun. São José dos Pinhais, *Oliveira 153* (MBM); Serra do Mar, *Braga 550* (MO, RB, US); Alto da Serra, Mun. Sete Barras, *Hatschbach 26892* (MBM, NA); Piraí, Mun. Tijucas do Sul, *Hatschbach 40187* (BH, MBM); Serra do Mar, desvio Ypiranga, *Dusén in 19 Sep. 1908* (BR, G, GH, LE, MICH, MO, PH, S, UC, Z); Vossoroca, Mun. Tijucas do Sul, *Kummrow 329* (MBM); Rincão, Mun. Tijucas do Sul, *Hatschbach 40471* (MBM). SANTA

CATARINA: Rio Novo, Mun. Aguas Mornas, *Klein & Bresolin 10547* (HBR); Faxinal, Biguaçu, Mun. Antônio Carlos, *Reitz C956* (HBR, MO, PACA, RB); *Rambo 50392* (PACA); Fazenda Coprowsky, Alto Bendito Novo, Zinco, Mun. Benedito Novo, *Bresolin & Rocco 683* (HBR); Morro Spitzkopf, Mun. Blumenau, *Reitz & Klein 9202* (CM, G, HBR, MO); *Smith & Reitz 6279* (HBR, R, RSA, US); Morro do Barão, Mun. Botuverá, *Reitz & Klein 18015* (HBR, MO, RSA); Morro da Bateia, Mun. Brusque, *Reitz C1914* (HBR, MO, US); Morro do Iquererim, Mun. Campo Alegre, *Smith & Klein 7384* (HBR, MO, R, RSA, US); Morro do Ribeirão, Mun. Florianópolis, *Klein 7166* (FLOR, HBR, MO, RSA); Lajeado Alto, Guabiruba, *Souza et al. 609, 613, 620, 621, 625* (FLOR); Monte Crista, São Francisco do Sul, Mun. Garuva, *Reitz & Klein 10027* (HBR, MO, RSA); Hôrto Florestal, Mun. Ibirama, *Klein 1975* (F, HBR, MO, PACA, RSA); Alto Cachoeira Grande, Aguas Mornas, *Klein & Bresolin 10751* (HBR); Morro do Baú, Mun. Itajaí, *Reitz 2104* (HBR, MO, RSA, US); Morro da Fazenda, Mun. Itajaí, *Reitz & Klein 1740* (HBR, MO, RSA), *1875* (MO); Joinville, *Schwacke 4961* (R, RB); Joinville, estrada Dona Francisca, *Reitz & Klein 4220* (HBR, MO, RSA); Morro da Ressacada, Mun. Itajaí, *Klein 1868* (HBR, MO, S, US); Serra da Pedra, Mun. Jacinto Machado, *Reitz C318* (GH, HBR, MO), *856* (PACA); Serra do Malhacoco, Praia Grande, Mun. Jacinto Machado, *Reitz C1456* (GH, HBR, MO); Encruzilhada a Serril, Mun. Lajes, *Lourteig 2287* (DS, HBR, NY, P, R, US); Serra Geral-Encruzilhada, Mun. Lajes, *Smith & Klein 8020* (HBR, MO, R, RSA, US); Pinhal da Companhia, Mun. Lauro Müller-Uruçanga, *Reitz & Klein 2849* (HBR, MO, UC, US); Bom Jardim da Serra, descent of Serra Geral to Lauro Müller, *Berry & Falkenberg 4520, 4521* (MBM, MO); *Falkenberg 2317* (FLOR, MO); Braço Joaquim, Mun. Luiz Alves, *Reitz & Klein 2685* (B, BR, HBR, K, MO, RSA); Octacilio Costa, *Pereira & Pabst 8016* (HB, M, PEL, RB); Anitópolis, Mun. Palhoça, *Klein 491* (HBR, MO, RSA, UC); Morro do Cambirela, Mun. Palhoça, *Klein & Bresolin 9297* (FLOR, HBR, MO); *Rambo 50332* (PACA); Serra da Boa Vista, São José, Mun. Rancho Queimado, *Reitz & Klein 5485* (HBR, MO), *10727* (HBR, MO, RSA); Rancho Queimado, road to Boa Vista, *Ramamoorthy & Reitz 1159, 1160* (MBM, MO); Boa Vista, *Ramamoorthy & Reitz 1163* (MBM, MO), *1167, 1168* (MO); Takuartas, near Boa Vista, *Ramamoorthy & Reitz 1164, 1165* (MO); Rio dos Bugres, *Schwacke in 5 July 1885* (P); Serra do Matador, Mun. Rio do Sul, *Reitz & Klein 7321* (G, HBR, MO, NY, UC, US); km 195–203 of road Rio do Sul–Curitibanos, Mun. Pouso Redondo, *Berry & Falkenberg 4501* ($n = 44$), *4502, 4504* ($n = 44$) (all MBM, MO); *Falkenberg 2318, 2321, 2322, 2325* (FLOR); slopes of Serra Geral from Itaimbezinho to Praia Grande, *Falkenberg 2370, 2376, 2377* (FLOR); *Falkenberg et al. 3750, 3751* (FLOR), *3752* ($n = 44$; FLOR); above Turvo to Serra da Rocinha, Mun. Timbé do Sul, *Matzenbacher 398* (ICN); 13–19 km above Timbé do Sul to Serra da Rocinha, *Falkenberg et al. 3753* ($n = 44$), *3754, 3755* (FLOR); Serra da Rocinha, border RS and SC states, 22 km above Timbé do Sul, *Falkenberg et al. 3756, 3757, 3760, 3761, 3766* (FLOR); Cerro Azul, Mun. Timbó, *Berry & Falkenberg 4500* (MBM, MO); 0.5–4 km E of escarpment of Serra Geral between Uribici and Braço do Norte, *Falkenberg et al. 3792–3796* (FLOR); 1–2 km W of escarpment of Serra Geral, towards Uribici, *Falkenberg et al. 3788–3791* (FLOR); NE of Uribici, km 90 of road to Braço do Norte, *Falkenberg et al. 3783, 3785* (FLOR); Sabiá, Mun. Vidal Ramos, *Reitz & Klein 4274* (HBR, MO, NY, RSA, UC, US), *6657* (F, HB, HBR, MBM, MO, PACA, PEL, RSA); Sombrio, 10 m, Mun. Sombrio, *Reitz C1131* (MO, RSA #79111). RIO GRANDE DO SUL: Torres, Faxinal, 10 m, *Waechter 827* (ICN #41273); Josafá, Mun. Cambará do Sul, *Falkenberg 2339, 2341, 2343, 2345, 2347, 2349, 2350, 2354, 2357, 2372, 2378* (FLOR); Itaimbezinho, Parque Nacional Aparados da Serra, *Falkenberg 258, 270, 274, 278, 352, 356, 401* (FLOR); *Falkenberg et al. 3749* (FLOR); *Lindeman & Haas in 3 Dec. 1971* (F, ICN #9359, U); *Pedralli & Rego in 24 Apr. 1983* (FLOR); *Rambo 4310* (PACA), *45524* (MO), *45529* (PACA), *49363* (RSA), *53983* (B, RB, S), *58552* (B, HBR, MO, S); 20 km E of Tainhas on RS-020 to Terra de Areia, *Falkenberg et al. 3744* ($n = 44$), *3745* (FLOR); Serra da Rocinha, Aparados da Serra, *Rambo 8630* (PACA); Cambará, near São Francisco de Paula, *Rambo 36222* (ICN, PACA); Serra do Faxinal, near São Francisco de Paula, *Rambo 32099* (PACA); Fortaleza, Mun. Cambará do Sul, *Wasum & Wasum 2122* (US); *Wasum et al. 734* (US).

Fuchsia regia subsp. *serrae* is the only taxon in sect. *Quelusia* besides *F. brevilobis* with the sepals connate for over one-third of their length. It is unique in its persistent, crassate stipules and lustrous, subcoriaceous leaves with thick petioles. Unlike the other subspecies of *F. regia*, the sepals are usually recurved at anthesis and four-angled in bud.

This subspecies is most common along the crest and upper slopes of the "serras," the steep and very wet region on the eastern edge of the southern Brazilian planalto as it drops abruptly to the Atlantic coastal plains. The rugged terrain, with sheer drops of 800 m or more, such as those found in the Aparados da Serra in northern Rio Grande do Sul, creates a broad diversity of microhabitats reflected in the large degree of variability in different populations of this subspecies. For example, low, densely branched subshrubs characteristically grow in rock crevices on the steep drop-offs of the Aparados, while tall lianas with long, drooping branches are found in more protected, forested areas near the crest of the Serra.

The degree of sepal connation varies considerably in different parts of the range of *F. regia* subsp. *serrae*. In northern Paraná, where it occurs together with the long-tubed *F. brevilobis*, the sepals are often joined for half or more of their length. Along the Serra Geral in southern Santa Catarina and Rio Grande do Sul, however, the sepals are less joined than populations further north; in extreme cases, individuals like *Falkenberg 3744* and *3745* have the sepals joined for only 4–6 mm, but their thick, shiny leaves and nodose stipules are characteristic of subsp. *serrae*.

Along the edge and just inland from the steep drop-offs of the Serra Geral in Rio Grande do Sul

and southern Santa Catarina, a sharp ecotone occurs between the drier, flatter planalto and the wet, steep coastal slopes. In this area, *Fuchsia regia* subsp. *serrae* occurs sympatrically with the easternmost populations of *Fuchsia regia* subsp. *reitzii*, and the two subspecies intergrade extensively in areas such as Itaimbezinho, Serra da Rocinha, and the edge of the Serra Geral near Uribici and Bom Jardim da Serra in Santa Catarina. Further discussion and a list of intermediate, probable hybrid individuals between these two subspecies is found in the Appendix.

Towards the northern limits of the range of *Fuchsia regia* subsp. *serrae*, this subspecies also contacts populations of *Fuchsia regia* subsp. *regia*, especially in the Serra da Bocaina in northern São Paulo state. Populations of subsp. *serrae* predominate there on the lower, coastal slopes below 1,100 m, while subsp. *regia* occurs at higher elevations and further inland. Extensive intergradation between these two subspecies occurs on the upper coastal slopes of the Serra, where unusually pilose individuals are also found. Some of these individuals are octoploid, as in all the southern populations of subsp. *serrae*, while others are tetraploid, like some of the populations of subsp. *regia* from the Bocaina range and further north (Hoshino & Berry, 1989). Although *F. regia* subsp. *regia* reaches its southern limit at the Serra da Bocaina, populations of *Fuchsia* with mixed ploidy levels and dense pubescence occur south of the Bocaina area as far as Ubatuba in the Serra do Mar of north-central São Paulo state (Hoshino & Berry, 1989).

Fuchsia regia subsp. *serrae* also occurs sympatrically with *F. brevilobis* in several localities in Paraná. Although *F. regia* is octoploid in this area, and *F. brevilobis* is tetraploid, the occurrence of morphologically intermediate individuals indicates that hybridization has taken place between these taxa (see Appendix). The unusually long sepal tubes of populations of *F. regia* subsp. *serrae* in this area are characteristic of *F. brevilobis* and may be the result of introgression with this species.

Outside of its typical montane habitats, *F. regia* subsp. *serrae* has also been found in coastal restingas at sea level, near the Rio Grande do Sul–Santa Catarina border. Reitz (1961) first detected this apparent anomaly in the distribution of typically montane taxa, and found it to occur in at least ten other species that normally occur along the crest of the Serra Geral. The presence of these species in the restingas must represent recent chance introductions from the nearby serras, as the coastal plains of this area are only of Quaternary age (Klein, 1984).

9c. Fuchsia regia subsp. **reitzii** P. Berry, subsp. nov. TYPE: Brazil. Santa Catarina: Município São Joaquim, Fazenda de Laranja, São Joaquim, 1,400 m, 13 Jan. 1959, *P. Raulino Reitz & Roberto Klein 8135* (holotype, UC #240288; isotypes, B, BR, G, GH, HBR, ICN, K, NY, U). Figure 18.

Fuchsia pubescens Cambessèdes in St. Hilaire, Fl. Brasil. Merid. 2(17): 275, tab. 134. 1830. TYPE: Brazil: "in fields near the Rio Yapó in the part of São Paulo Province called Campos Geraes," currently in Paraná, Municípios Piraí do Sul and Jaguariaíva, May 1820, *Auguste de Saint Hilaire C² 1545* (holotype, P, on the same sheet with a small piece of *St. Hilaire 2276*, which is *F. coccinea* from Minas Gerais; isotypes, P, as *St. Hilaire C¹ 1545* and also mixed with *2276*, MPU). The holotype at P was annotated as the type specimen of *F. pubescens*, and Cambessèdes's illustration shows the verticillate leaves and flower and round fruits characteristic of *F. regia* subsp. *reitzii*. The other collection from Minas Gerais cited by Cambessèdes in his protologue is *F. coccinea*.

Frutex erectus scandensve 1–4 metralis, ramulis purpurascentibus subglabris vel dense puberulentibus vel pilosis ferruginescentibus, ramis cito excorticatis. Folia 3–4(–5) verticillata, elliptica ad anguste ovato-elliptica, apice acuta basi acuto-acuminata obtusave, nervis tertiariis conspicuis, margine glanduloso-serrulato, petiolis 3–7(–15) mm longis, stipulis lanceolatis membranaceis 0.8–1.4 mm longis. Flores verticillati, tubis floralibus cylindrico-fusiformibus 5–11 mm longis, sepalis anguste lanceolato-oblongis 17–28 mm longis, basi 2–6 mm connatis sub anthesi patentibus, petalis obovatis 10–15(–20) mm longis, 7–13 mm latis. Bacca globosa vel interdum ellipsoidea 10–16 mm longa, 9–12 mm lata, seminibus 1.6–2 mm longis, 1–1.3 mm latis. Numerus gameticus chromosomatum $n = 44$.

Erect to scandent shrubs 1–3 m high, or climbers in trees or brush to 4 m tall. Young branches purplish, subglabrous to densely puberulent or pilose, the pubescence ferrugineous in some plants; older stems with reddish to pale tan, readily exfoliating bark. Leaves in whorls of 3 or 4(–5), firmly membranous, (narrowly) elliptic to narrowly ovate-elliptic, 20–65(–90) mm long, 7–20(–40) mm wide, acute at the apex, acute to attenuate or obtuse at the base, dark dull green and subglabrous above, pale green and subglabrous to densely pubescent below with conspicuous tertiary venation, margin serrulate, usually with prominent glandular teeth ascending apically at a ± 45° angle, secondary veins 5–8 per side. Petioles 3–7(–15) mm long. Stipules lanceolate, 0.8–1.4 mm long, 0.4–1 mm wide, thick at the base, purple, drying dark, divergent to recurved with age, with apiculate, semipersistent tips. Flowers solitary or sometimes 2 per leaf axil, near branch tips; pedicels slender, 10–

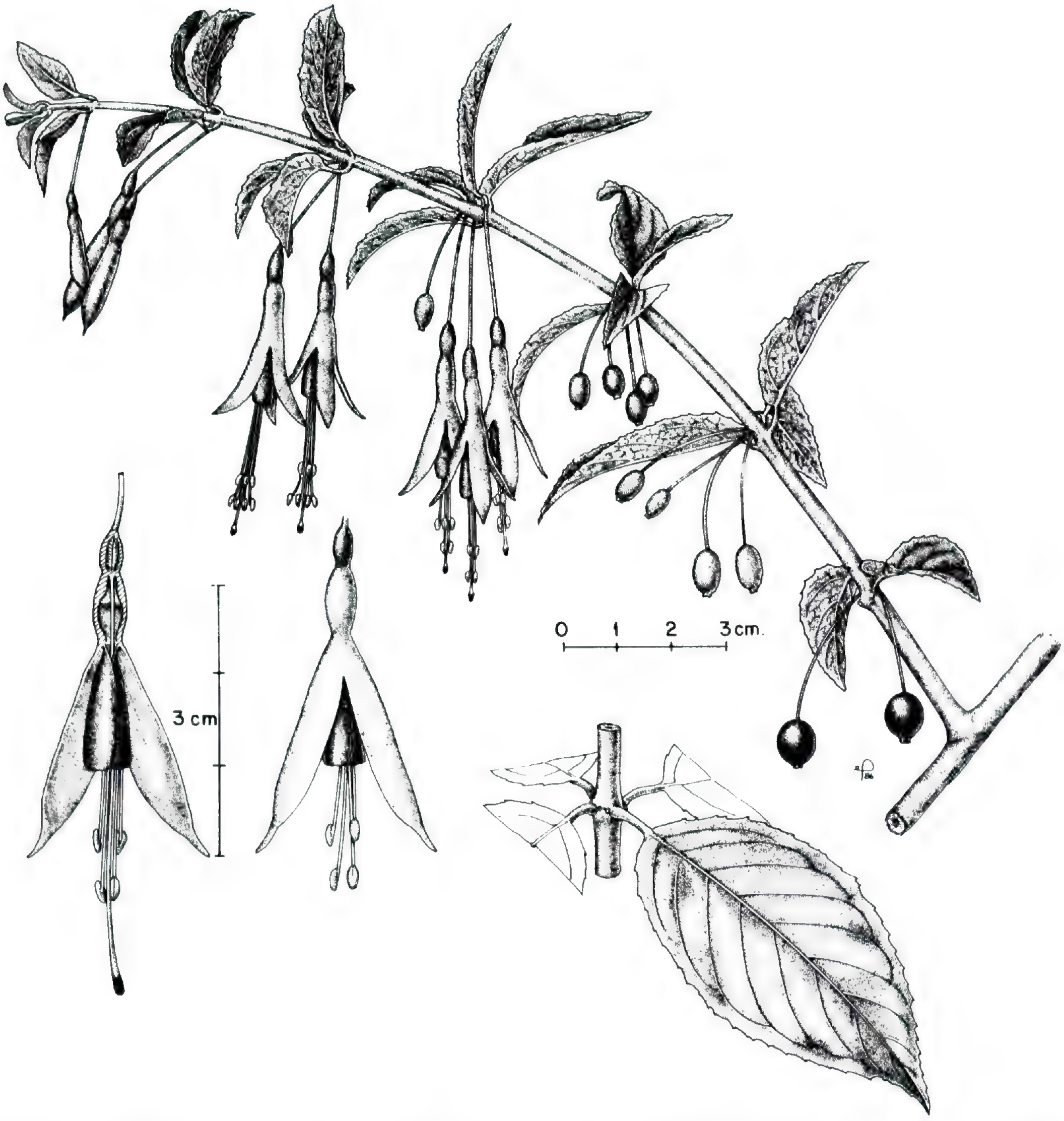

FIGURE 18. *Fuchsia regia* subsp. *reitzii*. Flowering branch, detail of flowers, and detail upper surface of basal leaf. From *Berry et al. 4512*.

35(–50) mm long, pendulous. Ovary oblong, (4–)5–9 mm long, 2–4 mm wide. Floral tube cylindrical-fusiform, 5–9(–11) mm long, 2–4(–6) mm wide, subglabrous to puberulent or loosely pilose outside, glabrous inside; nectary smooth, 2.5–5 mm high. Sepals 17–28 mm long, narrowly lance-oblong, connate at the base for 2–6 mm; free lobes 3–5(–6) mm wide at base, subacuminate at the apex, spreading at anthesis. Tube and sepals red. Petals purple, obovate, 10–15(–20) mm long, 7–13 mm wide. Filaments reddish, 25–45 mm and 20–38 mm long; anthers red-purple, oblong-elliptic, 2–2.5 mm long, 1–1.5 mm wide. Style glabrous to pilose in lower half; stigma clavate, 2–2.5 mm long, 1–1.5 mm wide, exserted 5–15 mm beyond the anthers. Berry globose to ellipsoid, shiny dark purple when ripe, (10–)12–16 mm long, 9–12 mm wide; seeds tan, 1.6–2 mm long, 1–1.3 mm wide. Gametic chromosome number $n = 44$.

Distribution (Fig. 15). Occurring principally in low wooded areas and usually along streams or seepages, on the planalto west of the Serra Geral and Serra do Mar in south-central Paraná, Santa Catarina, and Rio Grande do Sul, at 880–1,730 m. At the top of the escarpments of the coastal mountain ranges subsp. *reitzii* intergrades with *F. regia* subsp. *serrae*. Flowers mainly from November to March.

Additional specimens examined. BRAZIL. PARANÁ: General Carneiro, *Hatschbach et al. 13670* (U); 10 km N of Palmas, Mun. Palmas, *Hatschbach et al. 28175*,

28237 (MBM); Cachoeira dos Turcos, Mun. Guarapuava, *Hatschbach 25602* (MBM). SANTA CATARINA: Campo de Palmas, Mun. Agua Doce, *Smith & Klein 13421* (FLOR, HBR, MO, NY, RSA, SI, US); BR 153, Rio Roseira, 18 km S of Horizonte, Mun. Agua Doce, *Krapovickas & Cristóbal 33693* (CTES); 30 km S of Horizonte, *Smith & Klein 13421* (HBR); 8 km N of Caçador, Mun. Caçador, *Smith & Klein 8966* (HBR, MO, RSA, US); 12 km N of Caçador, *Smith & Klein 9145* (HBR, MO, R, RSA, US); 9–17 km W of Bom Jardim da Serra to São Joaquim, Mun. Bom Jardim da Serra, *Berry et al. 4510* (n = 44), *4511, 4512, 4513* (n = 44) (all MBM, MO); *Falkenberg 2269, 2270, 2273, 2275, 2277, 2279, 2280* (FLOR); 9 km E of Bom Jardim da Serra on road to Lauro Müller, Mun. Bom Jardim da Serra, *Berry et al. 4514–4516* (MBM, MO); *Falkenberg 2285, 2288* (FLOR); Bom Jardim da Serra, *Eskuche 1639-63* (SI); 5 km E of São Joaquim, Mun. São Joaquim, *Falkenberg et al. 3774–3776* (FLOR); road São Joaquim to Uribici, *Falkenberg et al. 3777* (FLOR; n = 44); Uribici, slopes and near summit of Morro da Igreja, *Falkenberg et al. 3778–3782* (FLOR); Uribici, km 90 of road to Braço do Norte, *Falkenberg et al. 3786* (FLOR); 0.5–1.5 km N of Várzea, road to Bom Jardim, *Falkenberg et al. 3771, 3772* (FLOR); Marombos, Mun. Curitibanos, *Klein 3287* (HBR, MO, RSA); Curitibanos, *Berry et al. 4506* (MBM, MO; n = 44); *Falkenberg 2247* (FLOR); 5 km W of Curitibanos on BR-470, *Berry et al. 4508* (MBM, MO); *Falkenberg 2253* (FLOR); Campo dos Padres, Mun. Bom Retiro, *Rambo 60135* (PACA); *Reitz 2342* (G, HBR, NY, U, UC, US), *5213* (PACA); *Smith & Klein 7652* (HBR, MO); Moratá, Ponte Miriad, *Reitz 4698* (RSA, S); 11 km E of Faxinal dos Guedes, *Smith & Klein 11853* (HBR, MO, R, RSA, US); descent of Serra Geral from Bom Jardim to Lauro Müller, *Berry et al. 4518* (MBM, MO); *Falkenberg 2305, 2307* (FLOR); 22 km above Timbé do Sul, Serra da Rocinha, Mun. Timbé do Sul, border with Rio Grande do Sul, *Falkenberg et al. 3758, 3759, 3763–3765* (FLOR); Bituruna, Fazenda Etienne, *Mello Filho 752* (R); BR-2, km 280, *Pabst et al. 6132* (HB, MBM, R); *Pereira & Pabst 6305* (RB); near Lajes, Mun. Lajes, *Lindeman & Haas 3703* (U); *Texeira & Texeira 3* (SP); *Rambo 49602* (MO, RSA, S); Campo de Areão, Mun. Sta. Cecília, *Reitz & Klein 14185* (HBR, MO, RSA); Ponte Alta do Sul, Mun. Ponte Alta, *Reitz & Klein 11294* (HBR, MO, US); São Francisco de Malta, Mun. São Joaquim, *Reitz 6662* (HB, HBR, MBM, MO, RSA); Fazenda de Laranja, São Joaquim, *Smith & Klein 7652* (HBR, R, RSA, US); 8 km NE of São Joaquim to Cruzeiro, *Smith & Klein 10277* (HBR, MO, R, RSA, US); Poço Preto, near Rio Timbó, Mun. Porto União, *Smith & Reitz 8670* (HBR, MO, R, RSA, US); 8 km SW of Fuck on BR-116, *Davidse et al. 11076* (MO, SP). RIO GRANDE DO SUL: Itaimbezinho, Parque Nacional Aparados da Serra, Mun. Cambará do Sul, *Falkenberg 361, 362, 2360* (FLOR); *Jarenkow in 6 Feb. 1983* (FLOR); *Rambo 49363* (PACA, RSA), *45585* (PACA), *53981* (SI); *Pirani & Yano 840* (SP); Tainhas, Mun. Cambará do Sul, *Vianna in 10 Feb. 1957* (ICN #1674); 10–11 km N of Tainhas on RS-020, *Falkenberg et al. 3746* (n = 44), *3747, 3748* (FLOR); 1–4 km N of Post Fiscal, NW of Serra da Rocinha, *Falkenberg et al. 3767* (n = 44), *3768, 3769* (FLOR); 1 km N of Silveira, *Falkenberg et al. 3770* (FLOR); 219 km N of Porto Alegre, *Lindeman & Haas 3734* (MBM); Serra da Rocinha, border RS-SC, Bom Jesus to Turvo, *Lindeman & Haas 9389* (ICN, U); *Rambo 53880* (B); *Sehman 4278* (B, PACA, SI); Bom Jesus, *Falkenberg 1234* (FLOR); Ausentes, Bom Jesus, *Falkenberg 1182, 1183* (FLOR); Cambará do Sul, *Falkenberg 263, 1119* (FLOR); *Rambo 36223* (ICN); Faxinal, Mun. Cambará do Sul, *Bonatto & Lima in 2 Apr. 1083* (FLOR); *Stehmann 450* (FLOR); *Sobral 2813* (FLOR); Esmeralda, Est. Ecol. Aracuri, *Jarenkow 60* (FLOR); Bom Jesus, Aparados da Serra, *Pabst 10201* (RB); *Rambo 8787* (PACA); Rio dos Touros, near Bom Jesus, *Rambo 8552* (PACA); Capela de São José, Aparados da Serra, Bom Jesus, *Smith & Klein 5914* (R, US); Cambará, São Francisco de Paula, *Rambo 36223* (PACA, S); Fazenda Bernardo Velho, Aparados da Serra, Bom Jesus, *Rambo 34864* (PACA, S); Aparados da Rocinha, Bom Jesus, *Rambo 45354* (PACA, S), *32487* (PACA); Passo do Guarda, Bom Jesus, *Rambo 51857* (PACA, S, US); Fazenda Englert, near São Francisco de Paula, *Rambo 54635* (B, PACA); near Montenegro, *Rambo 2204* (PACA); Agua Azul, near Caxias, *Henz in 3 Jan. 1947* (PACA #33277); Cerro do Umbu, near Osório, *Rambo 1284* (PACA); Caracol, near Canela, *Emrich in 6 Mar. 1946* (PACA #33277), *in 22 Mar. 1954* (PACA #54247); *Rambo 11998* (PACA); Vila Oliva, near Caxias, *Rambo 31024* (PACA), *31270* (R), *53880* (PACA), *56621* (PACA), *55021* (B, PACA); Passo do Socorro, near Vacaria, *Rambo 51576* (PACA, S), *51665* (PACA); 25 km N of Vacaria, *Pedersen 12739* (MO); 10 km S of Vacaria, *Lindeman & Haas 3734* (U); Fazenda da Ronda, near Vacaria, *Rambo 34864* (PACA, SI); Taimbé, São Francisco de Paula, *Sehnem 5125* (SI); Farroupilha, *Camargo 980* (PACA); Santa Rita, near Farroupilha, *Rambo 40172* (CAS, PACA, RSA), *45781* (MO, PACA, S), *45782* (PACA); Flores de Cunha, *Schultz 667* (ICN); Soledade near Passo Fundo, *Rambo 50039* (PACA); Jaquirana, São Francisco de Paula, *Rambo 51968* (PACA); Gramado-Cascata do Caracol, *Schweiger in Feb. 1924* (ICN #44812); Laje de Pedra, Canela, *Miotto 50* (ICN); Arroio Tatiuí, near Vila Assis, km 193 of BR-386, *Miotto et al. 184* (ICN); São Francisco de Paula, *Ferreira et al. 628* (ICN); no locality, *Waechter 1942* (ICN); *Rambo 9943* (PACA).

Fuchsia regia subsp. *reitzii* is distinguished by its whorled, membranous leaves with gland-serrate margins and a matte surface having more noticeable tertiary venation than the other subspecies of *F. regia*. Compared with *F. regia* subsp. *serrae*, the only other *Fuchsia* that grows near populations of subsp. *reitzii*, the sepals are much less joined and spreading (instead of recurved), the stipules are much less prominent, the leaf bases are more acute, and the berries are rounder. This subspecies is named in honor of P. Raulino Reitz of the Herbário Barbosa Rodrigues, Itajaí, Santa Catarina, who has made great contributions to the knowledge of the flora of Santa Catarina.

Subspecies *reitzii* is restricted to the planalto west of the coastal mountain ranges of southernmost Brazil. Its overall distribution in this area parallels that of *Araucaria angustifolia*, although it does not tolerate the shade of the dense conifer forests. Both species extend as far east as the edge of the coastal escarpments but end abruptly there

and do not appear on the seaward slopes or in the lower, coastal forest (Hueck, 1953).

Along the eastern edge of the planalto, where sharp drop-offs usually occur down to the Atlantic lowlands, the range of *F. regia* subsp. *reitzii* overlaps with *F. regia* subsp. *serrae*, which extends up from the moist, coastal slopes of the serras. A great deal of intergradation and variation exists in the *Fuchsia* populations of these areas, especially at the crest itself and just inland of the steep drop-offs. In some instances, the extreme local variability is indicative of hybrid swarms, while in other sites, odd variants are found that can extend beyond the normal limits of variation of either subspecies (see Appendix).

A number of unusually pubescent individuals, usually with conspicuously tan or ferrugineous hairs, occur in populations near the southern and western extremes of the range of subsp. *reitzii* in Rio Grande do Sul. Collections from the Farroupilha area, such as *Rambo 45781*, *45782*, and *40172* and *Camargo 980*, are uniformly pubescent, while others, such as *Rambo 31024* from Vila Oliva near Caxias, and *Rambo 51576* from Passo do Socorro near Vacaria, occur together with more typical subglabrous individuals of the subspecies.

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APPENDIX. Natural hybrids in *Fuchsia* sect. *Quelusia*

The main criterion used in detecting hybrids was the morphological intermediacy of several characters. In all cases, the putative parents were known to occur nearby.

1. *F. magellanica* × *F. lycioides*

F. macrostemma var. *parviflora* W. J. Hooker, Bot. Misc. 3: 309. TYPE: Chile. Valparaíso, 1832, *Bridges 199* (holotype, K—Benth.; isotype, CGE).

Specimens examined. CHILE. V REGION (VALPARAÍSO): Valparaíso, *Bertero 1006* (G, GH); in valleys near Valparaíso, *Bridges s.n.* (CGE, K—Hook.).

Representative cultivated specimens. CHILE: Juan

Fernández Islands, Más Atierra, *Meyer 9551* (MO). U.S.A. California: Berkeley, *Bracelin 1422* (BM). ZIMBABWE. Salisbury, *Biegel 5549* (K).

Fuchsia lycioides belongs to a different section, *Kierschlegeria*, and differs widely from *F. magellanica* in its small, alternate leaves, spinose leaf bases, smaller flowers with included stamens and reflexed sepals, and generally occurs in much drier habitats. Both species are tetraploid (Hoshino & Berry, 1989) and have been shown to be closely related by chloroplast DNA restriction site analysis (Sytsma & Smith, 1988). The ranges of the two species barely overlap in the hills around Valparaíso, where several natural hybrids were collected in the early 1800s. These plants are characterized by small flowers with larger, convolute petals than those of *F. lycioides*. The leaves are larger and more often opposite than in *F. lycioides*, with the characteristic dentation of *F. magellanica*. They also lack the spinose leaf bases typical of *F. lycioides*. The natural habitats where the early hybrids were collected have probably been totally eliminated by urban growth.

Hybrids of these two species appear quite often in cultivation and have sometimes been confused with the true *F. lycioides*, as in the cytological study of Chaudhuri (1956).

2. *F. regia* subsp. *regia* × *F. alpestris*

Specimens examined. BRAZIL. RIO DE JANEIRO: Pedra Dubois, Santa Maria Madalena, *Santos Lima & Brade 14240* (B, RB); *Plowman & de Lima 12885* (F, MO).

Both parental species occur locally on Pedra Dubois; the specimens cited above are intermediate in their short, fine pubescence, petiole length (6–10 mm), and flower size (floral tubes 10–12 mm long).

3. *F. regia* subsp. *serrae* × *F. brevilobis*

Specimens examined. BRAZIL. SÃO PAULO: Reserva Carlos Botelho, between Sete Barras and São Miguel Arcangel, 800 m, *Prance et al. 6896* (MBM). PARANÁ: 13 km W of Sesmaria and Rio Capivari, Mun. Bocaiúva do Sul, 815 m, *Berry et al. 4448* (MBM, MO; $n = 44$); road from Eng°. Lange train station and Prainhas, 310 m, *Cordeiro et al. in 16 Jan. 1987* (MBM; $n = 22$).

Fuchsia brevilobis is sympatric with *F. regia* subsp. *serrae* over most of its range but usually grows at lower elevations. These taxa are unique in the section in having their sepals connate for more than one-third of their length, but *F. brevilobis* has more membranous leaves that are narrower, shorter-petioled, and more pubescent than *F. regia* subsp. *serrae*, while the latter has more prominent, persistent stipules. The flowers of *F. regia* subsp. *serrae* also differ from *F. brevilobis* in their four-ridged buds, glabrous, nitid surface, and flaring sepal tube. The intermediate individuals cited above are from three different localities where the parent species are locally present. In the Capivari locality, the same hummingbird was observed visiting flowers of both species in succession.

Further experimental work on artificial hybrids of these two taxa is desirable, since only tetraploid counts have been obtained from *F. brevilobis*, and all individuals examined of *F. regia* subsp. *serrae* have been octoploid (Hoshino & Berry, 1989). The count obtained from *Cordeiro et al. in 16 Jan 1987* was tetraploid, indicating that it may only be a variant of *F. brevilobis*, and that of *Berry et al. 4448* was octoploid, as found in *F. regia* subsp. *serrae*.

4. *F. regia* subsp. *regia* × *F. campos-portoi*

Specimens examined. BRAZIL. RIO DE JANEIRO: Itatiaia, just above Hotel Brocken-Holsene, road to Abrigo Rebouças, 2,340 m, *Berry et al. 4440* (MO, RB; $n = 22$); Itatiaia, Agulhas Negras, *Lanstyak 253* (RB #61360).

Fuchsia campos-portoi is endemic to the high-altitude campos of Mount Itatiaia and is very distinctive in its small, narrow, strongly serrate leaves and small, short-tubed flowers. *Fuchsia regia* is common in forests at lower elevations on the same mountain range and occurs together with *F. campos-portoi* in thickets near the treeline above 2,200 m. Both specimens cited above are intermediate in leaf size, number of secondary veins, and floral features, such as the ratio of tube to sepal lengths. Meiosis in buds of *Berry et al. 4440* was normal, with the same chromosome number as recorded in local parental populations.

5. *F. regia* subsp. *regia* × *F. coccinea*

Specimens examined. BRAZIL. MINAS GERAIS: Serra do Itacolomi, near base of Pico do Itacolomi, 1,500–1,700 m, *Badini 22451* (OUPR); *Berry et al. 4546* ($n = 22$), *4547*, *4548* (MO, RB); *Falkenberg 3380* (FLOR); *Mello Barreto 9168* (R); Serra da Caraça, *Mello Barreto 7157* (BHMH).

Fuchsia coccinea typically grows in thickets amid the rocky, open campo of the highest peaks in Minas Gerais. On the Serra do Itacolomi, fire has destroyed much of the woody vegetation on the highest slopes; *F. coccinea* is now very rare in that area, and intermediate forms with *F. regia* are common. In the series of *Berry 4545–4550* and *Falkenberg 3380–3387*, some of the individ-

uals were treated under *F. coccinea*, but several of them show signs of introgression with *F. regia*, such as leaves that are larger or more coriaceous and rounder-based than individuals of isolated populations of *F. coccinea*. The collections cited above are clearly intermediate between the two species in key characters, such as petiole length, degree of leaf pubescence, and leaf shape. Both species are tetraploid in this locality, and the one hybrid examined cytologically was tetraploid with normal bivalent formation.

Both species are also known together from the Pico do Itambé, farther north in the Serra do Espinhaço. Although the collections of *Anderson et al. 35832* and *Furlan et al. 3058* were treated under *F. coccinea*, they both have unusually thick leaves for that species, as well as rounded rather than cordate leaf bases; these traits may be the result of introgression with sympatric populations of *F. regia*.

6. *F. regia* subsp. *regia* × *F. glazioviana*

Specimens examined. BRAZIL. RIO DE JANEIRO: Morro da Nova Caledônia, outskirts of Nova Friburgo, 1,810–1,950 m, *Berry et al. 4424*, *4427* (MO, RB), *4429* (RB), *4430* (MO, RB; $n = 22$).

As in the previous two cases, *F. glazioviana* is a local, high-elevation endemic that is sympatric with *F. regia* near the former's lower altitudinal limits. *Fuchsia glazioviana* has small, densely packed leaves and smaller, narrower flowers than *F. regia*. Most of the hybrids were found along roadsides in cleared areas, and one large patch of variable individuals was seen in an exposed area near the upper limit of the cloud forest. Local populations of both species are tetraploid, as was the one intermediate individual counted.

7. *F. regia* subsp. *serrae* × *F. regia* subsp. *regia*

Specimens examined. BRAZIL. SÃO PAULO–RIO DE JANEIRO BORDER AREA: Reserva Florestal da Bocaina, *Sucre et al. 2932* (AAU, MO, RB, US); Serra da Bocaina, road to old Estação de Fruticultura (now IBDF park HQ), *Duarte 7689* (MO, RB); *Handro 807* (SP); *Ramamoorthy & Vital 1176* (MO; $n = 44$); Bananal, Rio Bonito, Serra da Bocaina, 1,000–1,100 m, *Martinelli et al. 7779* (RB); Bananal, Sertão do Rio Vermelho, E of Bocaina, *Brade 15269* (RB); Sertão Bocaina, *Pabst 4744* (MO).

Populations of *F. regia* subsp. *serrae* and subsp. *regia* converge and intergrade extensively on the upper, seaward slopes of the Serra da Bocaina, close to the Rio de Janeiro–São Paulo border. *Fuchsia regia* subsp. *regia* reaches its southernmost limits in the Serra da Bocaina, occurring mostly at altitudes of 1,100–1,550 m on both sides of the Serra. *Fuchsia regia* subsp. *serrae* occurs exclusively on the lower, seaward slopes of the same range between 500 and 1,150 m, part of an almost continuous distribution down the coastal slopes of the Serra do Mar and Serra Geral as far as Rio Grande do Sul.

Varied intermediate forms between the two subspecies occur between 1,150 and 1,350 m on the upper slopes of the Serra da Bocaina, along the road from Cunha to Paraty. Most of the fuchsias in this area, including those cited in the above list, are unusually pubescent for *F. regia*. The degree of sepal connation and the thickness and persistence of the stipules, which generally distinguish these taxa, vary widely between individuals in this area, whereas populations higher up on the Serra and further inland are largely glabrous and fall well within the normal range of variation of *F. regia* subsp. *regia*. Hoshino & Berry (1989) reported tetraploid and octoploid individuals of *Fuchsia* from this area, further indicating the intergradation of the basically octoploid subsp. *serrae* and the mostly tetraploid subsp. *regia*. Hexaploid hybrids should be sought in mixed populations.

Although *F. regia* subsp. *regia* is not found further south in São Paulo, more populations of aberrant or intermediate individuals occur as far south as the Serra do Mar above Ubatuba, approximately 60 km south of the Bocaina massif. Tetraploid and octoploid individuals occur side by side at the Alto da Serra near the crest of the mountain (Hoshino & Berry, 1989), again with the unusual pubescence for *F. regia* and considerable variability in such traits as the degree of stipule development. In most other features, however, these individuals resemble *F. regia* subsp. *serrae* more closely than subsp. *regia*.

8. *F. regia* subsp. *serrae* × *F. regia* subsp. *reitzii*

Specimens examined. BRAZIL. SANTA CATARINA: top of Serra Geral and escarpments, km 22–25 from Lauro Müller to Bom Jardim da Serra, 1,270–1,450 m, *Berry et al. 4517*, *4519* (MBM, MO); *Falkenberg 2302* (FLOR); Rio Caveiras a Lajes, *Lutz in 29 Dec. 1949* (R #116687); Serra da Rocinha, border of Santa Catarina and Rio Grande do Sul, 1,250–1,280 m, 22 km above Timbé do Sul, *Falkenberg et al. 3762* (FLOR, MO; the whole series of *Falkenberg et al. 3756–3766* is a variable series of mostly intermediate variants); *Rambo 4604* (PACA); NW of Uribici, km 90 of road to Braço do Norte, 950 m, *Falkenberg et al. 3784* (FLOR, MO). RIO GRANDE DO SUL: Itaimbezinho, Aparados da Serra, *Falkenberg 261*, *264*, *275*, *354*, *357* (FLOR); *Pirani & Yano 839* (SP); *Rambo 49363*, *50150* (PACA); Caracol, near Canela, *Emrich in Feb. 1951* (PACA 50187); *Lindeman & Haas s.n.* (ICN #21790); 18 km N of Canela, Salto da Ferradura, *Schultz s.n.* (ICN #21032); Bom Jesus, *Fal-*

kenberg 1150 (FLOR); Taimbé, São Francisco de Paula, *Rambo 49363* (SI); Fazenda Bernardo Velho, Aparados da Serra, Bom Jesus, *Rambo 34864* (SI).

Both of these two subspecies are morphologically and ecologically distinct over most of their ranges, with *F. regia* subsp. *reitzii* confined to thickets in the southern planalto and *F. regia* subsp. *serrae* inhabiting the wet, seaward slopes of the coastal mountain ranges. *Fuchsia regia* subsp. *serrae* has nitid, subcoriaceous leaves with thick stipules and flowers with strongly connate, recurved sepals, while subsp. *reitzii* has thinner, more whorled leaves with serrate margins, thin stipules, and flowers with spreading, slightly connate sepals.

A narrow ecotone occurs all along the crest of the Serra do Mar and the Serra Geral in Santa Catarina and Rio Grande do Sul as the high rolling plains end and the steep coastal ranges drop abruptly to the Atlantic lowlands. Along this belt, which occurs sometimes just at the crest of the ridges and other times extends a few hundred meters or several kilometers inland, the two subspecies of *F. regia* converge and intergrade in a bewildering variety of variants, some of them exceeding the normal limits of variation of either parental subspecies.

The narrowest ecotone observed was at the Serra da Rocinha, on the Santa Catarina–Rio Grande do Sul border. In this area, the planalto is covered right to the edge by grassy campos, followed by steep drop-offs covered by a special "Aparados" flora adapted to the persistent rains and mists from the rising coastal air masses (Rambo, 1956). Along the rim of the serra cliffs, between 1,250 and 1,280 m, hybrid swarms of *F. regia* subsp. *serrae* and *reitzii* occur together with occasional plants that can be distinguished as parental, such as those included in the collection series of *Falkenberg et al. 3756–3766.*

Other areas where similar series of intermediates have been observed and collected include the Aparados da Serra at Itaimbezinho, in Rio Grande do Sul, and the area around the crest of the Serra Geral between Bom Jardim da Serra and Lauro Müller in Santa Catarina. Near the town of Urubici, Santa Catarina, plants of *F. regia* subsp. *serrae* occur farther inland from the crest of the Serra Geral, around the base of the Morro da Igreja and Campo dos Padres, the highest points in Santa Catarina. Where the two subspecies occurred sympatrically, as in the collection series of *Falkenberg et al. 3787–3791* (FLOR, MO; just W of the crest of the ridge between Urubici and Braço do Norte, at 1,030 m), some unusual variants of subsp. *serrae* were found with flowers less than half the normal size (*#3790*).

Both subspecies are octoploid and are characterized by variable numbers of multivalents during meiotic metaphase (Hoshino & Berry, 1989); the one intermediate individual examined had the same chromosome number and type of meiotic configuration.

OBSERVATIONS ON POLYPLOIDY IN *FUCHSIA* SECTS. *QUELUSIA* AND *KIERSCHLEGERIA* (ONAGRACEAE)[1]

Takuji Hoshino[2] *and Paul E. Berry*[3]

ABSTRACT

Chromosome numbers are reported for all eleven taxa currently recognized in *Fuchsia* sect. *Quelusia* and for *F. lycioides*, the sole member of sect. *Kierschlegeria*. Results are based on the study of individuals from 103 native populations and 13 cultivated plants. Most species and sections of *Fuchsia* are diploid ($n = x = 11$), but sects. *Quelusia* and *Kierschlegeria* are entirely polyploid, including the only naturally occurring octoploids in the genus. Polyploidy in these sections is always associated with 3(4)-aperturate pollen grains, instead of the normal 2-aperturate condition in the genus. All chromosome counts obtained from *F. lycioides* and from seven of the nine species in sect. *Quelusia* were tetraploid, but intraspecific variation in ploidy level was found in two Brazilian species of sect. *Quelusia*. The only wild individual examined of *F. alpestris* was tetraploid, whereas a cultivated specimen of this species from Europe was octoploid. In the widespread, polytypic *F. regia*, all individuals examined of subspecies *reitzii* and *serrae* were octoploid, but both tetraploid and octoploid populations were found in subsp. *regia*. Both ploidy levels were also found in the extreme northern range of subsp. *serrae*, in individuals that were morphologically intermediate with subsp. *regia*. This situation suggests that octoploidy has evolved recently and possibly repeatedly in sect. *Quelusia*, whereas tetraploidy probably originated in a common ancestor to sects. *Quelusia* and *Kierschlegeria*.

Fuchsia is one of the largest genera of the Onagraceae, with over 100 species occurring mostly in tropical montane cloud forests. It is placed in its own tribe, Fuchsieae, on the basis of its fleshy fruits and mostly 2-aperturate pollen. Chromosomes in *Fuchsia* are large and are heterogeneous in size for the family, with interphase nuclei having pycnotic areas that are variable in number, size, and density (Kurabayashi et al., 1962); these are unspecialized features shared with *Lopezia* and *Circaea*. All species examined in the genus have the basic chromosome number of the family, $x = 11$ (Raven, 1979), and none have the translocation systems or aneuploidy that are characteristic of other onagraceous genera such as *Oenothera* and *Clarkia*.

In recent efforts to improve our understanding of the relationships of the different species and sections of *Fuchsia*, the distribution of chromosome numbers has been determined for as many species as possible in the genus, together with extensive surveys of the palynology and foliar flavonoid chemistry of most taxa (Nowicke et al., 1984; Averett et al., 1986). To date, diploid chromosome counts ($n = 11$) have been obtained for 69 species and tetraploid counts ($n = 22$) for 10 species (Breedlove, 1969; Breedlove et al., 1982; Berry, 1982, 1985; Berry et al., 1988; Hoshino & Berry, 1988). Of the ten sections currently recognized in the genus (Berry et al., 1988), six are entirely diploid. The two largest sections, *Fuchsia* (61 species) and *Hemsleyella* (14 species), are predominantly diploid, but sect. *Fuchsia* has six known tetraploid or partly tetraploid species (Berry, 1982), and sect. *Hemsleyella* has two tetraploid species (Berry, 1985). This paper presents the results of

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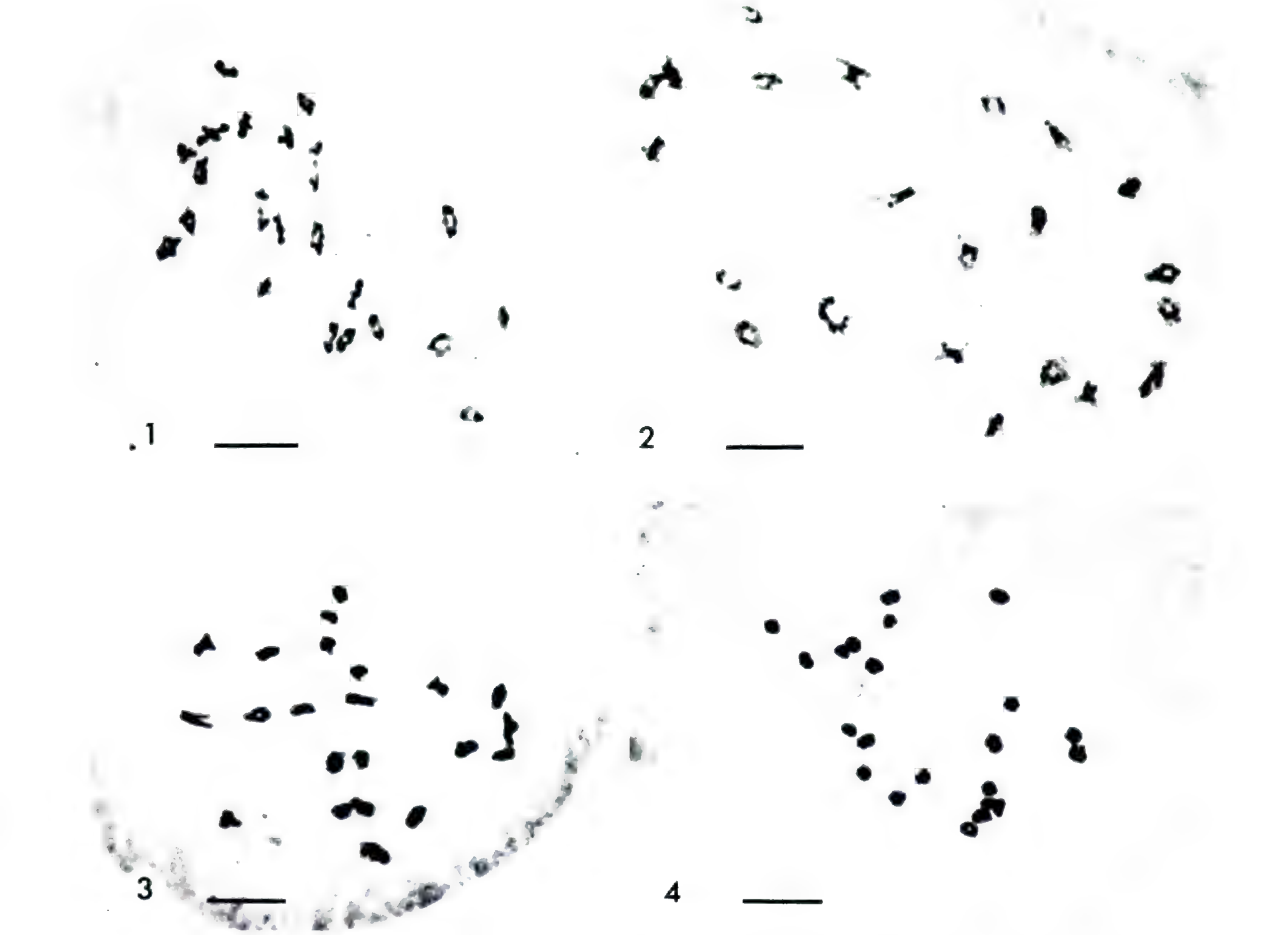
TABLE 1. Summary of chromosome numbers in *Fuchsia* sect. *Quelusia*.

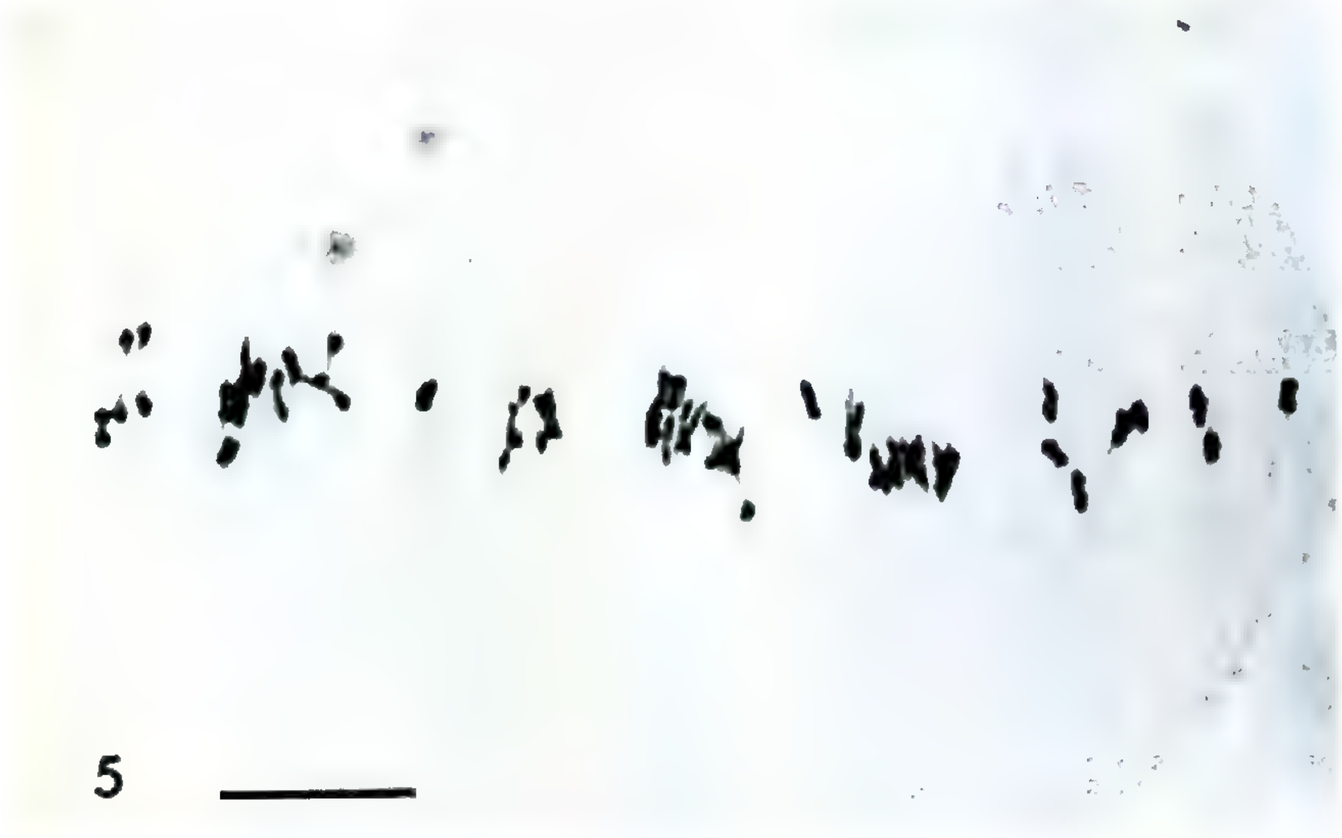
Taxon	Gametic Chromosome Number
F. alpestris Gardner	22, 44
F. bracelinae Munz	22
F. brevilobis P. Berry	22
F. campos-portoi Pilger & Schulze	22
F. coccinea Dryander	22
F. glazioviana Taubert	22
F. hatschbachii P. Berry	22
F. magellanica Lamarck	22
F. regia (Vellozo) Munz subsp. *regia*	22, 44
F. regia subsp. *reitzii* P. Berry	44
F. regia subsp. *serrae* P. Berry	44

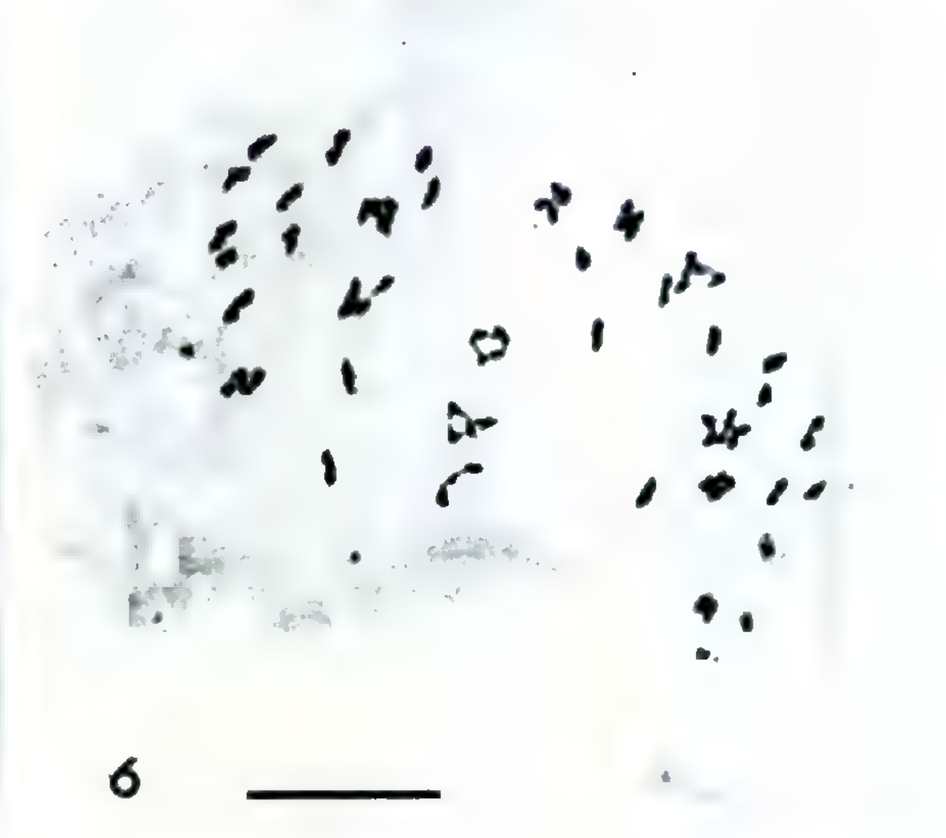
a comprehensive survey of the cytology of all 11 taxa of sect. *Quelusia*, concurrently with a systematic revision of the section (Berry, 1989). It also presents the first published counts for *Fuchsia lycioides*, the sole member of sect. *Kierschlegeria*.

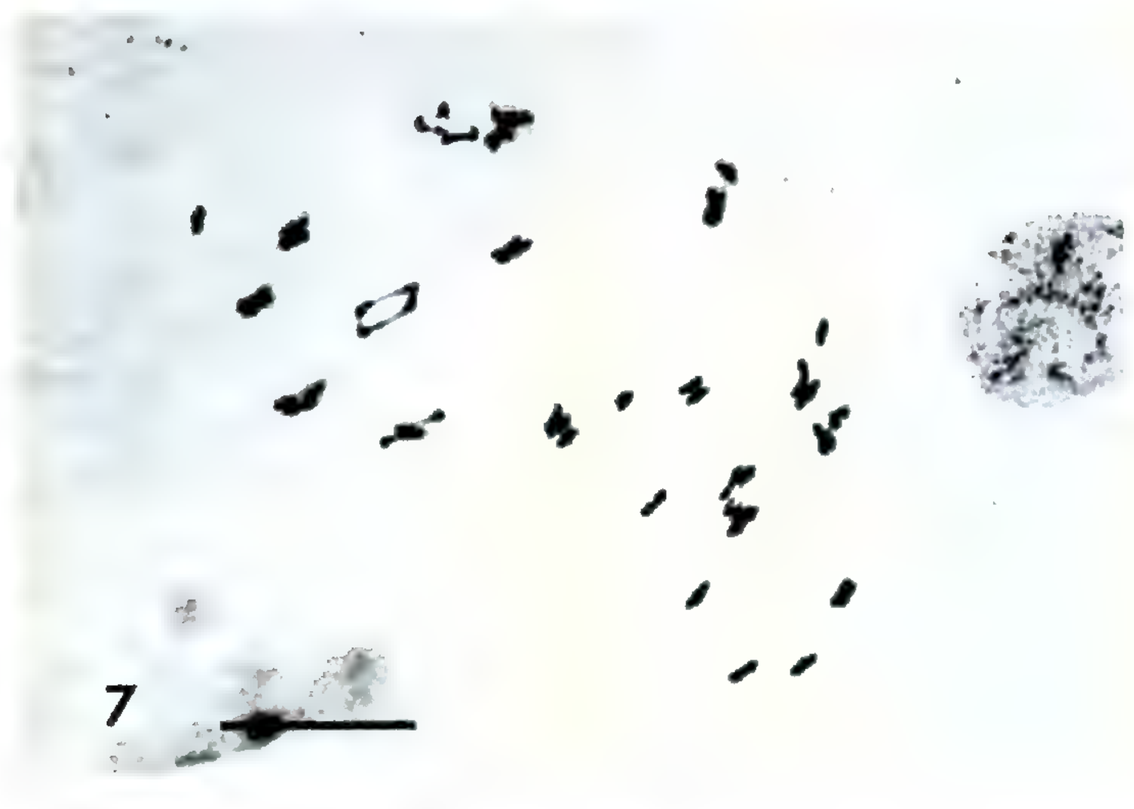
The only previous reports on chromosomes in sect. *Quelusia* were from *F. magellanica*. The first report by Warth (1923) was $n = 22$ for *F. coccinea*, but photographs in a subsequent publication (Warth, 1925) showed that this was a misidentification of *F. magellanica*. Johanssen (1929a, b) reported diploid counts of $n = 11$ for two horticultural selections of *F. magellanica*, but no vouchers or illustrations were provided to verify the identity of his plants, which were very likely misidentified (P. Raven, pers. comm.). A report of $2n = 44$ in *F. magellanica* by Haque (1952) also lacked vouchers. Chaudhuri (1956) made counts of $n = 22$ in *F. magellanica* and noted that it had



FIGURES 1–4. Photomicrographs of meiotic chromosomes of *Fuchsia* sect. *Quelusia*.—1. Metaphase I in *F. bracelinae* (*Berry et al. 4524*). $2n = 44$ (22II).—2. Diakinesis in *F. campos-portoi* (*Berry et al. 4435*). $2n = 44$ (22II).—3. Metaphase I in *F. coccinea* (*Berry et al. 4458*). $2n = 44$ (22II).—4. Metaphase I in *F. regia* subsp. *regia* (*Berry et al. 4544*). $2n = 44$ (22II). Scale bars = 10 μm.







FIGURES 5–8. Photomicrographs of meiotic metaphase chromosomes of *Fuchsia* sect. *Quelusia*.—5. *Fuchsia regia* subsp. *reitzii* (*Berry & Falkenberg 4510*). $2n = 88$ (15IV & 14II).—6. *Fuchsia regia* subsp. *serrae* (*Berry et al. 4492*). $2n = 88$ (9IV & 26II).—7. *Fuchsia regia* subsp. *serrae* (*Berry et al. 4493*). $2n = 88$ (17IV & 10II).—8. *Fuchsia regia* subsp. *reitzii* (probable hybrid with subsp. *serrae*, from *Berry & Falkenberg 4517*). $2n = 88$ (15IV & 14II). Scale bars = 20 μm.

distinctly shorter chromosomes than several diploid species he examined in the genus. Kurabayashi et al. (1962) examined two different collections of *F. magellanica*, which they also found to be tetraploid with short chromosomes. Although Chaudhuri (1956) reported a tetraploid count for *F. lycioides*, no voucher specimens were provided, and his description of this entity clearly indicates that it was a hybrid, probably of *F. magellanica* × *F. lycioides* parentage.

Materials and Methods

Meiotic chromosomes were examined in pollen mother cells of young buds fixed in Carnoy's solution (3 : 1 absolute ethanol to glacial acetic acid) for 24 hours, then transferred to 70% ethanol for storage. Anthers were squashed in 1% aceto-orcein.

Somatic chromosomes were studied in root tip apices, which were pretreated in 0.002 M aqueous 8-hydroxyquinoline for 6 hours at 5°C, then fixed in Carnoy's solution and macerated in 10% HCl for 6 minutes at 60°C. The root tips were stained in 1% aceto-orcein for 10 or 20 minutes and then squashed.

To establish pollen fertility, pollen grains were stained with Alexander's solution (Alexander, 1969).

Results

Chromosome counts from 40 different populations of native and cultivated individuals of *F. magellanica* were consistently tetraploid ($n = 22$; Table 1, Appendix). The populations sampled covered most of the range of this widespread species of southern Argentina and Chile, leaving little doubt that it is cytologically uniform throughout its range.

Counts of all other taxa in sect. *Quelusia* represent their first validated chromosome reports (Table 1). Seven Brazilian species, including the newly described *F. brevilobis* and *F. hatschbachii* (Berry, 1989), are all tetraploid, based on at least two counts for each species. The Chilean *F. lycioides*

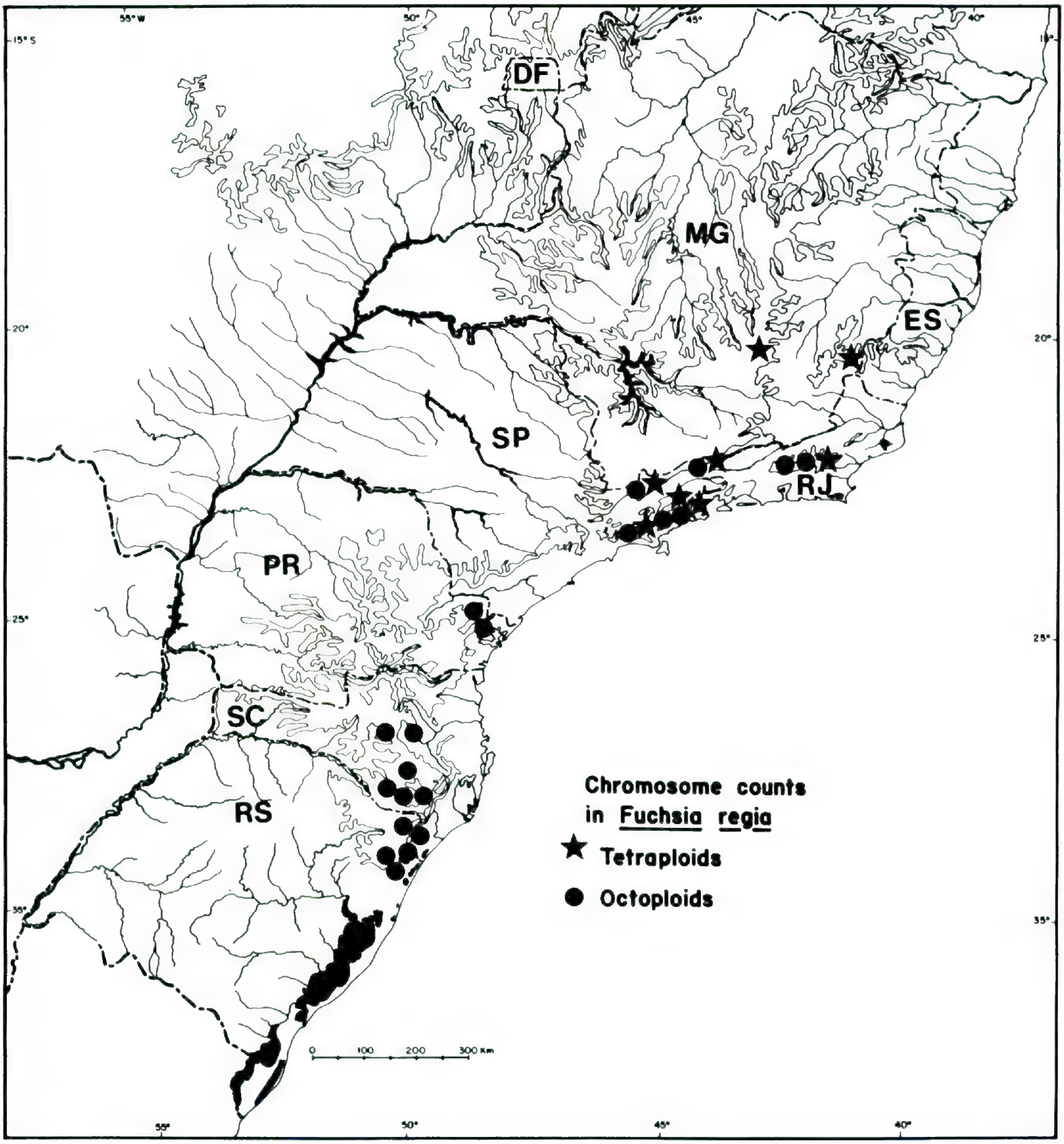
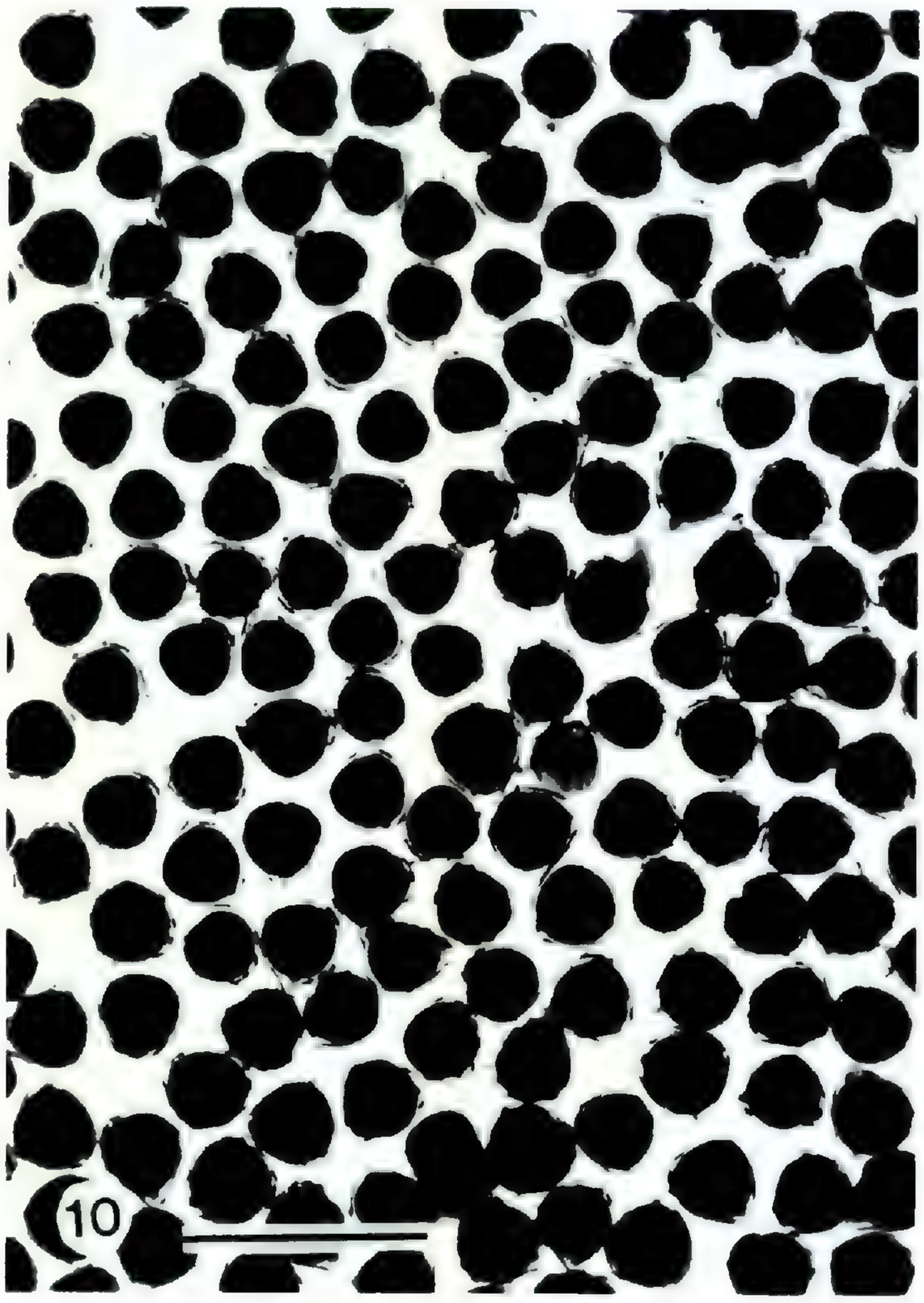


FIGURE 9. Geographical distributions of the different cytotypes of *Fuchsia regia* in southeastern Brazil. Pairs of capital letters refer to state abbreviations, RJ = Rio de Janeiro, etc. Contour lines indicated at 800 m.

(sect. *Kierschlegeria*) is also tetraploid. Normal bivalent formation was found in all tetraploid collections examined (Figs. 1–4). In the Brazilian *F. alpestris*, the single naturally occurring individual counted was tetraploid, but a plant of this species cultivated in Europe was octoploid.

Fuchsia regia, the most widespread species of the genus in Brazil, has tetraploid and octoploid populations (see Appendix). Populations from the southern half of its range were entirely octoploid, including all populations counted of subspecies *reitzii* and *serrae* and one naturally occurring hybrid between them. In most of the octoploids, numerous quadrivalents and bivalents were formed (Figs. 5–8).

Populations of *F. regia* subsp. *regia* with both tetraploid and octoploid individuals were found in northern São Paulo and southern Rio de Janeiro states (Appendix, Figure 9). The southernmost tetraploid individuals of *F. regia* came from north-central São Paulo State. These collections are morphologically intermediate, probable hybrids between subspecies *regia* and *serrae*. They also occurred sympatrically with octoploid individuals



FIGURES 10, 11. Photomicrographs of pollen grains from *Fuchsia* sect. *Quelusia*.—10. *Fuchsia regia* subsp. *serrae* ($2n = 88$) (*Ramamoorthy & Hatschbach 830*).—11. *Fuchsia regia* subsp. *regia* × *F. regia* subsp. *serrae* ($2n = 66$), artificial hybrid between *Ramamoorthy 683* (subsp. *regia*, $2n = 44$) and *Ramamoorthy & Hatschbach 830* (subsp. *serrae*, $2n = 88$), cultivated at Missouri Botanical Garden, *M2588*. Scale bars = 150 μm.

of *F. regia* subsp. *serrae*, but no hexaploid individuals were found in these areas. In Minas Gerais and other parts of Rio de Janeiro, all populations of subsp. *regia* sampled were tetraploid. The distribution of the different cytotypes of *F. regia* is shown in Figure 9.

Although meiosis was not observed in an artificial hexaploid hybrid between a tetraploid plant of *F. regia* subsp. *regia* and an octoploid one of subsp. *serrae*, more than 50% of the pollen grains of the hybrid were aborted. Both parents, however, showed fully stained and apparently viable pollen grains (Figs. 10, 11).

DISCUSSION

Sections *Kierschlegeria* and *Quelusia* are the only entirely polyploid sections of *Fuchsia*. In both groups, polyploidy is associated with 3-aperturate pollen, considered to be derived from the more common 2-aperturate condition in the genus (Nowicke et al., 1984). Despite differences between the two sections in viscin thread type (Nowicke et al., 1984), seed number and anatomy, sexual systems, and other morphological features (Berry, 1982), a preliminary chloroplast DNA restriction site analysis by Sytsma & Smith (1988) has shown the two sections to be more closely related to one another than to any other section of the genus. The results of a separate cladistic analysis of the species of these two sections by Berry (1989) were consistent with the hypothesis that tetraploidy evolved in a common ancestor. Since the other eight sections of the genus are predominantly diploid, including the South Pacific sect. *Skinnera* and all four Central American sections, it is clear that no existing member of sect. *Quelusia* or sect. *Kierschlegeria* could have directly given rise to those groups.

Octoploidy in natural populations of *Fuchsia* is known only in sect. *Quelusia*, where it has been detected primarily in *F. regia*, a species that also has tetraploid populations. Quadrivalents are common in the octoploid individuals examined, indicating a close chromosomal homology between the genomes that came together. Both the presence of different ploidy levels and the varying numbers of multivalents in *F. regia* indicate a recent origin of octoploidy in the genus. Whether the octoploidy detected in *F. alpestris* originated naturally or

under cultivation is not known, but the extent of the two different chromosome numbers needs to be examined further in nature. Cases of intraspecific polyploidy are widespread in the Onagraceae and have been recorded in over 40 species and 11 genera (Lewis, 1979).

The high level of pollen abortion in the artificial hexaploid between a tetraploid and an octoploid subspecies of *Fuchsia regia* is indicative of irregularities in meiotic pairing and disjunction, which may explain the absence of naturally occurring hexaploids among the individuals sampled in areas where tetraploids and octoploids both were found. Areas where tetraploid and octoploid populations of *F. regia* are known to occur sympatrically, such as the Serra da Bocaina and Campos do Jordão in northern São Paulo state, and the Itatiaia massif and the Serra dos Órgãos in Rio de Janeiro, should be sampled more intensively for naturally occurring hexaploids.

Within the Onagraceae, the pattern of polyploidy in *Fuchsia* sect. *Quelusia* is most similar to that of *Ludwigia*, where polyploidy has been a frequent and important part of the evolutionary strategy in most of the genus, with numerous cases of intraspecific polyploidy (Raven & Tai, 1979). Unlike the situation in tribe Onagreae, where polyploidy is associated with autogamy and aneuploidy in annual species, aneuploidy is unknown in *Fuchsia* and *Ludwigia*, and polyploid taxa are perennial and predominantly outcrossing. This clearly shows that the effects of polyploidy can vary widely in related genera, depending on factors such as the longevity of the species and the habitat in which they occur.

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Appendix I. Chromosome numbers in *Fuchsia* sects. *Quelusia* and *Kierschlegeria*.[4]

Fuchsia alpestris Gardner. Populations with $n = 22$.
Brazil. Rio de Janeiro: Teresópolis, *Berry et al. 4418*.
Fuchsia alpestris Gardner. Populations with $n = 44$.
Cultivated: The Netherlands, from plants long in cultivation in Europe, *Berry & Brako 001-86*.

[4] All counts were meiotic, except somatic counts indicated by "2*n*." Counts of Ramamoorthy collections were made by T. P. Ramamoorthy. Peter Raven counted both plants of *F. lycioides*; all other counts were made by the authors, except those with a cited reference. Only confirmed literature reports with vouchers or identifiable photographs were included. Unless otherwise indicated, voucher specimens are at the Missouri Botanical Garden (MO).

Fuchsia bracelinae Munz ($n = 22$).

BRAZIL. ESPÍRITO SANTO: Pico da Bandeira, *Berry et al. 4524, 4535*. MINAS GERAIS: Pico da Bandeira, *Berry et al. 4531*.

Fuchsia brevilobis P. Berry ($n = 22$).

BRAZIL: SÃO PAULO: 38 km NE of São Paulo–Paraná border, on Hwy. BR-116, *Davidse et al. 10902* ($n = 22$, $2n = 44$). PARANÁ: Mun. Bocaiúva do Sul, 3 km W of Sesmaria, *Berry & Juarez 4441*; Mun. Morretes, Porto de Cima, *Berry & Juarez 4495*; above Prainhas, *Cordeiro et al. 215* (MBM); below Estação Eng. Lange, road to Prainhas, *Cordeiro et al. 218* (MBM); Mun. Antonina, Cacatu, *Hatschbach et al. 50788* (MBM).

Fuchsia campos-portoi Pilger & Schulze ($n = 22$).

BRAZIL: RIO DE JANEIRO: Itatiaia, *Berry et al. 4435*, *Ramamoorthy & de Lima s.n.*

Fuchsia campos-portoi × *F. regia* subsp. *regia* (natural hybrid, $n = 22$).

BRAZIL: RIO DE JANEIRO: Itatiaia, *Berry et al. 4440*.

Fuchsia coccinea Dryander ($n = 22$).

BRAZIL: MINAS GERAIS: Serra da Piedade, *Berry et al. 4553, 4558*.

Fuchsia glazioviana Taubert ($n = 22$).

BRAZIL: RIO DE JANEIRO: Morro da Nova Caledônia, Nova Friburgo, *Berry et al. 4423, 4430* (probable introgressive hybrid with *F. regia* subsp. *regia*).

Fuchsia hatschbachii P. Berry ($n = 22$).

BRAZIL: PARANÁ: Mun. Campo Largo, Serra São Luis do Purunã, *Berry et al. 4458, 4461*; Mun. Bocaiúva do Sul, Bacaetava, *Kummrow et al. 2998* (MBM).

CULTIVATED: The Netherlands, from seed of *Berry 4464*, from Paraná, Brazil, *Berry & Brako 008-86*.

Fuchsia lycioides Andrews ($n = 22$).

CULTIVATED: University of California Botanical Garden, Berkeley, *UCBG # 53.1303-S2*, from seed of *Hartwig in 6 Oct. 1953*, from Punta Molles, Chile; University of California at Los Angeles, seedling from seed collected by D. M. Moore in Coquimbo, Chile ($2n = 44$; without voucher).

Fuchsia magellanica Lamarck ($n = 22$).

ARGENTINA: NEUQUÉN: Villa Angostura, Nahuel Huapi, *Diem 3614* ($2n = 44$), *3615* ($2n = 44$).

CHILE. BÍOBÍO (VIII Región): Concepción, Barrio Universitario, *Riquelme s.n.* ($2n = 44$); Las Canoas, Concepción to Chaimavida, *Riquelme s.n.* ($2n = 44$). LOS LAGOS (X Región): S of Valdivia, *Marticorena & Quezada 1671* ($2n = 44$), *1672* ($2n = 44$); Puente Rahue, Prov. Osorno, *Marticorena & Quezada 1676* ($2n = 44$); Frutillar Bajo, Prov. Llanquihue, *Marticorena & Quezada 1677* ($2n = 44$); Frutillar Bajo to Frutillar Alto, *Marticorena & Quezada 1678* ($2n = 44$); 2 km W of Llanquihue, *Marticorena & Quezada 1679* ($2n = 44$); 24 km S of Puerto Montt, *Marticorena & Quezada 1680* ($2n = 44$); El Avellanal, 8 km from Pargua, *Marticorena & Quezada 1682* ($2n = 44$); Prov. Chiloé, Chacao to Ancud, *Marticorena & Quezada 1683* ($2n = 44$); Paranqui to Curamo, Chiloé, *Marticorena & Quezada 1684* ($2n = 44$); 4 km from Castro to Quellón, Chiloé, *Marticorena & Quezada 1686* ($2n = 44$), *1687* ($2n = 44$); Lago Natri, Chiloé, *Marticorena & Quezada 1689* ($2n = 44$); Rio Mollueco, Castro to Quellón, *Marticorena & Quezada 1692* ($2n = 44$); 3 km past Coinco Alto, Castro to Quellón, *Marticorena & Quezada 1693* ($2n = 44$); Quellón, *Marticorena & Quezada 1694* ($2n = 44$); Dalcahue, Castro to Ancud, *Marticorena & Quezada 1696* ($2n = 44$); Estero Mechaico to Río San Antonio, Castro to Ancud, *Marticorena & Quezada 1698* ($2n = 44$); Chamiza, Prov. Llanquihue, *Marticorena & Quezada 1699* ($2n = 44$); 2 km from Correntoso to Lago Chapo, *Marticorena & Quezada 1703* ($2n = 44$); Lago Chapo, *Marticorena & Quezada 1704* ($2n = 44$); Santa Ida, Lago Llanquihue, *Marticorena & Quezada 1706* ($2n = 44$); Puerto Varas to Ensenada, Lago Llanquihue, *Marticorena & Quezada 1707* ($2n = 44$); Saltos de Petrohué, Parque Nacional Vicente Rosales, *Marticorena & Quezada 1708* ($2n = 44$); Petrohué, Lago Todos Los Santos, *Marticorena & Quezada 1709* ($2n = 44$); Río Cruzes, S of Lanco, Prov. Valdivia, *Marticorena & Quezada 1711* ($2n = 44$); Lastarria, Río Cautín, Prov. Cautín, *Marticorena & Quezada 1712* ($2n = 44$); 5 km S of Lautaro, Prov. Cautín, *Marticorena & Quezada 1713* ($2n = 44$); Corral, Valdivia, *Godoy s.n.* ($2n = 44$). MAGALLANES (XII Región): Punta Hatley, Seno Otway, *Pisano s.n.* ($2n = 44$); Fuerte Bulnes, Magellan Straits, *Pisano s.n.* ($2n = 44$).

CULTIVATED: Ireland, *Nelson 576* ($2n = 44$), *1162* ($2n = 44$, previously living at MO); California, at Univ. California Botanic Garden, Berkeley ($n = 22$, $2n = 44$; Kurabayashi et al., 1962); Germany ($n = 22$; photograph in Warth, 1925, as "*F. coccinea*").

Fuchsia regia (Vellozo) Munz subsp. *regia*. Populations with $n = 22$.

BRAZIL: RIO DE JANEIRO: Morro da Nova Caledônia, Nova Friburgo, *Berry et al. 4425, 4433, 4424* (probable hybrid with *F. glazioviana*); Itatiaia, road to Planalto, *Berry et al. 072, 074, 076, 082*. MINAS GERAIS: Tronqueiras to Vale Verde, Alto Caparaó, *Berry et al. 4543*; Serra do Itacolomi, Ouro Preto, *Berry et al. 4544, 4546* (probable introgressive hybrid with *F. coccinea*). SÃO PAULO: 17 km SE of Campos do Jordão, *Ramamoorthy 683* ($2n = 44$); Campos do Jordão, *Berry et al. 089, 090, 091*; Serra da Bocaina, *Berry et al. 083, 085*.

CULTIVATED: The Netherlands, from seed of *Berry 4425*, from Rio de Janeiro, Brazil, *Berry & Brako 019-86*.

Fuchsia regia (Vellozo) Munz subsp. *regia*. Populations with $n = 44$.

BRAZIL. RIO DE JANEIRO: Teresópolis, *Berry et al. 4419*; Itatiaia, Planalto, *Berry et al. 4439*; Serra dos Órgãos, *Falkenberg & al. 3743* (FLOR). SÃO PAULO: Campos do Jordão, *Ramamoorthy & Vital 673, 676, 680*; Serra da Bocaina, *Ramamoorthy & de Lima 1178*.

Fuchsia regia subsp. *reitzii* P. Berry ($n = 44$).

BRAZIL. SANTA CATARINA: Curitibanos, *Berry & Falkenberg 4506* (multivalents common); Bom Jardim to São Joaquim, *Berry & Falkenberg 4510* (multivalents common), *4513*; Bom Jardim da Serra to Lauro Müller, *Berry & Falkenberg 4517* (probable hybrid with *F. regia* subsp. *serrae*; multivalents common); Mun. Uribici, SW of Uribici, *Falkenberg et al. 3777* (FLOR). RIO GRANDE DO SUL: E of Tainhas on RS-486, *Falkenberg et al. 3746* (FLOR); Posto Fiscal, W of Serra de Rocinha, *Falkenberg et al. 3767* (FLOR).

CULTIVATED: The Netherlands, from seed of *Berry & Falkenberg 4510*, from Santa Catarina, Brazil, *Berry & Brako 013-86*.

Fuchsia regia subsp. *serrae* P. Berry ($n = 44$).

BRAZIL: SÃO PAULO: road between Mogi das Cruzes and

Bertioga, *Pirani & Yano 640* (SP). PARANÁ: Mun. Bocaiúva do Sul, 9 km W of Sesmaria, *Berry & Juarez 4448* (possible hybrid with *F. brevilobis*); 12 km W of Sesmaria, *Berry & Juarez 4450*; Estrada da Graciosa, Mun. Morretes, *Berry et al. 4492* (multivalents common), *4493*; Mun. Morretes, *Ramamoorthy & Hatschbach 829* ($n = 44$, $2n = 88$), *830*. SANTA CATARINA: Rio do Sul to Curitibanos, *Berry & Falkenberg 4501* (multivalents common); from Taimbezinho to Praia Grande, *Falkenberg et al. 3752* (FLOR); 13 km above Timbé do Sul, below Serra da Rocinha, *Falkenberg et al. 3753* (FLOR). RIO GRANDE DO SUL: 20 km E of Tainhas on RS-486, *Falkenberg et al. 3744* (FLOR).

CULTIVATED: The Netherlands, from seed of *Berry 4450*, from Paraná, Brazil, *Berry & Brako 023-86*; the Netherlands, from seed of *Berry 4504*, from Santa Catarina, Brazil, *Berry & Brako 024-86*.

Fuchsia regia: plants intermediate between subsp. *regia* and subsp. *serrae* ($n = 22, 44$).

plants intermediate between subsp. *regia* and subsp. *serrae* ($n = 22, 44$).

BRAZIL. RIO DE JANEIRO: above Parati to Cunha, *Berry et al. 097* ($n = 44$), *100* ($n = 22$). SÃO PAULO: Alto da Serra, W of Ubatuba, *Berry et al. 095* ($n = 22$), *096* ($n = 44$); Alto da Serra, above Caraguatatuba, *Berry et al. 092* ($n = 22$), *Ramamoorthy & Vital 688* ($n = 44$, previously living specimen at MO); Serra da Bocaina, *Ramamoorthy & de Lima 1176* ($n = 44$).

Fuchsia regia subsp. *regia* × *F. regia* subsp. *serrae* ($2n = 66$).

Artificial hybrid between *Ramamoorthy 683* (subsp. *regia*, $n = 22$) and *Ramamoorthy & Hatschbach 830* (subsp. *serrae*, $n = 44$), cultivated at Missouri Botanical Garden, *M2588*.

NOTES ON THE *CORDIA PANAMENSIS* COMPLEX (BORAGINACEAE) AND A NEW SPECIES FROM COLOMBIA

Cordia is a large pantropical genus of about 300 species, divided by most recent authors into six sections (Nowicke & Miller, in press). Section *Myxa*, with over 150 species, is the largest in the Neotropics and includes all but one of the paleotropical species (Miller, 1985). It is difficult taxonomically because most of the groups that can be recognized within the section have obscure boundaries.

One such group is the *Cordia panamensis* Riley group (Miller, 1985), which is widespread in Central America, the West Indies, and northern South America. This group is particularly problematic in terms of its definition within sect. *Myxa*, as well as species delimitations within it. It is loosely defined and may very well not be monophyletic, yet the species all share a similar appearance and are often confused in herbaria. The *C. panamensis* group is characterized by ovate to lanceolate, scabrous to scabrid, usually anisophyllous leaves that generally dry brown. All of the species except *C. anisophylla* J. S. Miller are dioecious. Perhaps *C. bicolor* A. DC. and *C. sellowiana* Cham. should be included, but *C. bicolor* does not dry brown, and both species differ in being homostylous.

Sculpturing on the surface of the endocarps appears to be useful in distinguishing species of *Cordia* sect. *Myxa* (Miller, in prep.) but has not yet been used for this. Dried fruits of various species of the *C. panamensis* group were soaked in 5% NaOH for two days to soften the exocarp and mesocarp, then washed in running water to remove outer tissues and expose the cleaned, outer surface of the endocarp. *Cordia gentryi* has an endocarp with raised, quadrangular areas (Fig. 1C); in *C. anisophylla* the raised areas are much longer (Fig. 1D). Other members of the group have rugulose (*C. panamensis*, Fig. 1E) to spinulose (*C. hebeclada* I. M. Johnston, Fig. 1F) endocarps.

Recent studies of members of the *C. panamensis* group have helped clarify the relationships of species in Central America (Miller, 1985, 1988) and Venezuela (Gaviria, 1987). The group is defined here as consisting of ten species, but problems still exist with differentiating *C. panamensis* and *C. macrophylla*. I have seen little material of *C. macrophylla* and have maintained it as separate following Johnston (1949). As part of a review of the *C. panamensis* group, several novel collections from Pacific coastal Colombia appear to represent an undescribed species.

KEY TO THE SPECIES OF THE *CORDIA PANAMENSIS* GROUP

1a. Leaf apices acute to obtuse.
  2a. Stems, petioles, and inflorescence branches with echinate hairs ..... *C. cymosa* (J. D. Smith) Standley
  2b. Stems, petioles, and inflorescence branches with simple hairs.
    3a. Petioles longer than 15 mm; twigs puberulent to strigillose; South America ..... *C. tetrandra* Aubl.
    3b. Petioles shorter than 15 mm; twigs velutinous to hirsute; West Indies ..... *C. sulcata* DC.
1b. Leaf apices acuminate to caudate.
  4a. Twigs strigillose, the hairs appressed, short, white or translucent.
    5a. Flowers distylous; corollas longer than 10 mm; mature fruits ellipsoid, longer than 8 mm ..... *C. anisophylla* J. S. Miller
    5b. Flowers dioecious; corollas shorter than 5 mm; mature fruits ovoid, shorter than 8 mm ..... *C. sericicalyx* DC.
  4b. Twigs with erect or curly hairs or densely short-velutinous, or if strigillose, the hairs brown.
    6a. Leaf apices caudate; mature fruits longer than 14 mm, glabrous ..... *C. gentryi* J. S. Miller
    6b. Leaf apices acuminate; fruits shorter than 14 mm or puberulent.
      7a. Branches of the inflorescences ferruginous-tomentose; fruits puberulent ..... *C. toqueve* Aubl.
      7b. Branches of the inflorescence velutinous to hirsute; fruits glabrous.
        8a. Stems hirsute to hispid.
          9a. Twigs shaggy-velutinous; Jamaica ..... *C. macrophylla* L.
          9b. Twigs hirsute; Mexico to South America, Trinidad, and Tobago ..... *C. panamensis* Riley

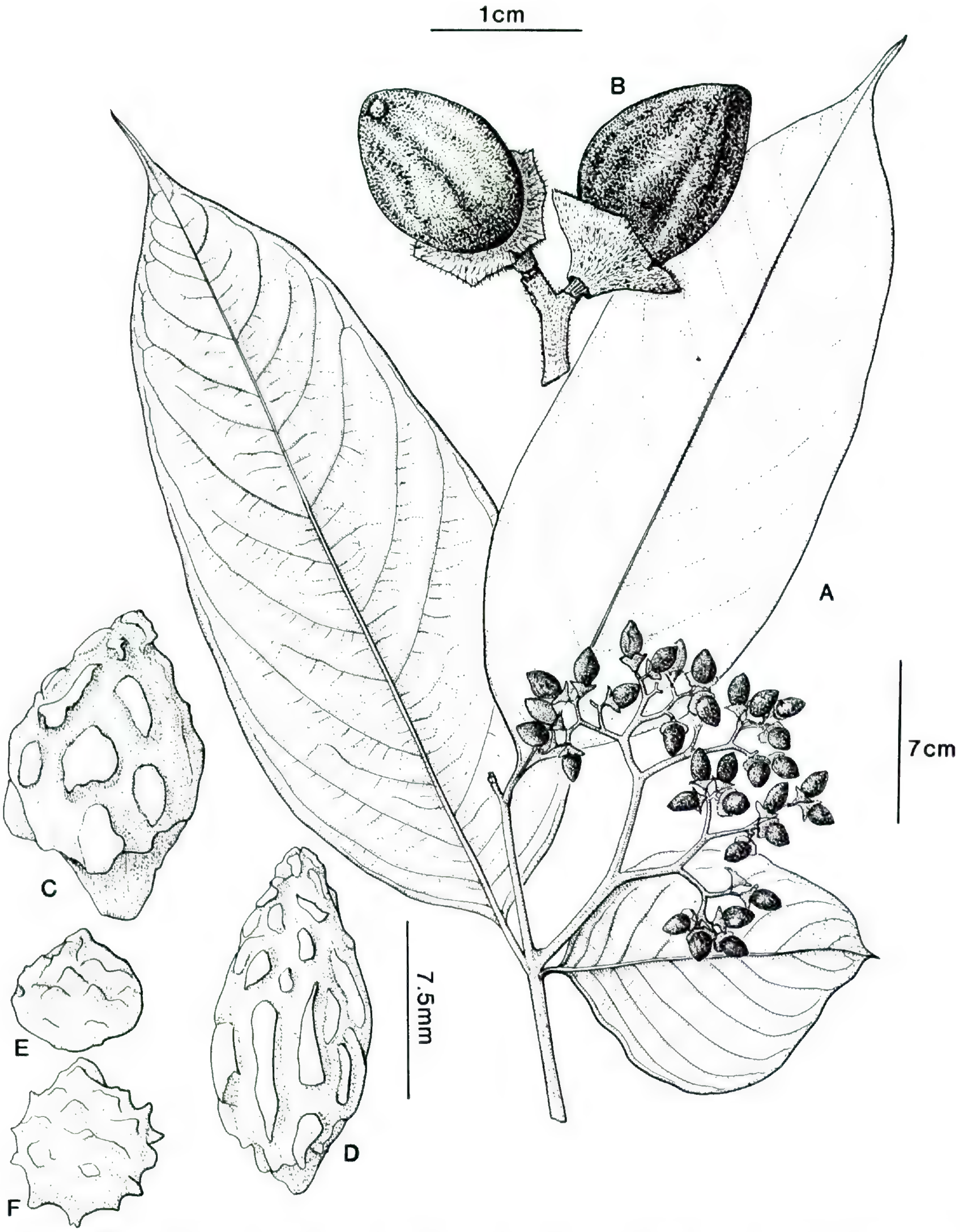

FIGURE 1. A–C. *Cordia gentryi* (*Gentry et al. 17874* (MO), Colombia).—A. Fruiting branch.—B. Fruits with persistent calyces. C. Dorsal view of endocarp. –D. *Cordia anisophylla* (*Mori & Kallunki 6373* (MO), Panama), dorsal view of endocarp.—E. *Cordia panamensis* (*Miller & Miller 961* (MO), Panama), dorsal view of endocarp. —F. *Cordia hebeclada* (*Gentry et al. 19686* (MO), Peru), dorsal view of endocarp.

8b. Stems pubescent to densely short velutinous.
9a. Fruits white; twigs hirsute to velutinous; upper leaf surface scabrous; West Indies ..... *C. sulcata* DC.
9b. Fruits yellow; twigs short and evenly golden brown velutinous; upper leaf surface glabrous to scabrid; Colombia, Ecuador, Peru ..... *C. hebeclada* I. M. Johnston

Cordia gentryi J. S. Miller, sp. nov. TYPE: Colombia. El Valle: Bajo Calima, Dindo area, 100 m, 11 July 1984, *A. Gentry, M. Monsalve & D. Wolfe 47874* (holotype, MO 3521285).

Arbor ad 8 m alta, ramunculis dense strigillosis ad puberulentis. Folia persistentia, petiolis 1.7–2.6 mm longis; laminae anisophyllae, folia maioribus ovatis, 30–35.3 cm longis, 10.7–13 cm latis, apice caudatis, basi obtusis, minoribus orbicularis, superficie scabrida, pagina inferiore grosse pubens. Flores ignoti. Fructus drupaceus, aurantiacus, endocarpo osseo, inaequilateraliter ovoideo, 16 mm longo, 10 mm lato.

Tree 8 m tall, the twigs densely puberulent with erect, brown hairs. Leaves persistent, dimorphic; petioles 1.7–2.6 mm long, canaliculate adaxially, puberulent, with erect, brown hairs; the larger blades narrowly ovate, 30–35.3 cm long, 10.7–13 cm wide, the apex caudate, 3–4 cm long, the base obtuse; smaller blades orbicular, 11–15.5 cm long, 9.5–14 cm wide, the apex abruptly short acuminate, the base rounded to acute, both types with the margin entire, the upper surface scabrous, the hairs translucent, appressed, the midrib raised, puberulent, the lower surface coarsely pubescent, with 6–10 pairs of secondary veins. Flowers unknown. Infructescence broadly cymose, ca. 13 cm broad. Fruits drupaceous, orange-yellow, the fruiting calyx slightly accrescent, unevenly 5-lobed, 9–11 mm broad, appearing torn along the margin, uniformly strigillose, somewhat sericeous inside, the mesocarp mucilaginous, the endocarp bony, inequilaterally ovoid, 16 mm long, 10 mm broad, the surface reticulate with raised quadrangular areas.

Distribution. *Cordia gentryi* is known from the Colombian provinces of Chocó and El Valle at elevations below 100 m in wet tropical forests.

Additional specimens examined. COLOMBIA. CHOCÓ: area of Baudó, on the right side of Río Baudó, about 13 km upstream from the estuary of Quebrada Carpio and the shore opposite Quebrada Cola Barquita, 11 Feb. 1967, *Fuchs & Zanella 21294* (MO). EL VALLE: Bajo Calima, ca. 10 km N of Buenaventura, Cartón de Colombia concession, transition between tropical wet and pluvial forest, ca. 50 m, 10 Dec. 1981, *Gentry 35508* (MO).

Cordia gentryi is most easily distinguished by its caudate leaf apex and large, orange-yellow fruits. It most resembles *C. panamensis* and *C. anisophylla* J. S. Miller. *Cordia panamensis* differs in having hirsute twigs and white fruits shorter than 7.5 mm. *Cordia anisophylla* differs in having thinner ellipsoid fruits 6–7.5 mm broad and less-prolonged leaf apices.

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NOTES

A NEW *ASPIDOGYNE* (ORCHIDACEAE) FROM VENEZUELAN GUAYANA

The genus *Aspidogyne* Garay is one of the recent segregates from *Erythrodes* Bl. (Garay, 1977) and comprises 27 species, widely distributed in the American tropics, primarily Brazil. They are small to medium-sized terrestrial, humicolous, to (rarely) subepiphytic herbs growing in mostly shady places of rain or cloud forests.

Aspidogyne belongs to the pantropical subtribe *Physurinae*, of seven genera. Among them, *Aspidogyne* can be recognized by the following combination of features: horizontal stigmata; elongate, erect column; and entire emarginate rostellum.

A revision of the *Aspidogyne* species of the Venezuelan Guayana for the orchid treatment in Steyermark's *Flora of the Venezuelan Guayana* has revealed a different identity for the species that appeared in Foldats (1970) as *Erythrodes picta* (Lyndley) Ames, a synonym of *Aspidogyne argentea* (Vell.) Garay. Foldats had already noted that the Venezuelan material cited under *E. picta* differed from the type, and suggested that it might represent a new variety. New evidence shows that the differences are sufficient for recognition of a new species, described below.

Aspidogyne steyermarkii Carnevali & Foldats, sp. nov. TYPE: Venezuela. Bolívar: cabeceras del Río Chicanán, Sierra de Lema, 80 km SW de El Dorado, 500 m, 6°5′N, 62°W, 22 Aug. 1967, *Steyermark 89371* (holotype, VEN; isotype, MO).

Species haec *A. argentea* (Vell.) Garay similis, at sepalo dorsali acuto, petalis non lobulatis, calcari cylindrico, labelli lobo centrali transvere rhombico recedit.

Terrestrial herbs, 9–19 cm high. Stems basally rhizomatose, creeping at the base, aphyllous, apically ascendent to erect, 2–6-foliate. Leaves deep olive-brown with red streaks on both sides of midrib and with the same colored spots near margin above, pale lavender with pale streaks and dots below, ovate to ovate-elliptic, acute, basally rounded to somewhat truncate, 7–28 mm long, 8–12 mm wide; petioles about 12 mm long, basally dilated and sheathing. Inflorescences of erect, laxly pauci- to pluriflorous racemes, 4.5–11 cm long, the peduncle densely pubescent. Flowers resupinate, small, with white tepals and labellum. Tepals uninnervate, subfleshy. Dorsal sepal elliptic, acute, 4 mm long, 1.2 mm wide; lateral sepals ovate-elliptic, subacute, basally attenuate, somewhat oblique, 5 mm long, 2 mm wide; petals narrowly obovate-elliptic, acute, 3.8 mm long, 1.1 mm wide. Labellum elliptic in overall outline, 5.1 mm long, 2.7 mm wide, contracted above its apical third, obovate below the contraction, dilated in a transversely rhombic terminal lobe above, 0.8 mm long, 1.2 mm wide, subacute. Spur cylindric, acute, slightly arched, 5.2 mm long, 0.7 mm thick. Column clavate, 3 mm long; rostellum aristate, acute.

This new species belongs in sect. *Argenteae* Garay. It is similar to *Aspidogyne argentea* (Vell.) Garay but differs by having acute (vs. rounded or obtuse) dorsal sepals, cylindric (vs. fusiform) spur, petals apically not lobulate, and the labellum with a transversely rhombic, subacute (vs. transversely obreniform, truncate, apiculate) apical lobe.

We are grateful to Lic. Bruno Manara for criticism of the Latin diagnosis and for the drawing.

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—Germán Carnevali and Ernesto Foldats, *both authors: Jardín Botánico de Caracas, Herbario Nacional de Venezuela, INPARQUES, Apartado 2156, Caracas 1010-A, Venezuela. Carnevali's current address: Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.*

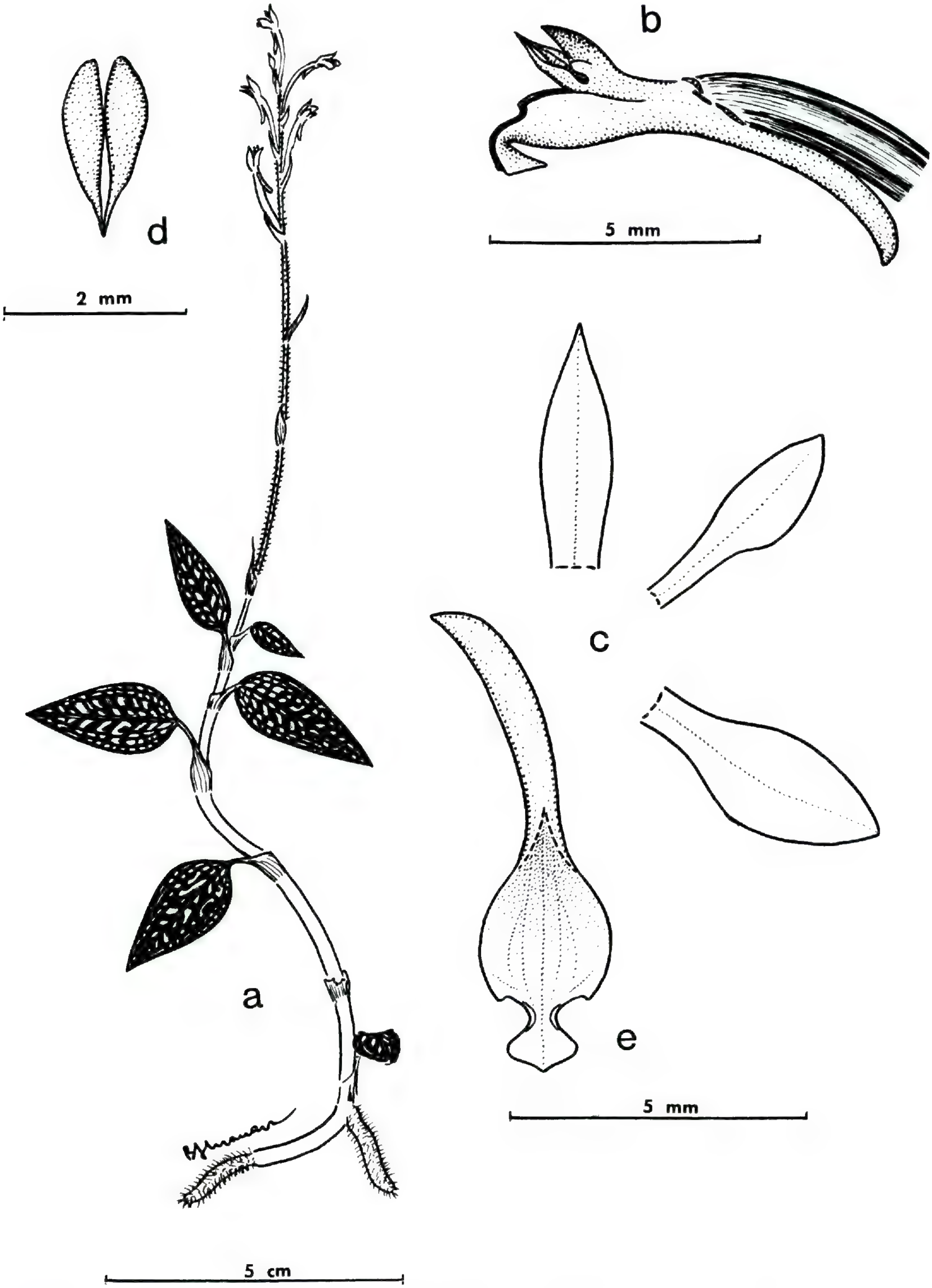

FIGURE 1. *Aspidogyne steyermarkii.*—a. Flowering habit.—b. Lateral view of labellum and column.—c. Perianth segments and labellum flattened.—d. Pollinia.—e. Labellum.

THREE NEW SPECIES OF *BOMAREA* (ALSTROEMERIACEAE) FROM MESOAMERICA

During preparation of the treatment of *Bomarea* Mirbel for the *Flora Mesoamericana*, I found three previously undescribed species in the Missouri Botanical Garden herbarium (MO). The types of all three species are from Panama, from where no new species have been described since the treatment of the genus in the *Flora of Panama* (Killip, 1945).

Characters of these new species common to all Alstroemeriaceae (Dahlgren et al., 1985) are: sepals 3; petals 3; stamens 6 with anthers pseudobasifixed (the tip of the filament inserted in a deep

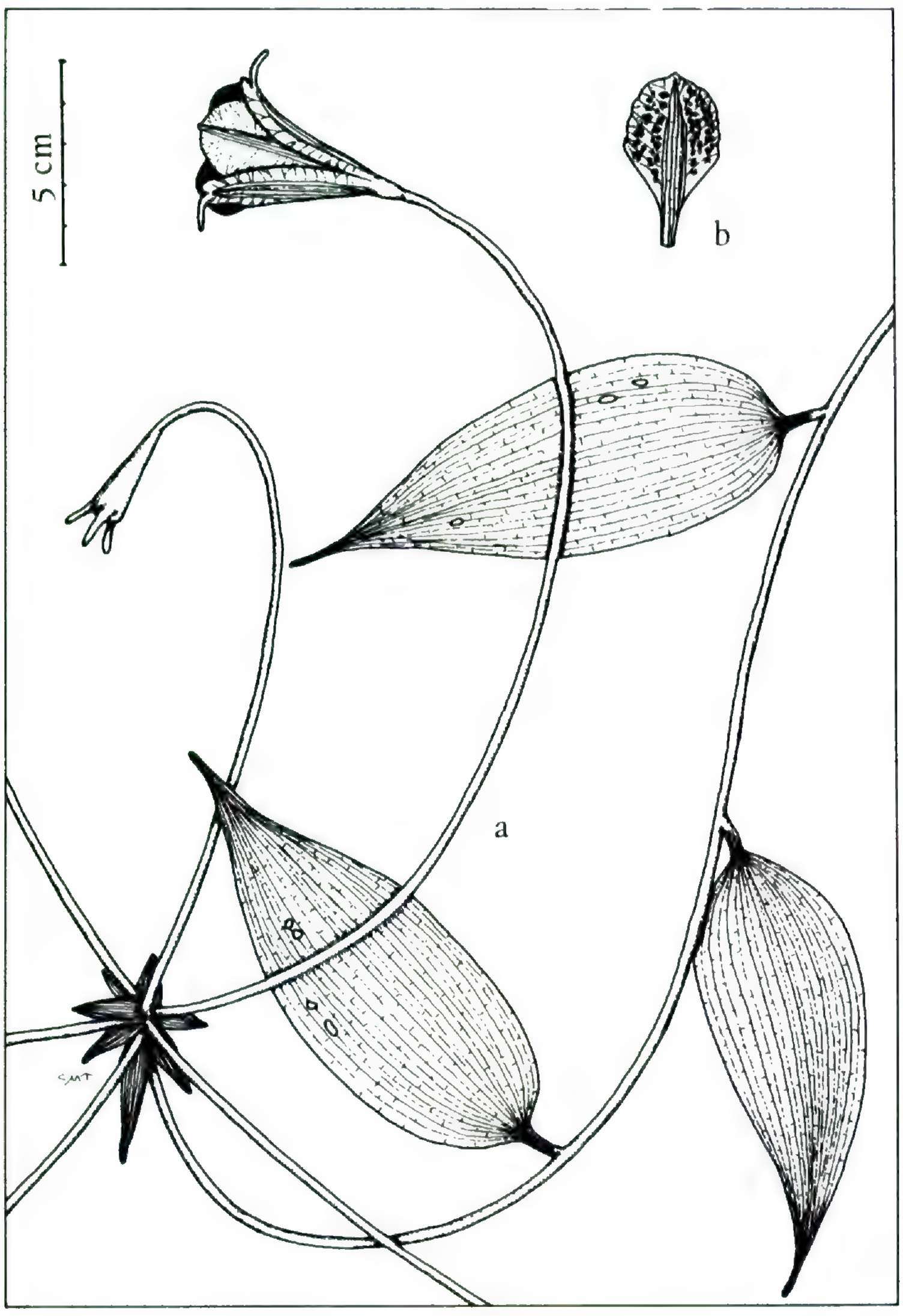

FIGURE 1. *Bomarea caudatisepala.*—a. Plant showing two inflorescence rays.—b. Petal, inside surface (same scale as a). (From holotype, with one leaf from *Sytsma et al. 4871.*)

pit) and introrsely dehiscent; style 1 with 3 stigmatic branches. Like all other Mesoamerican species of *Bomarea*, the new species have fully inferior ovaries and loculicidally dehiscent, capsular fruits. Stem diameter is measured between the first and second leaves below the umbel; length of compound umbel rays is measured from the involucre to base of the uppermost ovary.

Bomarea caudatisepala Gereau, sp. nov. TYPE: Panama. Chiriquí: 8°46′N, 82°25′W, upper NE slopes of Cerro Pate de Macho and along soggy ridge of Continental Divide, 1,900–2,000 m, 19 June 1987, *Croat 66496* (holotype, MO; isotype, PMA). Figure 1.

Herba volubilis caule glabro ad parce puberulo sub umbella. FOLIUM: lamina ovato-lanceolata, 6.9–12.5 cm longa × 2.7–4.5 cm lata, superne glabra, inferne secus nervos glabra ad parce crispato-pubescente. UMBELLA: bracteis involucralibus 5–8, 3.1–3.8 cm longis × 0.4–0.5 cm latis, glabris; radiis 6–14, 17.1–26.2 cm longis, saltem versus apicem parce fulvo-puberulis, simplicibus ebracteolatisque. FLOS: sepalis oblongo-lanceolatis, 3.6–4.0 cm longis × 0.9 cm latis, externe aurantiacis, unoquoque sepalo cornu viridi 7–10 mm longo sub apice 2–4 mm inserto munito; petalis obovatis, 3.8–4.3 cm longis × 1.6–1.7 cm latis, sepala per 2–5 mm excedentibus, externe aurantiacis, interne flavo-aurantiacis ad viridibus, purpureo-maculatis; ovario anguste obconico, sub anthesi 7–10 mm longo × 3–5 mm lato, parce fulvo-puberulo.

Vine; stem 2.0–2.5 mm diam., glabrous throughout to sparsely puberulent just below the umbel. Petiole 10–13 mm long; leaf blade ovate-lanceolate, 6.9–12.5 × 2.7–4.5 cm (L/W ratio = 2.6–3.0), glabrous above, glabrous to sparsely crisp-pubescent on the nerves beneath. Involucral bracts 5–8, 3.1–3.8 × 0.4–0.5 cm, glabrous; rays of the umbel 6–14, 17.1–26.2 cm long, sparsely brown-puberulent at least toward the tip, unbranched and ebracteolate. Sepals oblong-lanceolate, 3.6–4.0 × ca. 0.9 cm, externally orange with a green horn 7–10 mm long inserted 2–4 mm below the tip; petals obovate, 3.8–4.3 × 1.6–1.7 cm, exceeding the sepals by 2–5 mm, orange without, yellowish orange to green with purplish spots within; filaments 2.9–3.0 mm long; anthers 4.0–6.0 × 1.9–2.4 mm; ovary narrowly obconic, 7–10 × 3–5 at anthesis, sparsely brown puberulent; style 10–14 mm long; stigmatic branches 1.4–1.9 mm long.

Known only from three collections on Cerro Pate de Macho, in cloud forest and elfin forest at 1,700–2,100 m elevation.

Additional collections examined. PANAMA. CHIRIQUÍ: Cerro Pate Macho NE of Boquete, S slope along path to Finca Serrano, near the crest at ca. 2,000 m, 26 May 1981, *Andersson & Sytsma 1307* (GB, MO); SE slopes and summit Cerro Pate Macho, trail from Río Palo Alto, 4 km NE of Boquete, 1,700–2,100 m, 26 May 1981, *Sytsma, Knapp & Andersson 4871* (MO).

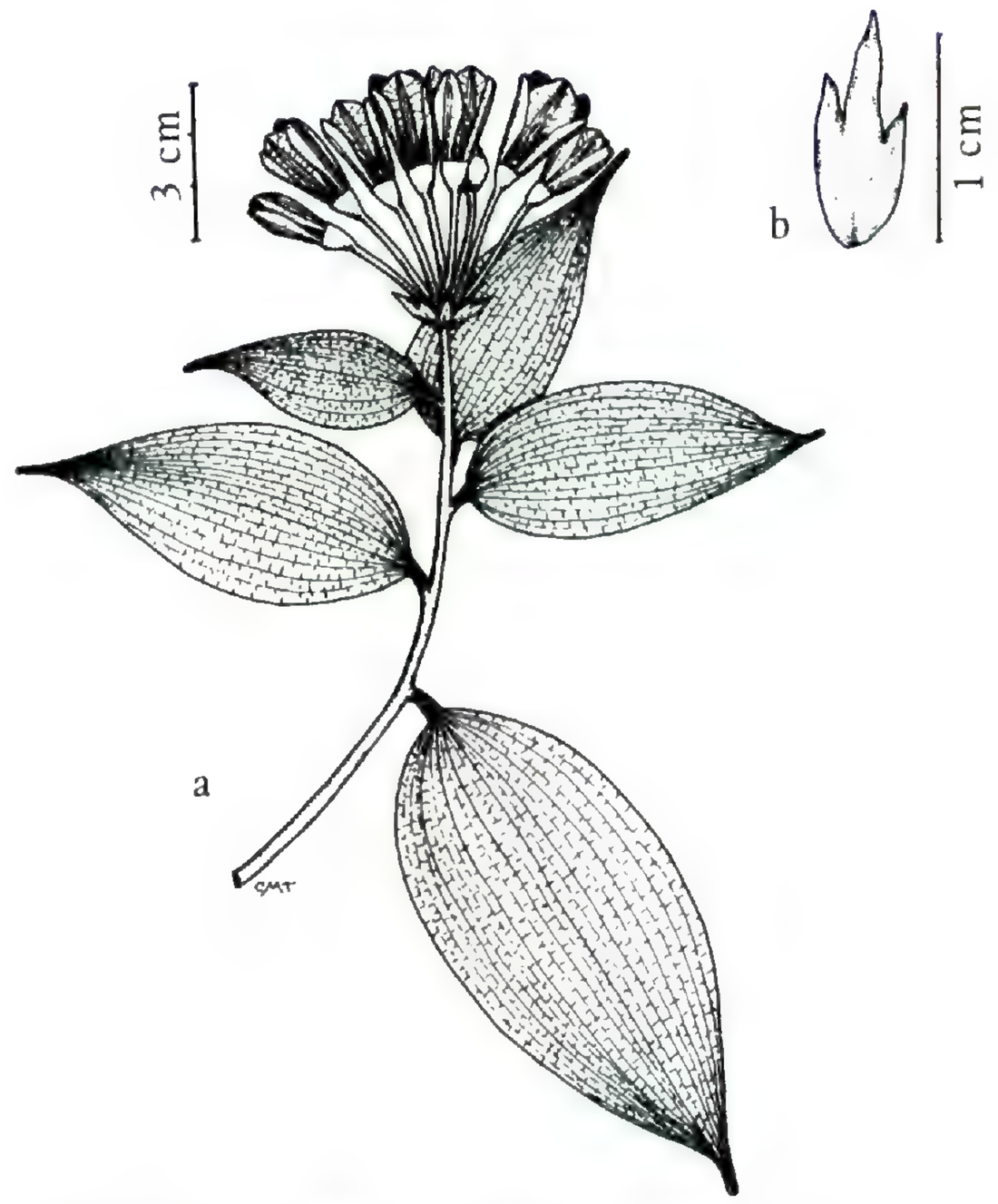

FIGURE 2. *Bomarea suberecta.*—a. Apex of plant with inflorescence.—b. Involucral bract. (From *McPherson 9333*, with one bud from holotype.)

This new species of uncertain affinity is easily distinguished from all other Mesoamerican *Bomarea* by the presence of a horn just below the tip of each sepal. Andean species with horned sepals all have much smaller flowers and further differ from *B. caudatisepala* in having very short umbel rays (*B. caudata* Killip, *B. cornigera* Herbert) or compound inflorescences (*B. cornuta* Herbert).

Bomarea suberecta Gereau, sp. nov. TYPE: Panama. Chiriquí: slope of Cerro Respinga above town of Cerro Punta, 2,500 m, 9 Aug. 1972, *W. G. & J. J. D'Arcy 6587* (holotype, MO). Figure 2.

Herba volubilis vel plerumque suberecta ad erecta, ubi erecta usque ad 2 m alta foliis inferioribus ad squamas reductis; rhizomate radices fibrosas in tumores tuberosos terminantes emittente; caule glabro ad puberulo pilis multicellularibus sub umbella. FOLIUM: lamina late ovata ad ovato-lanceolata, (6.0–)8.2–15.3 cm longa × 3.3–7.2 cm lata, utrinque glabra. UMBELLA: bracteis involucralibus 4–5, 0.9–2.0 cm longis × 0.4–0.6 cm latis, profunde trifidis lobo centrali lateralibus multo longiore, glabris; radiis 5–12, 2.2–4.3 cm longis, dense fulvo-puberulis, simplicibus, ebracteolatis vel (in typo tantum) supra medium bracteolam ca. 5 mm longam gerentibus. FLOS: sepalis oblongo-lanceolatis, 1.7–2.0 cm longis × 0.5–0.7 cm latis, base rubris ad aurantiacis sursum flavescentibus

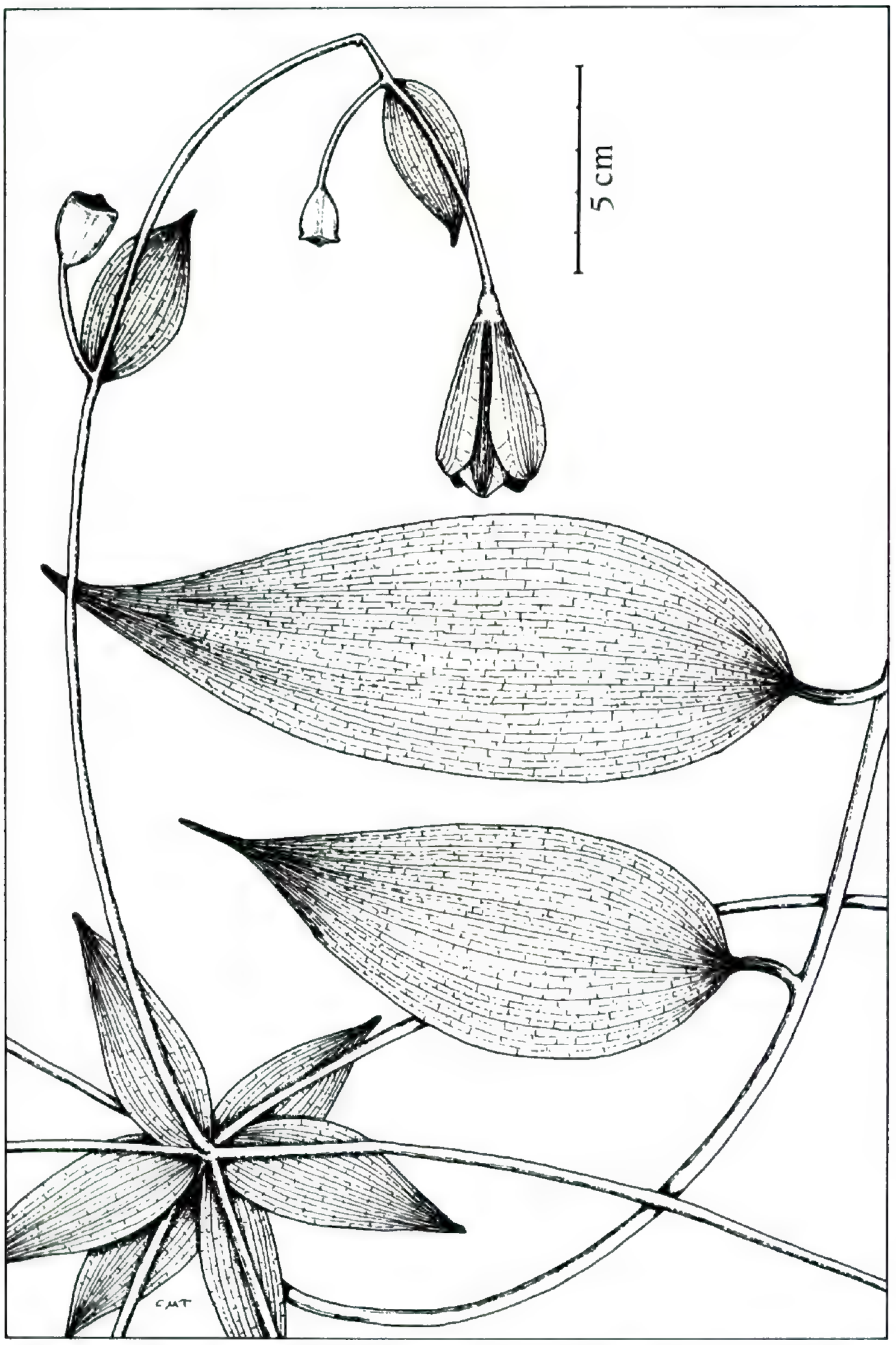

FIGURE 3. *Bomarea bracteolata*. Apex of plant showing one inflorescence ray. (From holotype.)

petalis obovatis, 1.8–2.2 cm longis × 0.7–1.0 cm latis, sepala per 1–3 mm excedentibus, flavis ad aurantiacis; ovario late obovoideo, sub anthesi 4–7 mm longo × 3–5 mm lato, dense fulvo-puberulo.

Vine or more often a suberect to erect herb to 2 m from a creeping rhizome with fibrous roots terminating in tuberous swellings, the lower leaves reduced to scales when plant erect; stem 1.9–4.9 mm diam., glabrous to short-puberulent with multicellular hairs just below the umbel. Petiole 7–16 mm long; leaf blade broadly ovate to ovate-lanceolate, (6.0–)8.2–15.3 × 3.3–7.2 cm (L/W ratio = 1.7–2.7(–3.0)), glabrous above and beneath. Involucral bracts 4–5, 0.9–2.0 × 0.4–0.6 cm, deeply trifid with central lobe much longer than lateral lobes, glabrous; rays of the umbel 5–12, 2.2–4.3 cm long, densely brown puberulent, unbranched, ebracteolate or bearing (only in type) above the middle a bracteole ca. 5 mm long. Sepals oblong-lanceolate, 1.7–2.0 × 0.5–0.7 cm, red to orange at the base, shading to yellow above and green at the tip; petals obovate, 1.8–2.2 × 0.7–1.0 cm, exceeding the sepals by 1–3 mm, yellow to orange; filaments 10–14 mm long; anthers 2.3–3.5 × 1.0–1.6 mm; ovary broadly obovoid, 4–7 × 3–5 mm at anthesis, densely brown puberulent; style 7–15 mm long; stigmatic branches 1.2–3.1 mm long.

Known from the vicinity of Cerro Punta and Cerro Pando (on Costa Rican frontier) in Panama, and from the Atlantic slope of the Cordillera de Talamanca in adjacent Costa Rica, in montane rain forest, *Quercus* forest, and elfin forest at 1,900–2,750 m elevation.

Additional collections examined. PANAMA. CHIRIQUÍ: Cerro Punta, 2,100 m, 3 July 1966, *Blum, Olson & Rasmussen 2428* (MO); Las Nubes, ca. 2,000 m, 7 Aug. 1984, *Croat 26454* (MO), *26472* (MO, PMA); above

Cerro Punta, 2,000 m, 9 May 1971, *D'Arcy 5365* (MO); 8°55′N, 82°44′W, E slopes of Cerro Pando, 2,000–2,300 m, 15 Oct. 1981, *Knapp 1650* (MO); 8°50′N, 82°35′W, road from Cerro Punta village towards Boquete near Bajo Grande, ca. 2,100 m, 5 June 1986, *McPherson 9333* (MO); 8°52′N, 82°33′W, Cerro Punta, along ridge to watershed to Bocas del Toro, 2,200 m, 26 Jan. 1985, *van der Werff & Herrera 6436* (MO, PMA); 8°50′N, 82°44′W, Santa Clara to Cerro Pando, 28 Feb. 1985, *van der Werff & Herrera 7252* (MO, PMA). COSTA RICA. LIMÓN: 9°00′–12′N, 82°57′–59′W, unnamed cordillera between Río Terbi and Río Siní, 2,300–2,500 m, 11 Sep. 1984, *Davidse, Herrera Ch. & Grayum 28957* (MO), 2,400–2,750 m, 13 Sep. 1984, *29046* (CR, MO); 9°14′–15′N, 82°59′W, Kámuk massif, ridge between Río Tararia and NE-most páramo, 1,900–2,300 m, 16 Sep. 1984, *Davidse & Herrera Ch. 29206* (MO).

This new species is distinguished by its deeply trifid involucral bracts; these organs are entire in all other known members of the genus. In Mesoamerica, the new species could only be confused with *B. acutifolia* (Link & Otto) Herbert. In addition to its entire involucral bracts, *B. acutifolia* has larger flowers (petals 2.6–3.9 cm long) than *B. suberecta* and a consistently twining or trailing habit. The suberect to weakly vining habit of *B. suberecta* is otherwise only known in a few Andean species, most notably *B. ovata* (Cav.) Mirbel.

Bomarea bracteolata Gereau, sp. nov. TYPE: Panama. Chiriquí: 8°45′N, 82°15′W, Fortuna Dam, above Gualaca, on forested slopes behind forestry experimental station, ca. 1,200 m, 9 March 1985, *McPherson 6706* (holotype, MO; isotype, PMA, not seen; other isotypes distributed as *B. allenii*). Figure 3.

Herba volubilis caule glabro. FOLIUM: lamina ovato-lanceolata, 13.0–17.5 cm longa × 4.9–6.6 cm lata, superne glabra, inferne secus nervos hyalino-hirsutula pilis multicellularibus complanatis, inter nervos puberula. UMBELLA: bracteis involucralibus 5–10, 4.2–8.8 cm longis × 1.8–3.7 cm latis, superne puberulis; radiis 5–14, 14.9–42.3 cm longis, glabris, bivel trifurcatis, unoquoque ramo bracteola foliacea suffulto, ima 3.6–7.0 cm longa. FLOS: sepalis oblongo-lanceolatis, 4.1–4.8 cm longis × 1.2–1.6 cm latis, rubris vel glauco-salmoneis; petalis anguste obovatis, (3.8–)4.6–5.1 cm longis × (0.8–)1.2–1.3 cm latis, sepalis 3 mm brevioribus ad 3 mm longioribus, externe rubellis, interne pallide viridibus ad flavo-albescentibus, maculis nigris vel atro-purpureis obsitis; ovario obconico, sub anthesi ca. 7 mm longo × 3–4 mm lato, glabro.

Vine; stem 2.3–4.9 mm diam., glabrous. Petiole 16–41 mm long; leaf blade ovate-lanceolate, 13.0–17.5 × 4.9–6.6 cm (L/W ratio = 2.5–2.7), glabrous above, hyaline-hirsutulous with flattened multicellular hairs on the nerves and puberulent between the nerves beneath. Involucral bracts 5–10, 4.2–8.8 × 1.8–3.7 cm, puberulent above; rays of the umbel 5–14, 14.9–42.3 cm long, glabrous, 2- or 3-branched, each branch subtended by a leaflike bracteole, the lowest bracteole 3.6–7.0 cm long. Sepals oblong-lanceolate, 4.1–4.8 × 1.2–1.6 cm, red or glacous pink-salmon; petals narrowly obovate, (3.8–)4.6–5.1 × (0.8–)1.2–1.3 cm, from 3 mm shorter to 3 mm longer than the sepals, reddish without, pale green or yellow-white with black or dark purple spots within; filaments ca. 36 mm long; anthers ca. 5.6 × 2.1 mm; ovary obconic, ca. 7 × 3–4 mm at anthesis, glabrous; style ca. 36 mm long; stigmatic branches ca. 2.7 mm long.

Known from the provinces of Chiriquí and Veraguas in Panama, in premontane wet forest at 750–1,350 m elevation.

Additional collections examined. PANAMA. CHIRIQUÍ: type locality, 9 Mar. 1985, *McPherson 6704* (MO, PMA); 8°45′N, 82°15′W, Fortuna Dam, in valley S of lake, 1,200–1,300 m, 25 Dec. 1986, *McPherson & Aranda 10126* (MO, PMA). VERAGUAS: vicinity of Santa Fé, slopes of Cerro Tute, 750 m, 25 Mar. 1947, *Allen 4367* (MO); Cerro Tute, trail past agricultural school near Santa Fé, 1,200 m, 17 Sep. 1979, *Antonio 1853* (MO); 8°32′N, 81°07′W, trail to Cerro Tute, above Escuela Agrícola Alto de Piedra just W of Santa Fé, 800–1,350 m, 5 June 1982, *Knapp & Dressler 5456* (MO).

Bomarea bracteolata is probably most closely related to *B. allenii* Killip, the only other large-flowered Mesoamerican *Bomarea* with branched umbel rays. These species differ in sepal length (4.1–4.8 cm in *B. bracteolata*, 5.3–6.5 cm in *B. allenii*), lower leaf surface (pubescent in *B. bracteolata*, glabrous in *B. allenii*), and length/width ratio of leaf blades (2.5–2.7 in *B. bracteolata*, 4.0–5.4 in *B. allenii*). The inflorescence and flowers of *B. bracteolata* are very similar to those of *B. kranzlinii* Baker of Colombia (cf. *Stein & McDade 3205*, MO), but the latter species has smaller bracts and bracteoles and narrower leaves that are glabrous beneath.

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HOSTA YINGERI (LILIACEAE/FUNKIACEAE): A NEW SPECIES FROM KOREA

The genus *Hosta* Tratt. includes ca. 22–25 species of rhizomatous herbaceous perennials from Japan, China, and Korea. The genus is well known to gardeners in the United States, Europe, and New Zealand, since the species and cultivars are widely grown in shady gardens for their attractive foliage and flowers (Aden, 1988). They are also grown as ornamentals and eaten cooked in China, Japan, and Korea. Traditionally *Hosta* has been placed in the Liliaceae (e.g., Cronquist, 1981) or in the Funkiaceae (Dahlgren et al., 1985) along with *Hesperocallis* A. Gray and *Leucocrinum* Nutt. ex A. Gray, both from western North America.

Bailey (1930) and Stearn (1931) noted that *Hosta* is a taxonomically difficult genus with confused nomenclature. Although a number of papers have been published on *Hosta* during the past 50 years, there has been little improvement in our understanding of the genus. The matter has been largely complicated by broad (Fujita, 1976) or narrow (Maekawa, 1940) species concepts and confusion caused by cultivars. The plants have relatively few good diagnostic features that can be observed in pressed and dried herbarium specimens (Hylander, 1954). In an attempt to improve our knowledge of *Hosta*, my associates Carleen Jones, Myong Chung, and Haynes Currie and I have been attempting to assemble a collection of living hostas. Several years ago Barry R. Yinger, then of the U.S. National Arboretum, supplied seeds of several accessions of *Hosta* collected from Taehuksan Island, a remote island off the southwestern coast of Korea. Examination of my cultivated plants and field-collected vouchers at NA reveals a new species, named in honor of the collector, Barry Yinger.

Hosta yingeri S. B. Jones, sp. nov. TYPE: Korea. Cholla Namdo, Shin An Gun, Huksan Myon, Taehuksan Island, east side of Yeri village, 34.40N, 125.6E. Among rocks on northwest-facing talus slope, shade, on cut-over hillside, ca. 60 m, common, 23 Sep. 1985, *B. R. Yinger, T. R. Dudley, J. C. Raulston, A. P. Wharton & Y. J. Chang 3616* (holotype, NA). Figure 1.

Lamina folii elliptica-lanceolata vel anguste-ovata, semierecta; apex acuminatus, petiolus valde sulcatus, basis laminae paullatim in petiolum attenuata; petiolus superne alatus et inferne paullatim angustatus; scapus viridis glaber levis, racemo laxo multifloro terminatus, bracteis parvis instructus; flores non-secundi, perianthium sex-partitum, tubiforme-infundibuliforme; stamina tria + tria, libera, exserta, declinata, in base perianthii affixa; tria filamenta elongata.

Plants glabrous, herbaceous perennials from short, clumpy rhizomes. Leaves ascending obliquely, spirally arranged at base of stem; petioles 3–7(–15) cm long, 2–5 mm wide at the middle of the petiole, greenish or sometimes with purple spots, winged; blades 4–15(–21) cm long, 2.2–7(–11) cm wide, elliptic-lanceolate or narrowly ovate, rigid and heavy-textured, acuminate at the apex, gradually narrowed at the base into the petiole, having a V-type fold in the base of the blade extending down into the petiole, the veins of upper leaf surface inconspicous when fresh, the veins of lower leaf surface in 3–4(–6) pairs of prominent, smooth lateral veins on either side of the midrib. Scapes 2–4 times longer than the leaves, erect, smooth, usually with 1–2 linear-lanceolate bracts below the inflorescence, 1–2 cm long, 2–3 mm wide; raceme 20–25-flowered, the flowers equally arranged around the central axis of the raceme; pedicels 1.2–2 cm long, longer than the subtending bracts; bracts flat, greenish, papillose at the apex, 8–12 mm long, 2–3 mm wide. Perianth (fresh) whitish purple, tubular-funnelform, ca. 3.6–4 cm long; tube slender, ca. 1.8–2 cm long, ca. 5 mm wide, white inside; throat white with purple between each lobe, veins not intensely colored; limb ca. 1.8–2 cm long, lobes 6, ca. 5 mm wide, inner surface light purple; tops of the flower buds purplish. Stamens distinct, 3 + 3, conspicuously exserted; filaments white, attached to the base of the perianth tube, strongly declined, then curving upwards, one set ca. 3.1 cm long, the other ca. 4.4 cm long, the filaments attached to the connective of the anthers in a groovelike pit; the anthers ca. 3 mm long, white beneath, black above. Style filiform, ca. 4.5 cm long, exserted beyond the stamens; stigma small, capitate, moist. Capsules cylindric,

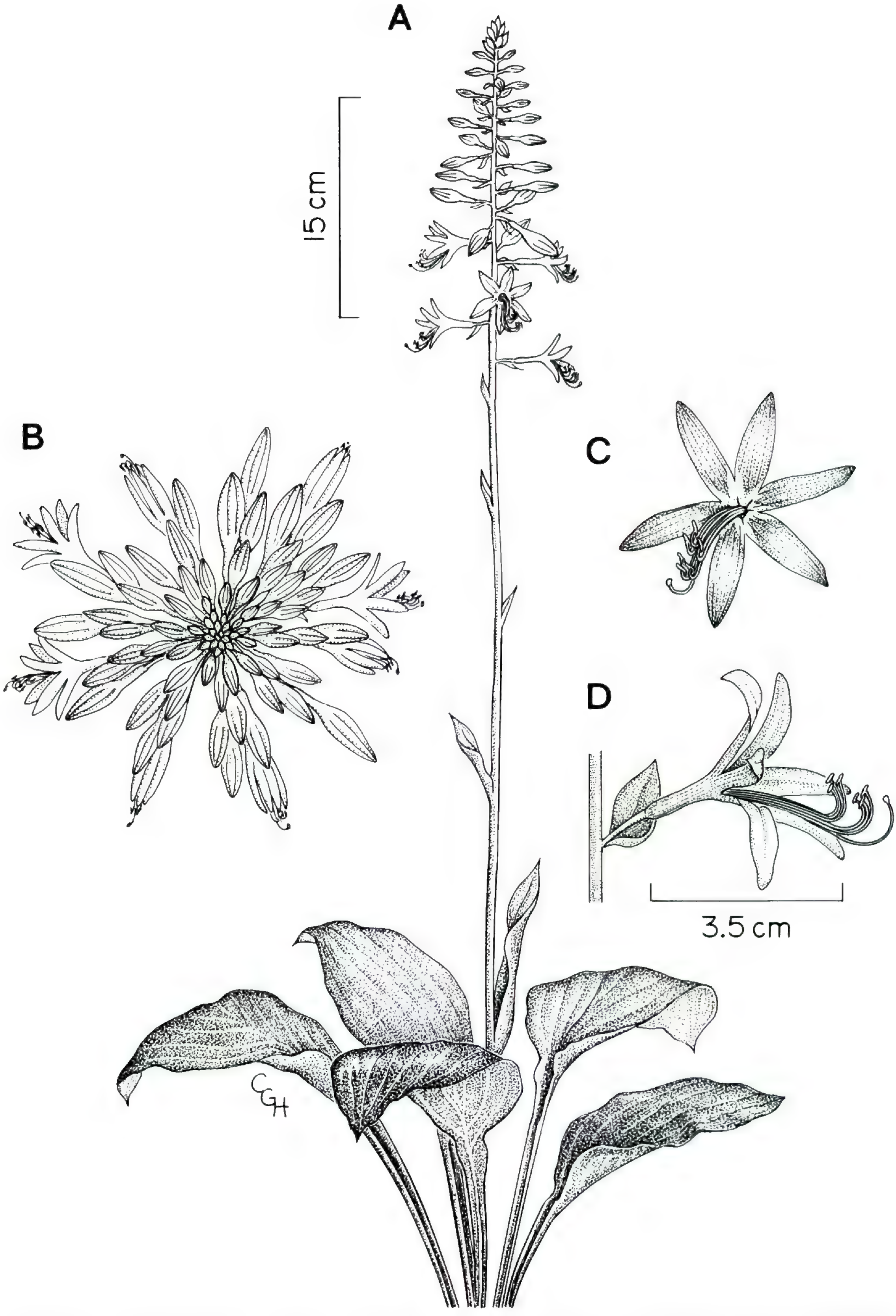

FIGURE 1. *Hosta yingeri.*—A. Habit.—B. Downward view of the raceme axis showing the flowers spread evenly around the central axis of the inflorescence.—C. Flower viewed from front.—D. Flower viewed from the side. (Drawing prepared by Carol L. Gubbins Hahn from fresh material of garden-grown seedlings of holotype collection.)

2.5–3 cm long, 4.5–6 mm wide; seeds black, flattened, winged, ca. 8.4 mm long, ca. 3.4 mm wide; cotyledon small, undifferentiated.

Flowering in August and September in Korea and in my garden located in northeast Georgia in August; fruiting and maturing seed in September and October.

Paratypes. KOREA. TAEHUKSAN ISLAND: garden-grown material of same collection as holotype, *Yinger et al.* (GA); *Yinger et al. 3585* (NA) and garden-grown material (GA); *Yinger et al. 3244, 3610* (NA) and garden-grown material (GA); Sohuksan Island, *Yinger et al. 3164* (NA).

Hosta yingeri is distinct from other species of *Hosta* in its relatively thick, adaxially dark green leaves. This feature may be an adaptation to its coastal habitat, growing at 2–60 m above sea level. It is also distinguished by its delicate raceme of flowers spread evenly around the central axis of the inflorescence; typically, *Hosta* has subsecund racemes. An additional diagnostic feature of *H. yingeri* is the exceptional length of the second set of stamens, with both sets exserted well beyond the perianth. Our living material has been compared with representative accessions of all species of *Hosta* in our garden and with loans of herbarium material. *Hosta yingeri* is an attractive and interesting new species with horticultural potential. It appears to be associated with Maekawa's (1940) subgenus *Bryocles*, section *Tardanthae*. *Hosta yingeri* does not resemble our garden-grown material of *H. tsushimensis* obtained from the National Arboretum.

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LINDSAEA MESARUM, A NEW FERN SPECIES FROM THE RORAIMA SANDSTONE

When the present author published his revision of the New World species of *Lindsaea* (Kramer, 1957), the collection *Tate 430* (NY) was cited as a probably distinct but as yet insufficiently known, undescribed taxon. This taxon is now known by over 20 collections and is therefore described as new.

Lindsaea mesarum Kramer, sp. nov. TYPE: Venezuela. Bolívar: Distr. Piar, summit of Murisipán-tepuí, Aparamá Range, 5°53′N, 62°03′W, sandstone mesa, cracks of rock, 2,200 m *B. K. Holst 3548* (holotype, MO; isotype, Z). Figure 1.

Rhizoma breviter repens, squamis parvis, fuscis vestitum. Folia approximata; petiolus obscurus, abaxialiter rotundatus vel superne applanatus. Lamina bipinnata, pinnis primariis paucis, usque ad 3 pro latere et terminali conformi; rhachis primaria abaxialiter biangularis vel sulcata, secundariae subacute biangulares. Pinnulae numerosae, coriaceae, in sicco obscurae, semi-ovatae vel subtriangulares, margine anteriori recto, plerumque inciso, incisionibus paucis, haud profundis, inconspicuis sed pro lamina omni numquam carentibus. Venae immersae, simplices vel unifurcatae, liberae. Sori interrupti incisionibus marginis, vel continui ad pinnulas minores; indusium firmum, marginem subaequans. Sporae triletae.

Rhizome rather short-creeping, 1.5–2.5 mm diam.; scales fuscous, small, narrowly triangular with broad base, acuminate, ca. 1 × 0.2 mm, ca. 8-seriate at base. Leaves a few–several mm apart; petiole usually lustrous, atropurpureous to black, smooth but the basal part bearing some small wart-like bases of shed scales: adaxial (sometimes also abaxial) side flattened (near the apex) to faintly sulcate, abaxial side otherwise rounded; length ca. 12–22 cm, equaling the lamina to much exceeding it. Lamina narrowly oblong, ca. 10–20 cm long, paucijugate-bipinnate, or a few once-pinnate or subbipinnate sterile leaves present beside the bipinnate fertile ones; primary rachis dark reddish to blackish brown, abaxially faintly biangular to distinctly sulcate. Pinnae from 1 odd one to more often 1–3 pairs and a conform terminal one, moderately to very strongly ascending, hence the width of the lamina quite variable; lateral pinnae with a petiolule of ca. 8 mm, 7–10(–16) cm long, up to 15 mm wide, somewhat narrowed near the base, gradually and strongly tapering to the apex. Secondary rachises medium to dark brown, dull, adaxially sulcate, the groove bordered by rounded ridges, abaxially subacutely biangular. Pinnules close to contiguous or even overlapping, coriaceous, often blackish when dry, dull or adaxially sublustrous, dimidiate, spreading or somewhat ascending, up to ca. 25 well-developed ones to a side, above these some much-reduced pinnules, a few finally confluent into a short, pinnatifid pinna-apex. Larger pinnules ca. 6–9 mm long, 3.5–5 mm wide, about 1.5 times as long as wide, semiovate to subtriangular, base cuneate, posterior margin straight or convex, anterior margin approximately straight, entire or more often distantly and shallowly incised to ca. 0.5 mm, the lobes flanking the incisions mostly touching to overlapping, thus the incisions inconspicuous. Inner margin of pinnules straight, diverging from the rachidule, an outer margin not developed; all margins, especially the posterior, sclerotic, apex subacute to obtuse but not rounded. Sterile pinnules very shallowly and rather irregularly crenate. Veins immersed but somewhat evident, adaxially often slightly impressed in dry specimens, free, simple or the inner forked above the base, ca. 5–8 vein-ends per pinnule present. Sori occupying the anterior margin, interrupted, or in small pinnules continuous, (1–)2–5 per pinnule, each on 1–4(–6) vein-ends, ca. 1.5–4 mm long; indusium firm, entire, often somewhat undulate (not sinuate!), about equaling the margin, ca. 0.4 mm wide. Spores trilete, subtetrahedral, tawny, smooth, with prominent laesura, ca. 35 μm (proximal) × 26 μm (lateral view).

Paratypes. VENEZUELA. BOLÍVAR: Distr. Piar, Aparamá Range, Camarcaibaraí-tepuí, 2,400 m, shaded ledge, *B. K. Holst 3632* (MO, Z); Murisipán-tepuí, 2,350 m, eroded sandstone mesa, *Holst, Steyermark & Liesner 2947* (MO, Z); summit of Auyan-tepuí, 2,140 m, sandy ground under large rock, *Steyermark, Carreño E., McDiarmid & Brewer-Carías 116035* (UC); Chimantá Massif, Apacará-tepuí, ca. 2,200 m, *Steyermark, Huber & Carreño E. 128445* (MO, UC). AMAZONAS: Dept. Atabapo, Cerro de Marahuaco above Salto Los Monos, 2,255 m, base of rock, *Liesner 17973* (MO), *18003* (MO, Z); same locality, 2,520–2,650 m, *Steyermark & Holst*

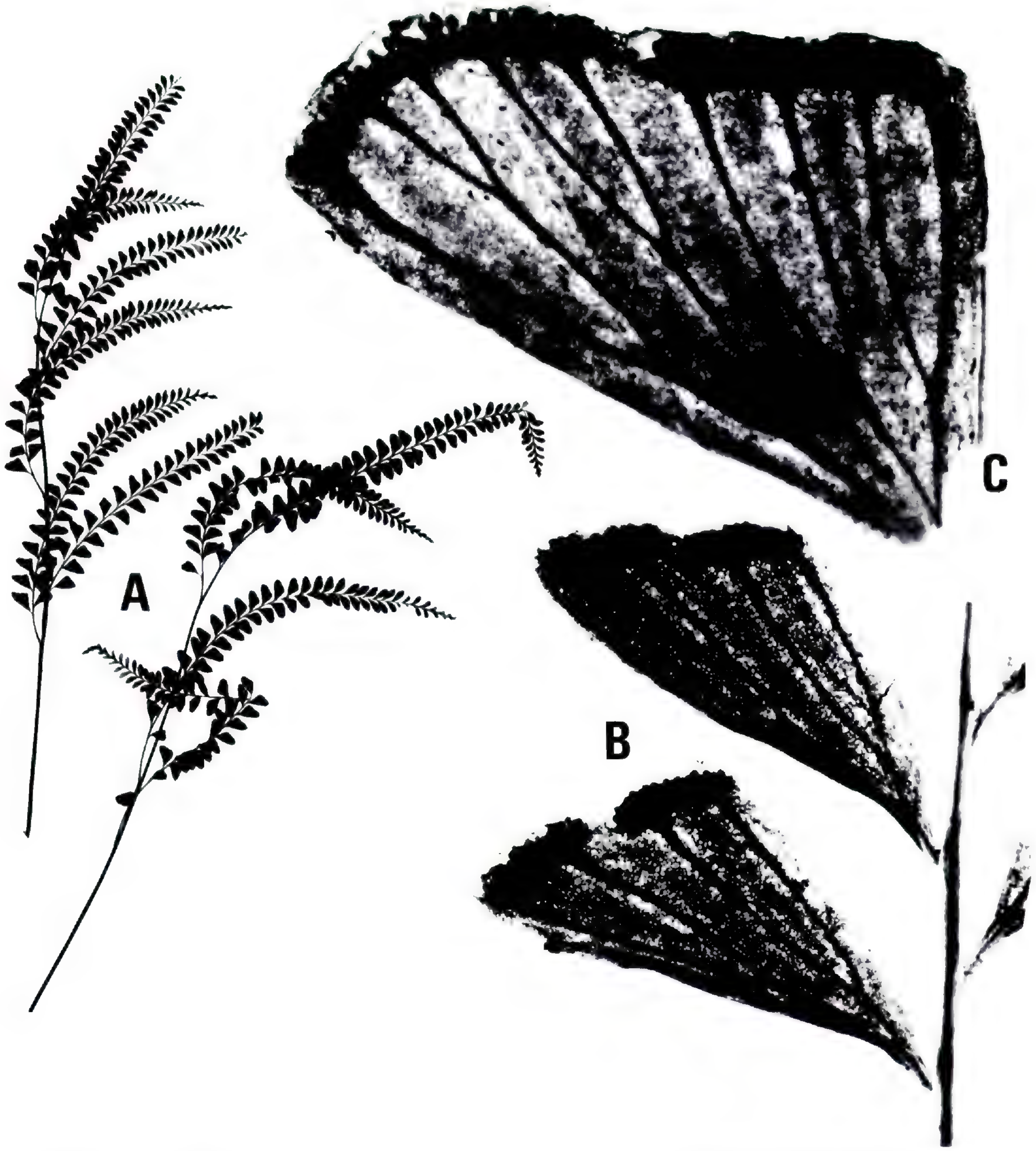

FIGURE 1. *Lindsaea mesarum*—A. Two laminas, × ½.—B. Part of secondary rachis with two pinnules, ×13. —C. A single pinnule, ×20. All from *Holst, Steyermark & Liesner 2947* (Z).

130808 (MO, Z); same locality, 2,580–2,600 m, *Steyermark & Delascio 129253* (UC); same locality, summit, 2,800 m, *Steyermark & Delascio 129096* (MO); same locality, *Steyermark & Delascio 129214* (NY); Cerro Marahuaca-Fhuif, summit, 2,480–2,500 m, *Steyermark, Guariglia, Holmgren, Luteyn & Mori 126072, 125979* (NY); same locality, 2,580 m, same collectors *125947* (NY); Cerro Marahuaca-Shiho, summit, 2,450–2,480 m, same collectors *126351* (NY); same locality, 2,480 m, same collectors *126289* (NY); same locality, 2,450 m, same collectors *126351* (NY); Cerro Duida, Ridge 25, *Tate 430* (NY); Cerro de la Neblina, 3 km ENE of Pico Zoloaga, 1,900–2,000 m, *Stein & Gentry 1606* (MO); same locality, S slopes of Cañon Grande, 1,770–1,850 m, *Croat 59509* (MO); Dept. Río Negro, Cerro de la Neblina, ridge on Venezuela–Brazil border, 2,000 m, *W. W. Thomas & Plowman 3073* (MO, NY, UC).

The following, almost sterile collection may also belong to this species: Cerro de la Neblina, *Liesner 16023* (MO, UC).

All collections are from cracks and crevices of sandstone rocks, from sandy soil in open thickets or other vegetation, or from open forest with *Bonnetia roraimae* (where recorded), between ca.

1,800 and 2,800 m. The species is often described as being locally common.

The interrupted sori were at first taken for an abnormality due to incomplete fertility of the leaves, as is often seen in the genus. The constancy of the character, however, leaves no doubt about its being a distinctive feature of the species.

Lindsaea mesarum resembles *L. stricta* (Sw.) Dryander var. *jamesoniiformis* Kramer in habit, but this is certainly due to convergence. The two taxa occur in the same habitat and are sometimes collected next to each other. The closest relative of *L. mesarum* is *L. klotzschiana* Moritz ex Ettingsh., which has thinner, much more pronouncedly incised pinnules and larger rhizome scales. Another probable relative is *L. parkeri* (Hooker) Kuhn subsp. *steyermarkiana* Kramer, a little-known taxon of somewhat uncertain status; it has thinner pinnules that are much less narrowed towards the apex. If the inconspicuous incisions of the anterior margin of the pinnules of *L. mesarum* are overlooked, it will key out to *L. stricta* (Sw.) Dryander in the present author's key (Kramer, 1957); from this it can be distinguished by its smaller rhizome scales, and the forms of *L. stricta* with dark leaf axes have strongly rounded pinnules.

The author is indebted to the Curators of the Herbaria MO, NY, and UC for lending and/or donating material, and to Mr. A. Zuppiger, Zürich, for preparing the illustration.

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—K. U. Kramer, *Institut für Systematische Botanik der Universität Zürich, Zollikerstrasse 107, CH-8008 Zürich, Switzerland.*

TWO NEW SPECIES OF *PASSIFLORA* SECTION *DECALOBA* (PASSIFLORACEAE) FROM COSTA RICA

Living collections of two species of *Passiflora* L. section *Decaloba* DC. were made in Costa Rica and subsequently studied in cultivation. Both were found to represent undescribed species. The study of the living plants as well as herbarium specimens has allowed the following detailed descriptions. Color names follow the standardized English names system of the ISCC-NBS (1965).

Passiflora nubicola MacDougal, sp. nov. TYPE: cultivated at Duke University, 1980, from stem of *MacDougal 220* collected 27 Aug. 1977 in: Costa Rica. Puntarenas: Cordillera de Tilarán, road through Monteverde Cloud Forest Reserve, Pacific slope just below continental divide, ca. 1,540 m, *MacDougal 220GR* (holotype, DUKE; isotypes, BM, CR, MEXU, MO). Figure 1.

Passiflora scandens; petioli eglandulosi; folia bilobata vel trilobata, lobis obtusis vel truncatis, angulo inter lobos laterales 70–90(–100)°, lobis lateralibus quam centrali subaequalibus vel longioribus, marginibus integris; bracteae ad 1.4 mm longae; flores parvi albidi subpendentes; coronae filamenta uniseriata vel biseriata, filamentis exterioribus luteolis 2–3 mm longis; operculum plicatum; ovarium glabrum; semina 8–10 sulcata.

Gracile climbing perennial herb 1.5–3(–4) m long, lightly and minutely puberulent throughout at shoot tip (except laminas) with antrorsely appressed trichomes 0.04–0.10 mm long, becoming very sparsely puberulent or glabrescent on mature structures. Stem 1.5–3 mm diam., perennial with little secondary growth (several-year-old stems 3 mm diam., dark green, not woody), obtusely sub-5-angulate (drying acutely sulcate-striate) and 5–6-carinate, the carinae becoming verrucose and somewhat scabrous below; posture of shoot tip cernuous; phyllotaxy 2/5. Stipules 1–2(–2.5) × 0.15–0.25 mm, linear-triangular, falcate at base, necrescent. Petioles 0.8–2(–2.8) cm, eglandular. Laminas 2.2–4(–4.6) × 4–6(–9.2) cm at fertile nodes, depressed-obovate to strongly depressed-obovate or semicircular in general outline, adaxially glabrous, often with slight variegation consisting of a few discontinuous patches of white between (not along) the primary and secondary veins, abaxially very sparsely puberulent with trichomes restricted to primary and secondary veins, sometimes flushed purplish (especially new growth), margins entire, sparsely puberulent to nearly glabrous, shallowly (2–)3-lobed less than 0.15 the distance to the obtuse base, the lateral lobes obtuse to rounded or truncate, the central lobe (obsolete to) obtuse or truncate and sometimes emarginate, the angle between the primary lateral veins 70–90(–100)°, the ratio of lateral to central vein lengths 1.0–1.4, the ratio of laminar width to length 1.5–2.1; laminar nectaries 8–14(–18) per leaf (to 26 on immature plants), borne abaxially between the primary veins, often appearing light yellowish adaxially, the most proximal pair only occasionally strictly axillary but not enlarged; leaves of juvenile plants similar, variegated, vein ratio close to 1.0; seedlings unknown. Tendrils straight during development at shoot apex. Prophyll of vegetative ramifying bud 1, lanceolate, acuminate. Peduncles 1.0–2.0 cm, geminate, uniflorous; bracts 3, 0.7–1.4 × 0.05–0.25 mm, usually borne near apex of peduncle, linear-triangular, often involute near base and appearing narrowly lanceolate, early necrescent, stramineous. Flowers ca. 1.7–2 cm diam., subpendent, whitish with green and yellow corona, slightly sweetly odorous; floral stipe (3.0–)4–6.0 mm (to 5–9 mm in fruit); hypanthium 5–5.5 mm diam.; sepals 7.5–11 × 2.6–4.4 mm, oblong to oblong-lanceolate, rounded, ecorniculate, pale yellow-green abaxially, whitish adaxially; petals 5.0–7.5 × 2.4–3.4 mm, oblong to ovate-oblong, rounded, white; filamentous corona in 1–2 series, the outer filaments ca. 23–25, 2–3 mm, simply curved and spreading, thickest near the base, abaxially flattened, slightly laterally compressed, the apex obtuse or rounded, light yellowish green basally, bright yellow toward apex; inner series (if present) 1.8–2.2 mm, capillary, clavate or dilated at the apex, inclined toward androgynophore; operculum 0.9–1.5 mm, membra-

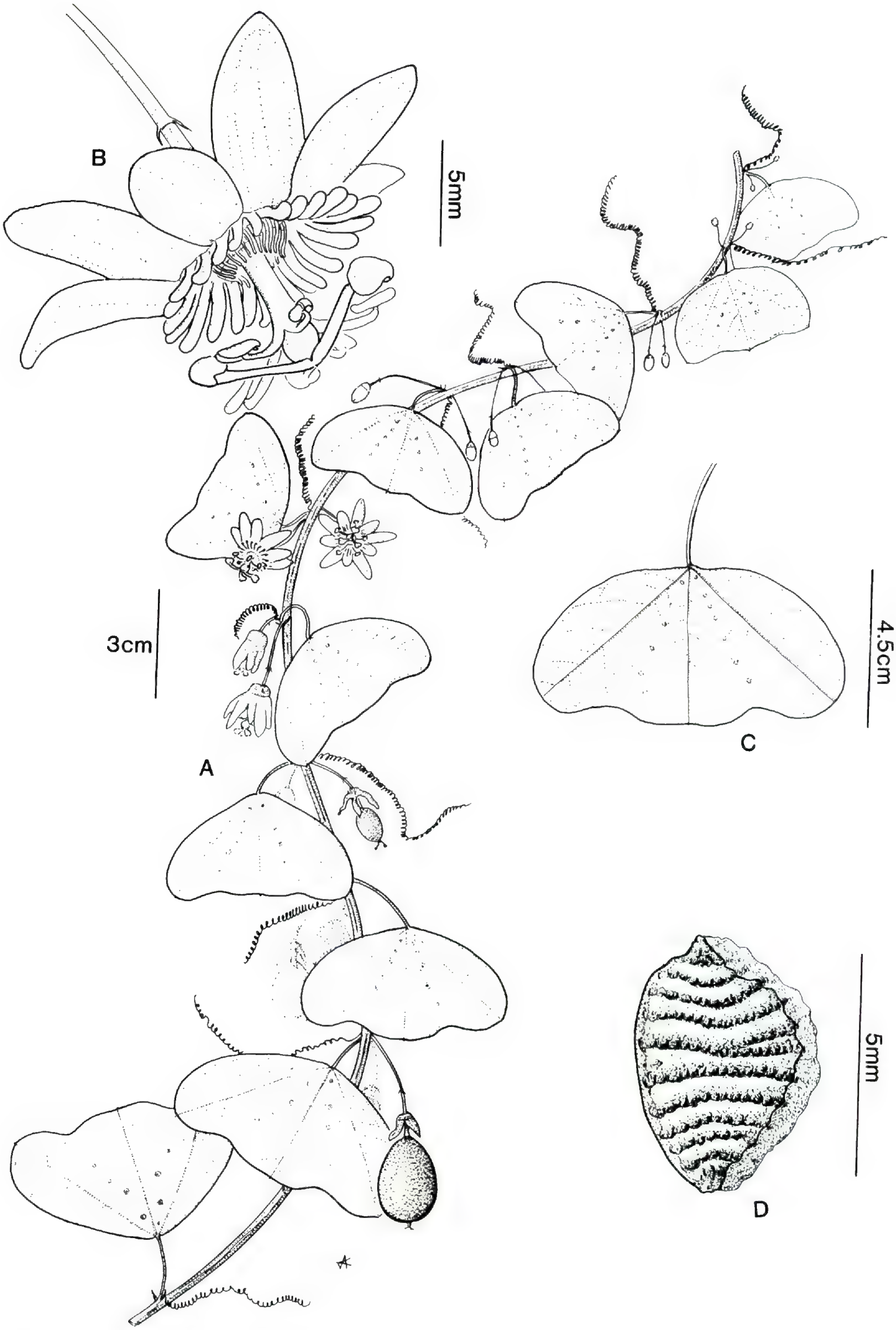

FIGURE 1. *Passiflora nubicola.*—A. Habit (*MacDougal 220GR*).—B. Flower (*MacDougal 220GR*).—C. Large leaf (*Brenes 6158*).—D. Seed with raphe (*Dryer 460*).

nous, plicate, pale yellow-green; nectary-trough without a raised annulus; limen (disk) ca. 2.5–2.7 mm diam., not colored or spotted; staminal filaments connate for 4.7–5.9 mm along the very pale green androgynophore, the free portions ca. 3–4 mm, pale yellowish green; anthers 2.2–2.5 mm, not marked with purple; ovary 2.0 × 1.8–2.0 mm, widely obovoid to widely ellipsoid, glabrous, light yellow green; styles ca. 4–5 mm, light yellow green; stigmas 1.5–2.4 mm diam., capitate. Fruit 1.8–2.5 × 1.8–2.1 cm, widely ellipsoid to very widely obovoid, obtusely trigonous in cross section, exocarp purplish or bluish black, glaucous, mesocarp spongy, white; arils no longer than seeds, clear, gelatinous; seeds 3.6–4.2(–4.5) mm long, 2.5–2.9 mm wide, 1.5–1.6 mm thick, obovate (to widely obovate), very slightly obcampylotropous (or nearly symmetric), transversely sulcate with (7–)8–10 sulcae, the ridges verrucose or knobbed, the chalazal beak erect to slightly inclined away from raphe. Chromosome number $n = 6$.

Additional specimens examined. COSTA RICA. ALAJUELA: Finca Johanson, Los Angeles de San Ramón, [ca. 10°09′N, 84°29′W], 11–12 Mar. 1928 (fl), *Brenes 6019* (F); camino de Finca Johanson, Los Angeles de San Ramón, 4 May 1928 (fl), *Brenes 6158* (F); road to Peñas Blancas from Monteverde ca. 2 km from continental divide, Atlantic slope, 1,400 m, 13 Apr. 1981 (fl, fr), *Knapp & Mallet 857* (TEX); road to Peñas Blancas ca. 3–4 km from divide, Atlantic slope, 1,300 m, 13 Apr. 1981 (fl), *Knapp & Mallet 858* (TEX). CARTAGO: Tapantí, 1,300–1,700 m, 26 Oct. 1983 (fl), *Chácon et al. 1530* (CR); ca. 1 km N and downstream of the junction of the Río Dos Amigos and the Río Grande de Orosi on the road to Tapantí, 1,500 m, 10 Aug. 1980, *MacDougal 1244* (DUKE). PUNTARENAS: vertiente Pacífico, Reserva, Monteverde, 1,520–1,580 m, 17 July 1976 (fr), *Dryer 460* (CR, F); 14 June 1977 (fr), *Dryer 1449* (F); 27 Aug. 1977, *MacDougal 220* (DUKE).

This small and inconspicuous passionflower is known from four areas of lower montane rainforest in Costa Rica. *Passiflora nubicola* grows at edges of primary forest, in treefalls, or along trails, where its thin wiry dark green stems trail over fallen logs and among grasses, bushes, and small trees. The leaves are similar in shape to those of a juvenile *P. biflora* Lam., and their flecks of white variegation are similarly distributed. The flower also resembles that of a miniature *P. biflora*, but in the Orosi valley possesses only one row of coronal filaments. The species is closely related to *P. biflora*.

At the Monteverde Reserve, the main herbivore of this species is *Heliconius clysonimus* (J. Mallet, pers. comm.).

The clone from the same plant as the holotype of this species was grown at Duke University 1977–1983, and the chromosome count was determined from the clones of this plant. Floral anthesis was around 0830 hrs. in the greenhouse, with the flowers closing in the early afternoon. No fruits were set by autogamy during cultivation, and more than 40 attempts at self-pollination also failed to produce fruit. *Passiflora nubicola* was very fertile in both directions with *P. biflora* (*MacDougal 260GR & 275GR*), yielding well-seeded fruit and vigorous F_1 progeny. Those progeny, generally morphologically intermediate in vegetative and reproductive character states, had variously malformed flowers and were sterile, producing no viable pollen. Fruits (with hybrid embryos) produced on *P. nubicola* matured in 45–48 days and contained 35–64 seeds per fruit (N = 13 fruits).

The epithet means "cloud-dweller," in reference to its habitat of misty forest.

Passiflora gilbertiana MacDougal, sp. nov. TYPE: Costa Rica. San José: along roadcut 18.2 km S of Villa Mills on Pan-American Highway, 7,700 ft, 10 Aug. 1977, *L. E. Gilbert 8* (holotype, LL; isotypes: F, MO, MSC). Figures 2, 3B.

Passiflora scandens; petioli eglandulosi; folia supra vittata, infra purpureata vel atrovinoseata, bilobata vel trilobata, lobis lateralibus acuminatis vel acutis, interdum rotundis, lobo centrali acuto vel obtuso, raro rotundo, interdum obsoleto, angulo inter lobos laterales 13–21°, lobis lateralibus quam centrali subaequalibus vel brevioribus, marginibus integris; bracteae 0.8–4.5(–5.7) mm longae; flores parvi virelli et aurei erectiusculi, odorem stercoreum exhalentes; coronae filamenta uniseriata vel biseriata, filamentis exterioribus filiformis, aureis, 5–7 mm longis; operculum plicatum; ovarium pubescens; semina 6–8 sulcata.

Perennial climber 2–4 m long, minutely ± puberulent throughout (except laminas) with (0.06–)0.10–0.15(–0.20)-mm suberect or slightly antrorsely appressed trichomes, the shoot tip densely minutely puberulent, becoming moderately (to sparsely) puberulent below. Stem 1.5–5 mm diam., with normal secondary growth below, subterete (drying angular), striate; posture of shoot tip cernuous; phyllotaxy 2/5. Stipules (1.7–)2.5–4.5(–6.0) × (0.2–)0.3–0.5(–0.7) mm, falcate, narrowly lanceolate to linear-triangular, very dark purplish, distally stramineous, yellow, or brown and necrescent. Petioles 0.8–3.5 cm (to 5 cm in juveniles), eglandular, adaxially puberulent, abaxially glabrous or sparsely puberulent. Laminas (4–)6–13(–17.5) × (1.7–)2.5–6.5 cm at fertile nodes, elliptic to narrowly obovate or oblong-obovate in general outline, adaxially glabrous or nearly so with a few trichomes proximally on primary veins, olive

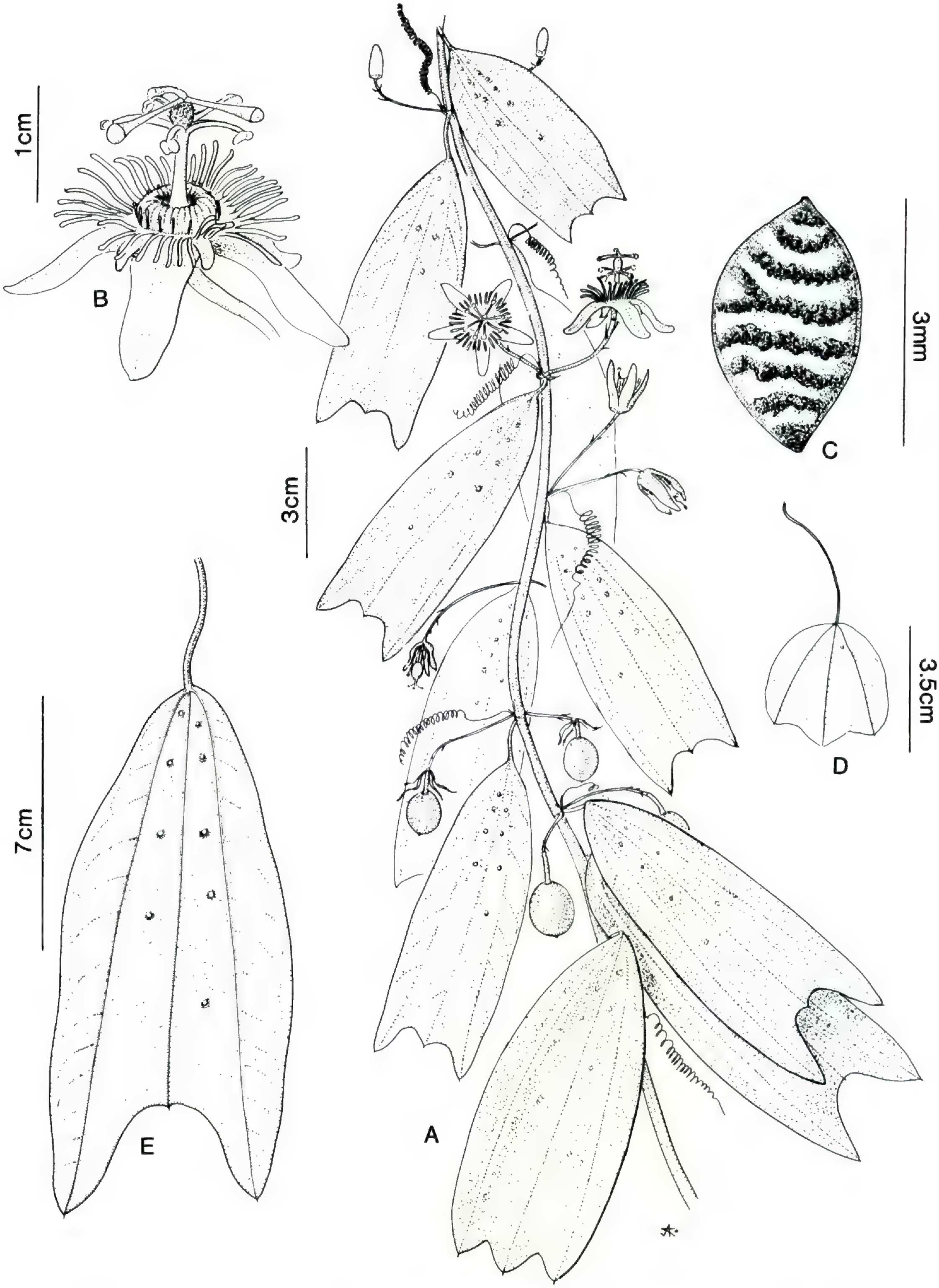

FIGURE 2. *Passiflora gilbertiana*.—A. Habit (*MacDougal 655*).—B. Flower (*MacDougal 655*).—C. Seed (*Gilbert 8*).—D. Leaf of seedling (*MacDougal 1432*).—E. Large leaf from below reproductive nodes (*MacDougal 1431*).

green or flushed purplish, striped with white or pale greenish yellow the length of the 2 lateral veins and sometimes along the basal part of the central vein, abaxially sparsely puberulent to glabrescent with trichomes mainly restricted to the primary and secondary veins, very deep purplish red to very dark reddish purple, becoming greenish on older leaves, the margins entire, puberulent to sparsely puberulent with 0.06–0.10-mm trichomes, very shallowly 3-lobed or shallowly 2-lobed for 0.04–0.15(–0.25) the distance to the cuneate to obtuse (or narrowly rounded) base, the lobes acuminate to acute, sometimes rounded at the very apex, or the central lobe obtuse to obsolete, the angle between the primary lateral veins 13–21°, the ratio of lateral to central vein lengths 0.94–1.2(–1.3), the ratio of laminar width to length 0.35–0.50; laminar nectaries (5–)9–14(–17) per leaf (fewer on seedlings), borne abaxially between the primary veins, ocellate with purple border, appearing light yellowish adaxially, the most proximal pair not strictly axillary or enlarged; leaves of juvenile plants similar, to 18 × 10 cm, with slightly larger lobe angle and relative width; leaves of seedlings with lobe angle 40–60°, central lobe on first leaves longest, then subequal in length, nearly as wide as long. Tendrils straight during development at shoot apex. Prophyll of vegetative ramifying bud 1, broadly lanceolate and often tridentate, acuminate, very dark purple. Peduncles 2.4–3.8(–4.4) cm, geminate, uniflorous; bracts 3, (0.8–)1.7–4(–5.7) × (0.1–)0.2–0.4 mm, linear-triangular, very dark purplish proximally, stramineous, yellowish, or brownish and necrescent apically. Flowers ca. 2 cm diam., suberect, pale greenish with a golden corona, with a strong putrid odor of scatole; floral stipe 4.0–6(–8.0) mm; hypanthium 6 mm diam.; sepals 11–15 × 3.0–4.5(–6.0) mm, narrowly triangular-oblong or lanceolate-oblong, rounded, ecorniculate, lightly but evenly puberulent to apex, very light yellow green on both sides; petals 2.0–3.5 × 1.0–1.5 mm, narrowly oblong-ovate to ovate, rounded, very light yellow-green; filamentous corona in 1–2 series, the outer filaments ca. 46–50, 5–7 mm, strongly spreading and only slightly and simply curved, cylindrical and gradually slightly ampliate toward the rounded apex, pale yellow, yellow-green, or whitish basally, the remainder vivid yellow; the inner filaments (if present) 0.6–1.2 mm, expressed mainly in the sepal sectors, slightly clavate, erect; operculum 1.8–2.4 mm, membranous, plicate, cream to yellow; nectary-trough without raised annulus; limen (disk) ca. 2 mm diam., pentagonal, bright yellow; androgynophore pale at base, dark pink to grayish purplish red distally; staminal filaments connate (6.2–)7.5–8(–9.0) mm along androgynophore, the free portions 5–6 mm, dark pink at base, light yellow-green distally; anthers 2.0–2.2 mm, not marked with purple; ovary 1.8–2.5 × 1.4–2.1 mm, widely ellipsoid to subglobose, densely puberulent, dark green; styles ca. 6 mm, light yellow green; stigmas ca. 1 mm diam., clavate-capitate. Fruit 1.2–1.4 cm diam., subglobose to widely ellipsoid, lightly puberulent, purplish or bluish black; arils translucent white, length unknown; seeds (2.9–)3.1–3.3 mm long, 1.9–2.1 mm wide, 1.1–1.2 mm thick, obovate, nearly symmetric to very slightly campylotropous, transversely sulcate with (6–)7–8 sulcae, the ridges coarsely verrucose or knobbed, the chalazal beak very slightly inclined toward raphe.

Additional specimens examined. COSTA RICA. SAN JOSÉ: clone of Gilbert's type collection cultivated at Duke University 1980–1984, *MacDougal 655* (BM, CR, DUKE, HUA, MEXU, TEX); from type locality, Aug. 1980, *MacDougal 1431* (CR, DUKE, MO), *1432* (DUKE); side roads along the Pan-American Hwy. ca. 10–15 km N of San Isidro de General, near kms 118–116, at the crossing of the Río Paymer, and N along the road from there, 1,500–1,600 m, 8 Aug. 1981, *Taylor 1120* (DUKE); along the Interamerican Hwy. above San Isidro de General, ca. 15 km N at river crossing, 1,500 m, 5 Mar. 1985, *Taylor & Skotak 4771* (DUKE, MO).

Passiflora gilbertiana is remarkable for its variegated reddish purple leaves and stinking golden flowers. It is a member of a species group of Central American passionflowers in section *Decaloba* characterized by bilobed variegated leaves, greenish to yellow perianth, filiform unbanded outer coronal filaments, and notable reduction in the size of the petals relative to the sepals. This group is part of section *Decaloba* but was not recognized by Killip (1938), who scattered its component species among several of his invalid "series" of section *Decaloba*. Within the group, the new species is most closely related to *P. jorullensis* H.B.K. of Mexico, *P. apetala* Killip of Costa Rica and Panama (Fig. 3), and an undescribed relative of *P. apetala* from the mountainous border of Mexico and Guatemala. Its distinctive characteristics include its long narrow leaf with a relatively small interlobe angle and more strongly expressed red to purple coloration, retention of conspicuous laminar variegation at maturity, and yellow flower with small petals and second (inner) series of coronal filaments. The inner series of coronal filaments varies as to presence or absence within the species. In *Taylor & Skotak 4771* the series is well developed, numbering ca. 40; in the type it is absent. However, the cultivation of somatic clones (*MacDougal 655*) from the type plant revealed that the expression of the second

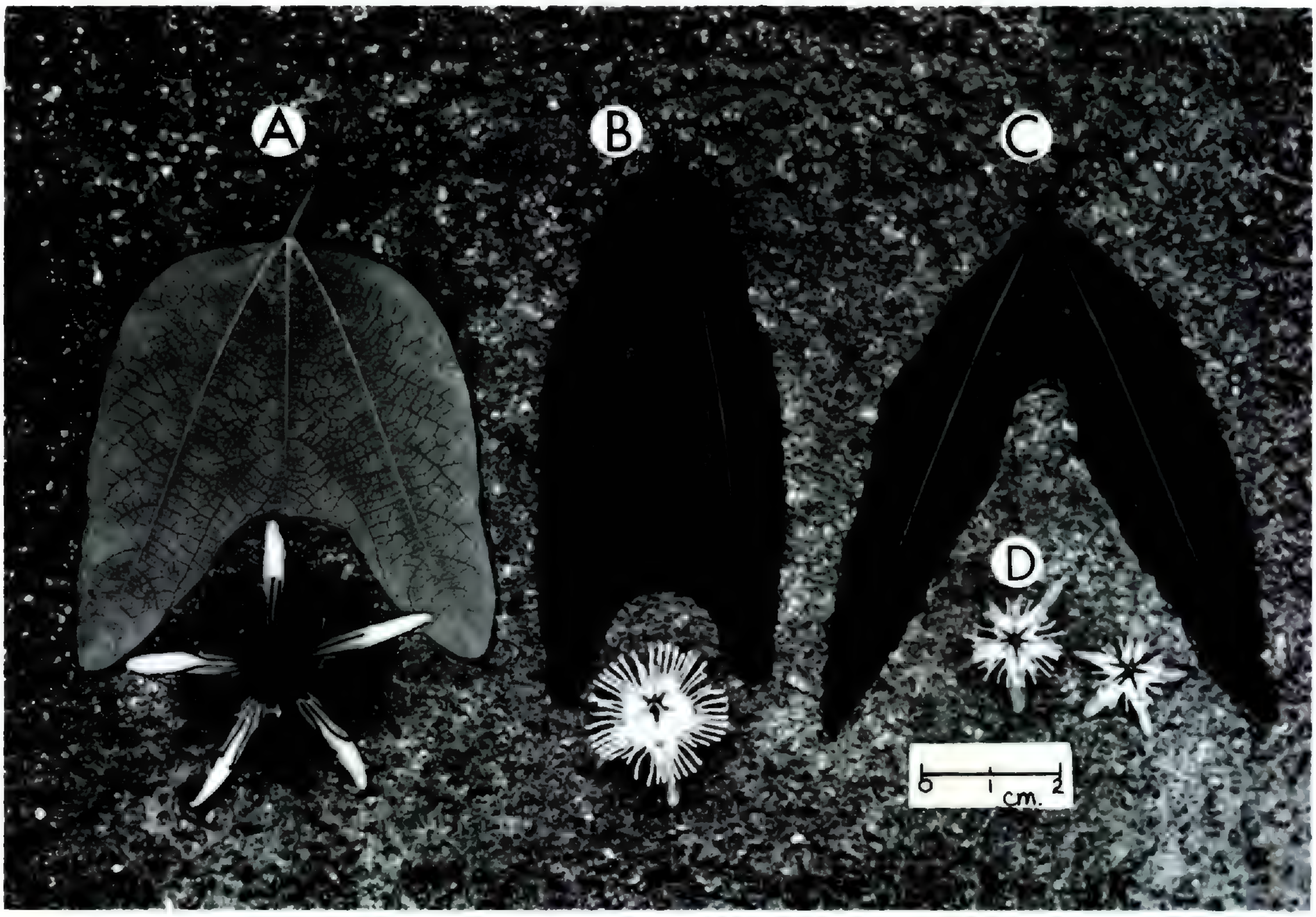

FIGURE 3. Comparison of leaves and flowers of three closely related species.—A. *Passiflora jorullensis* (*MacDougal 368*).—B. *Passiflora gilbertiana* (*MacDougal 655*).—C. *Passiflora apetala* (*MacDougal 467*).—D. *Passiflora apetala*, flower only (*MacDougal 450*).

filamentous series was variable within this individual, with (0–)5–12(–20) filaments per flower. The expression changed gradually along the stem, at times stronger, at times weaker, perhaps dependent on environmental conditions. In certain cases the expression seemed to be related to the position of the flower on the vine, with smaller flowers near the end of flowering axillary branches completely lacking the second series.

On the label of the type is the collector's note "odor of pigpen." The flowers of this new species share this strong odor (described as between "stercoraire et putride" by Planchon, 1849) with *P. jorullensis* (pers. obs.). Gilbert also noted on the type label "visited by hummingbirds," but the same day he also observed a single wasp at a flower (pers. comm.). It is thus probably significant that *P. jorullensis*, with a nearly identical odor, is primarily wasp-pollinated at least in some part of Mexico (MacDougal, unpubl.).

The habitat at the type locality is treefalls and partially shaded thickets along a dirt road on steep slopes in the lower reaches of *Alnus* forest. Plants there climbed over bushes and trailed into small *Alnus* and *Piper* trees. An important herbivore at the type locality is a yellow flea beetle that is an undescribed species of *Monomacra* (from *MacDougal 1431*, voucher identified by C. Duckett, deposited in the Cornell University Insect Collection). Several of the cited specimens show characteristic damage by flea beetles.

A clone from the type collection was cultivated at Duke University and from there was distributed to several commercial greenhouses in California and made available for sale to the public by 1980. In cultivation the plant bloomed from the morning to afternoon, with anthesis around 0930 hrs. and flower closing in mid to late afternoon. The stigmas, although lowered to anther level into the afternoon, were not receptive after ca. 1230 hrs. No fruits were set by autogamy during cultivation, but during limited hand-pollinations, 6 of 11 self-pollinations before 1230 hrs. produced mature fruit containing 19–31 seeds per fruit.

Mr. Patrick Worley, a commercial plant hybridizer, crossed a clone of the type with *P. biflora*, *P. ornithoura* Masters (*MacDougal 623*), and *P. jorullensis* (*MacDougal 368*); many F_1 progeny were grown to maturity and all flowered. Pollen viability was not examined. In each case the unpleasant odor was conserved. One especially ornamental individual of the cross with *P. jorullensis*

was named "Sunburst" and has been available to the public from several nurseries since 1983.

I take great pleasure in naming this species for its discoverer, Lawrence E. Gilbert of The University of Texas at Austin, whose seminal contributions to the understanding of the ecology of the Passifloraceae and their herbivores are well known. Dr. Gilbert first suggested the study of passionflowers to me and has aroused and guided an interest in these plants in many other students. It is particularly gratifying to name this plant because I had the privilege of being with Dr. Gilbert the day he discovered it and gathered the type collection. He immediately suspected it to be undescribed and his exuberance kindled in me what has become a career.

Many of the observations given here were made at Duke University, and I gratefully acknowledge Donald E. Stone for his inspiration and guidance during my graduate studies. Thanks are due the Organization for Tropical Studies for their summer field course that introduced me to Lawrence Gilbert and to these Costa Rican passionflowers. The staff of the Duke University greenhouses provided many years of favorable conditions for passionflower vines, and the Jessie Smith Noyes Foundation generously provided postdoctoral support for research on this family at the Missouri Botanical Garden. The drawings were prepared by John Myers.

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PASSIFLORA MAYARUM, A NEW SPECIES RELATED TO *P. PROLATA* IN SUBGENUS *PASSIFLORA* (PASSIFLORACEAE)

Collections from Central America made since the time of Killip's (1938) monumental monograph of the American Passifloraceae have allowed a clearer delineation of a number of taxa, and in some cases have confirmed his suspicions that certain specimens might represent undescribed species. Such is the case with *Passiflora prolata* Masters and its apparent sister species newly described here.

Passiflora mayarum MacDougal, sp. nov. TYPE: Mexico. Quintana Roo: roadside secondary scrub 3 km N of San José de la Montaña on road N of Tomás Garrido (ca. 75 km W of Chetumal), 100 m, 9 May 1982, *Chater et al. 89* (holotype, MO; isotype, BM). Figures 1A, C, 2.

Passiflora (subgenus *Passiflora*) scandens, puberula, trichomatibus 0.05–0.25 mm longis; stipulae 10–22 × 0.4–1.0 mm; petioli 2(–4)-glandulosi; folia trilobata, lobis acuminatis vel caudatis, marginibus serratis vel serrulatis; bracteae 4.8–6.6 × 2.0–3.4 cm, ovato-ellipticae, acuminatae; coronae filamenta 6–8-seriata; operculum ad apicem in lacinias divisum; ovarium glabrum vel raro puberulum. *Passiflora prolata* affinis est.

Vine, size unknown, puberulent throughout except glabrous or nearly so on tendrils, adaxial surface of lamina, flowers, and sometimes adaxial surface of bracts. Trichomes 0.05–0.20(–0.25) mm, erect and straight or curved. Stems subterete to obtusely subangular, striate, apparently not hollow. Stipules (10–)13–18(–22) × 0.4–1.0 mm, linear-narrowly oblanceolate (or linear-triangular to linear-narrowly lanceolate), long-attenuate, tardily deciduous, glandular-denticulate; petioles 2(–4)-glandular ¼–¾ the distance to the appex (or if 4-glandular, rarely 1 pair near the apex), the nectaries sessile or up to 1 × (0.7–)1–2.2 mm, (crateriform to) patelliform; laminas 10–13 × 9–14 cm, glandular-serrate(-serrulate), not variegated, glabrous adaxially except the primary veins puberulent at least half their length, 3-lobed for 0.4–0.7 the distance to the base, the lobes lanceolate to narrowly ovate-oblong, acuminate to short-caudate; laminar nectaries marginal, 2–5 slightly enlarged teeth borne in each lobe sinus, enlarged teeth absent at base of lamina. Prophylls of vegetative ramifying bud 2, 1–2 mm long, lanceolate, equal or one smaller. Peduncle 1 per node, 1.5–4(–5.0) cm, uniflorous; bracts 4.8–6.6 × 2.0–3.4 cm, valvate in bud, free to the base, ovate-elliptic, conspicuously 2–4(–6)-glandular at the margin basally, otherwise entire or the basal ½ obscurely glandular-denticulate, acuminate to long-acuminate, yellow green, deciduous in fruit, adaxial surface puberulent or glabrous with puberulent main veins and a narrow band of tomentum along margin, the venation basally acrodromous with prominent intramarginal veins. Perianth white, longest coronal filaments purplish to violet, white at the apex, banded white basally; floral stipe ca. 12–14 mm (to 20 mm in fruit); hypanthium ca. 5–6 mm long, ca. 13–14 mm diam., puberulent; sepals 24–34 × 7–12 mm, lanceolate-triangular, puberulent, sometimes only sparsely so, subapically with an arista (8–)10–18 mm; petals 24–34 × 6–9 mm, oblong-lanceolate; coronal filaments in 6–8 series, the 2 outermost similar, often apically tortuous, the outer 26–32 mm, the second series broader at their base and ca. 3–6 mm shorter, the next (3–)4–5 series tuberculate or 1–5(–7) mm, the innermost series 6–10 mm, banded purple and white; operculum basally connate for 2–4.5 mm, membranous, the margin erose or short-fimbriate and often slightly plicate, with a subapical and slightly deflexed series of fimbriae or filaments 1–3(–5) mm long; nectar ring (annulus) present in the middle of the nectary; limen (disk) ca. 6–8 mm diam. around the widely broadened base of the androgynophore, ca. 3 mm above the floor of the nectary; staminal filaments connate 10–13 mm along androgynophore, the free portions 8–9 mm, glabrous; anthers 10–12 mm; ovary 5–6.5 × 2–3.2 mm, narrowly ovoid-ellipsoid, glabrous (rarely sparsely puberulent); styles 10–11 mm including stigmas, glabrous; stigmas 4 mm wide, deeply bilobed. Fruit 7.5–9 × 4.5–5 cm, ellipsoid, greenish

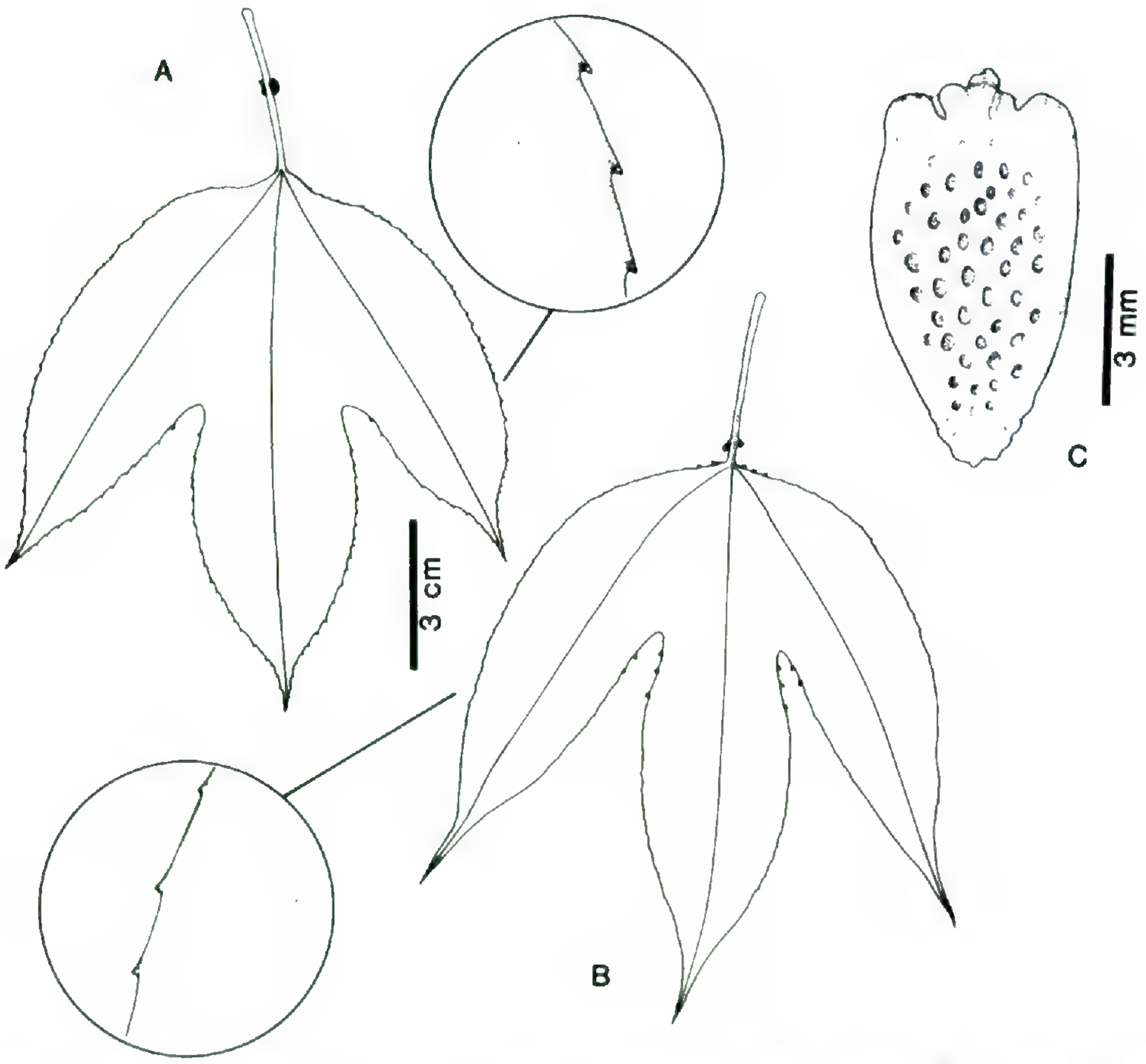

FIGURE 1.—A. Leaf of *Passiflora mayarum* with detail of marginal teeth (*Téllez & Cabrera 2429*).—B. Leaf of *P. prolata* with detail of marginal teeth (*MacDougal 596*).—C. Seed of *P. mayarum* (*Téllez & Cabrera 2429*).

yellow to yellow, estipitate; arils longer than the seeds, color and flavor unknown; seeds 7.2–8.0 mm long × 4.0–4.5 mm wide × 1.9 mm thick, obovate, strongly compressed, nearly bilaterally symmetric with the chalazal end squared and shallowly 3-dentate, brown, reticulate-foveate with 35–46 foveae.

Habitat and distribution. This species grows in the Caribbean lowlands of northern Guatemala, western Belize, and the southern part of the Yucatán Peninsula (Fig. 2). The collections come from elevations of 20–250 m, except for two collections from one station at 550 m in Belize. The habitat is usually open or partially open vegetation. Although the information is not present on the specimen's label, Bartlett (1935: 20) stated that his collection *12840* was collected in the wooded swamp vegetation called *escobal*, which is a vegetation type dominated by the *escoba* palm, *Cryosophila*. This edaphic climax occurs in the Petén and Yucatán on wet soil surrounding water holes ("aguadas") and as the transitional zone between the inundated areas of the wooded swamps ("bajos") and the well-drained "high bush" uplands (Bartlett, 1935; Lundell, 1937). However, most of the collections are from disturbed and more well-drained habitats, namely, roadsides and secondary areas in low forest, *selva mediana subperennifolia*, or *selva alta subperennifolia* (Rzedowski, 1978).

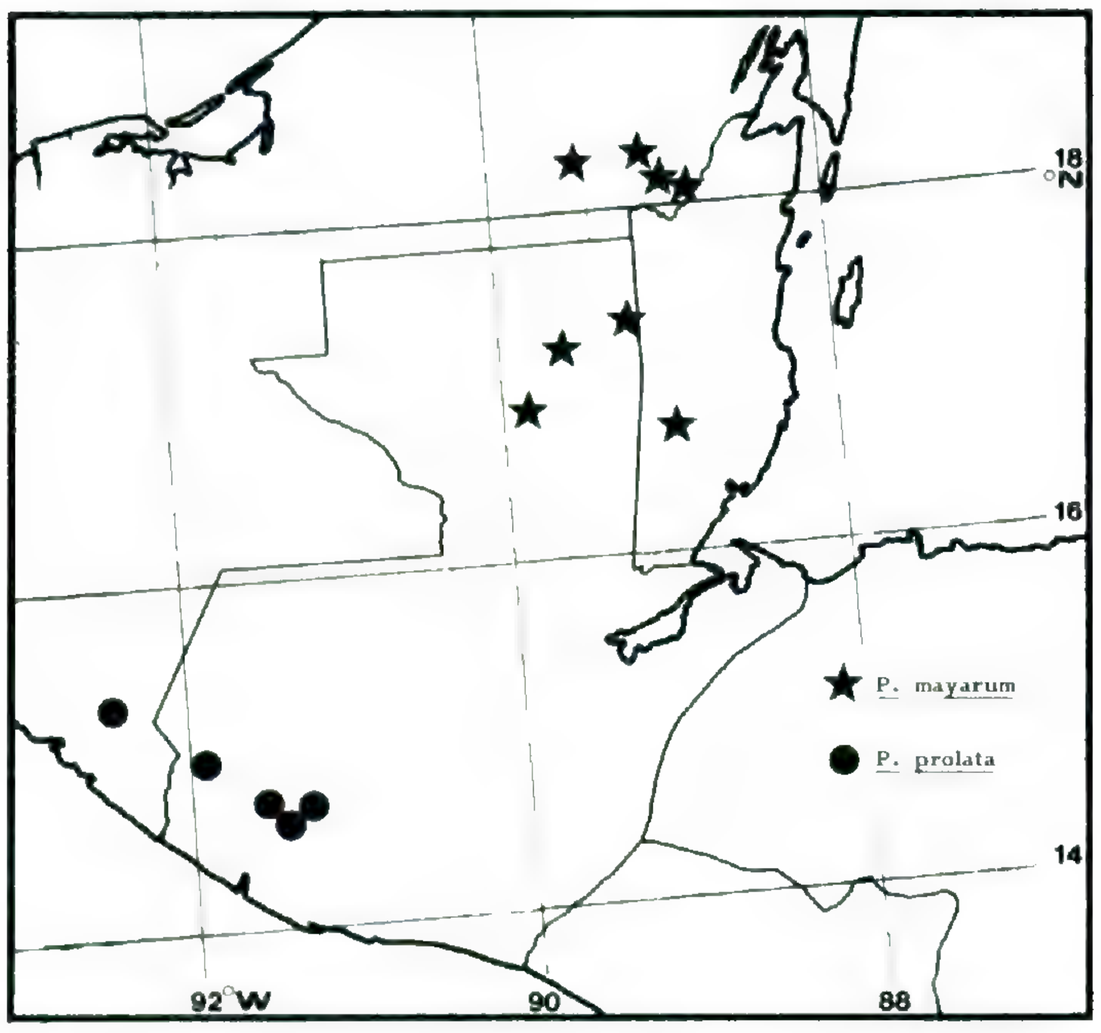

FIGURE 2. Map of Guatemala, Belize, and neighboring countries showing distributions of *Passiflora mayarum* and *P. prolata*.

Phenology. The few collections known suggest that reproduction occurs primarily during the wet season from April through November. One sheet, however, was collected in flower at the end of December. Although the type has nearly mature fruit, fully mature fruit and seeds are known only from *Téllez & Cabrera 2429*.

Vernacular name. "Granadilla" (*Tún O. 372*).

Additional specimens examined. MEXICO. CAMPECHE: 30 km al S de Xpujil, 22 Apr. 1982, *Cabrera & Cabrera 2482* (MEXU, MO). QUINTANA ROO: 8 km al S de Tres Garantias, sobre el camino a Tomás Garrido, 22 Dec. 1982, *Cabrera & Cabrera 4174* (MEXU, MO); 24 km al N de La Unión, 7 May 1980, *Téllez & Cabrera 2100* (MEXU, MO); 15 km al S de Ejido Laguna OM, 8 June 1980, *Téllez & Cabrera 2429* (MEXU, MO). BELIZE. CAYO: between Millionario and Cuevas, 30 May 1973, *Dwyer 10823* (MO); vic. Millionario, 1,800 ft., 30 May 1973, *A. Gentry 7733* (MO). GUATEMALA. PETÉN: Dos Arroyos to Yal'och, 2 May 1931, *Bartlett 12840* (MICH, US—fragment; photos: F, NY, US); ca. 5 mi. S of Tikal National Park, 19 June 1973, *Dwyer 11269* (MEXU, MO); S of Tikal National Park, 19 June 1973, *A. Gentry 8338* (MO—2 sheets, US); camino de El Remate en el Km 59, Parque Nacional de Tikal, 24 Oct. 1969, *Tún O. 372* (F, NY, US); Santa Elena, en el camino para San Andrés, Km 4, lado saliente, 4 Oct. 1969, *Tún O. 1374* (F).

Passiflora mayarum is most similar to and is undoubtedly very closely related to *P. prolata* from the premontane to montane broad-leaved forests of the Pacific watershed of Guatemala and Chiapas, Mexico. Except for the vestiture, the two have similar leaves and nearly identical glandular bracts. At the time of his 1938 monograph, Killip knew *Passiflora prolata* only from the type. He knew the related species newly described here from a single collection by Bartlett (*12840*). He had identified that sheet as *P. prolata* (Killip, 1936), but later expressed some misgivings. In his monograph (1938: 389) he stated, "I am referring the Bartlett collection to *P. prolata* with some hesitation, as the stem and under surface of the leaves are puberulent and the petiolar glands are not quite as in the type. It comes, moreover, from the lowlands." The more recent collections of both species confirm that the two are separate morphologically and ecologically. Neither fruit nor seeds are known from *P. prolata*, so it is impossible to compare the two species on these points. They may be distinguished by the following key.

1a. Stems and leaves glabrous except for slight pubescence or puberulence at the nodes, on the sides of the adaxial primary laminar veins, and sometimes on the petiole. Stipules 7–10 mm long, acuminate. Petioles glandular in the distal half, the glands 0.3–0.8 mm diam. and usually longer than wide. Laminar lobes conspicuously long-acuminate; laminar margin serrulate, often only denticulate apically, usually nectariferous at the junction of the petiole. Bracts glabrous abaxially. Hypanthium and sepals glabrous. Habitat elevation 700–2,000 m ..... *P. prolata*

1b. Stems and leaves puberulent except the lamina glabrous adaxially with the primary veins puberulent. Stipules 10–22 mm long, long-attenuate. Petioles glandular at a variable position, the glands 0.7–2.2 mm diam. and wider than long. Laminar lobes acuminate to short-caudate; laminar margin uniformly serrate (to serrulate), not nectariferous at the junction of the petiole. Bracts puberulent abaxially. Hypanthium puberulent, sepals puberulent or only sparsely so. Habitat elevation 20–550 m ..... *P. mayarum*

Not having seen the type of *P. prolata* (*Lehmann 1630*—G-BOIS), I have relied on the protologue and five more recent collections, including one of my own, that match the protologue. Three of these collections were identified as *P. prolata* by Killip (who saw the type), and one was collected within 30 km of the type locality at a similar elevation. The flowers of *P. prolata* and *P. mayarum* appear to be rather similar, apparently borne above the horizontal plane, with two prominent series of purplish outer coronal filaments, several reduced intermediate series, and a well-developed inclined inner series. The operculum in both is similar, although that of *P. mayarum* has shorter subapical filaments. I have seen the flower of *P. prolata* only from *Matuda 16479* (F), in which the intermediate coronal series are reduced to variably expressed series of tubercles. It is not possible to determine clearly the relative length of the two outer series except to say that they are roughly similar in this poorly pressed specimen. Given the lack of comparative reproductive material and the coronal variation that occurs within related species, I have for now distinguished the two species mainly by vegetative characteristics.

The leaves of *P. mayarum* tend to be less deeply lobed, but there is considerable overlap with *P. prolata*. The quality and quantity of the indument differ: the few trichomes that occur on the leaves and nodes of *P. prolata* are ca. 0.2–0.4 mm instead of 0.05–0.25 mm long. Despite the variation in their vestiture, the bracts of both species always have a narrow band of dense tomentum along the margin adaxially. The trichomes are crispate, and those of adjacent bracts are interlocked during the development of the bud, keeping the bracts valvate. This marginal band of crispate tomentum occurs in number of species of *Passiflora* and is correlated with foliaceous valvate bracts. The ovary of *P. mayarum* is glabrous in all collections examined except *Tún O. 1374*, in which it is sparsely puberulent.

Some of the Mexican collections of the new species were distributed as *P. platyloba* Killip and are cited as such in Sousa & Cabrera (1983).

Passiflora mayarum and *P. prolata* belong to subgenus *Passiflora*, where they share characteristics with species that Killip (1938) included in his informal "series" *Serratifoliae* and *Incarnatae*.

Killip placed *P. prolata* next to *P. incarnata* L. as one of six species in *Incarnatae*, which was distinguished within subgenus *Passiflora* (as subgenus "*Granadilla*") as having unwinged stems, free bracts, narrow stipules, lobed leaves, eglandular sepals, filamentous corona in more than two series, petiolar glands present, and denticulate or fimbriate operculum. That delineation is fraught with difficulties since most of those character states are undoubtedly plesiomorphic for the subgenus. Except for the lobed leaves, it also fits the species put in the *Serratifoliae* group. An understanding of the relationships among these species and the granadillas as a whole awaits a revision of subgenus *Passiflora*. *Passiflora mayarum* is probably genetically close enough to the commercially important *P. edulis* Sims to warrant investigation into using it as a rootstock or as a source of genetic improvement for the commercial passionfruit. It is especially notable that *P. mayarum* has been collected growing in warm wet soil, the kind of conditions that induce fungus-related failure of the commercial crop.

The epithet *mayarum* refers to the native distribution of this species, centered in the heart of the Mayan Old Empire.

I am grateful to the Jessie Smith Noyes Foundation for postdoctoral support for research on passionflowers, to the curators of the herbaria listed above, and to John Myers for the drawing.

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TWO NEW SPECIES OF *TOURNEFORTIA* (BORAGINACEAE) FROM COLOMBIA

Recent collecting efforts in western Colombia have yielded two very distinct and undescribed species of *Tournefortia* L. Both are members of sect. *Tournefortia*, a pantropical group with its center of diversity in Andean South America. Species of *Tournefortia* from this area remain confused, since the most recent taxonomic treatment available is de Candolle's (1845). Macbride (1960) covered the species from Peru, but his treatment is regional and incomplete. Killip prepared an unpublished treatment of the Andean species. The following two species are new.

Tournefortia brantii James S. Miller, sp. nov. TYPE: Colombia. Antioquia: Mpio. Valdivia; road to Briceño, 1.1 km W of the Medellín–Caucasia highway, pasture, and secondary forest adjacent to road, 7°03′N, 75°28′W, 1,800 m, *A. E. Brant & O. Escobar 1293* (holotype, MO 3531269). Figure 1.

Arbor parva ad 3 m alta, ramunculis villosis. Folia opposita, ovata ad elliptica, 9–17 cm longa, 5–9.5 cm lata, apice acuminato, basi cuneata ad decurrenti, supra pubescentia, infra villosa. Inflorescentia cymosa, bis dichotome ramosa, pedunculo 4–11 mm longo. Sepala lineari-lanceolata, 3–5 mm longa; corolla alba, 5 mm longa, lobis 5, ovatis, 1 mm longis, tubo 4–5 mm longo, strigoso. Fructus non visi.

Small tree 3 m tall, the twigs villous, the hairs erect, 1–2 mm long, brown. Leaves opposite; petioles 5–12 mm long, villous, the hairs erect, 1–2 mm long, brown; leaf blades ovate to nearly elliptic, 9–17 cm long, 5–9.5 cm wide, the apex acuminate, the base cuneate to decurrent, the margin entire but appearing ciliate from hairs of the upper surface, the secondary veins 8–9, ascending, arising from the midrib at 30°–50°, the tertiary and quaternary veins clearly visible on the lower surface, ramifying reticulately, the upper surface pubescent, the hairs erect, ca. 1 mm long, translucent white to clear, approaching villous along the midrib, the lower surface villous, densely so along the midrib and secondary veins. Inflorescence a twice dichotomously branched cyme, the peduncle 4–11 mm long, villous, the hairs erect, 1–2 mm long, brown, the fertile branches 3–9 cm long, the flowers borne densely at early anthesis, 1–2 mm apart, the fertile branches later becoming more lax, the flowers then 3–5 mm apart. Flowers bisexual, with the stigma borne beneath the anthers; sepals 5, free to the base, linear-lanceolate, 3–5 mm long, unequal in length, densely brown strigose; corolla white, tubular with 5 spreading lobes, 5 mm long, the lobes ovate, 1 mm long, the tube 4–5 mm long, brown strigose, densely so near the apex, sparsely so near the base; stamens 5, the anthers borne just beneath the mouth of the corolla tube, nearly sessile, ellipsoid, 0.8 mm long; ovary ovoid, 1 mm tall, the style 3 mm long, the stigma conical. Fruits unknown.

Tournefortia brantii is a member of sect. *Tournefortia* and belongs to a group of about 10 poorly defined species that have opposite leaves. These species occur from Costa Rica through Colombia, Ecuador, Peru, and into Bolivia and are centered in the northern Andes. While problems exist with species delimitation among the opposite-leaved species of *Tournefortia*, *T. brantii* is distinct among the South American species by having dark brown indument and sepals to 5 mm long. It is most similar to *T. johnstonii* Standley, a species of Panama (Miller, 1988), which differs in having sepals longer than 6 mm and a corolla tube 8–10 mm long. The other species of *Tournefortia* with opposite leaves in Colombia, *T. pauciflora* Nowicke and *T. scabrida* Kunth, differ in having shorter calyces and less prominant indument on the twigs (Nowicke, 1974).

Tournefortia spicata James S. Miller, sp. nov. TYPE: Colombia. Nariño: Mpio. Tumaco, 80 km from Tumaco along road to Pasto, in wet area of primary forest, near *Orbignya* palms and streams, "Guayacana," 19 July 1984, *M. J. Balick, L. E. Forero P., S. R. King & N. Hernández 1667* (holotype, MO 3531270). Figure 2.

MISSOURI
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HERBARIUM

№ 3531269

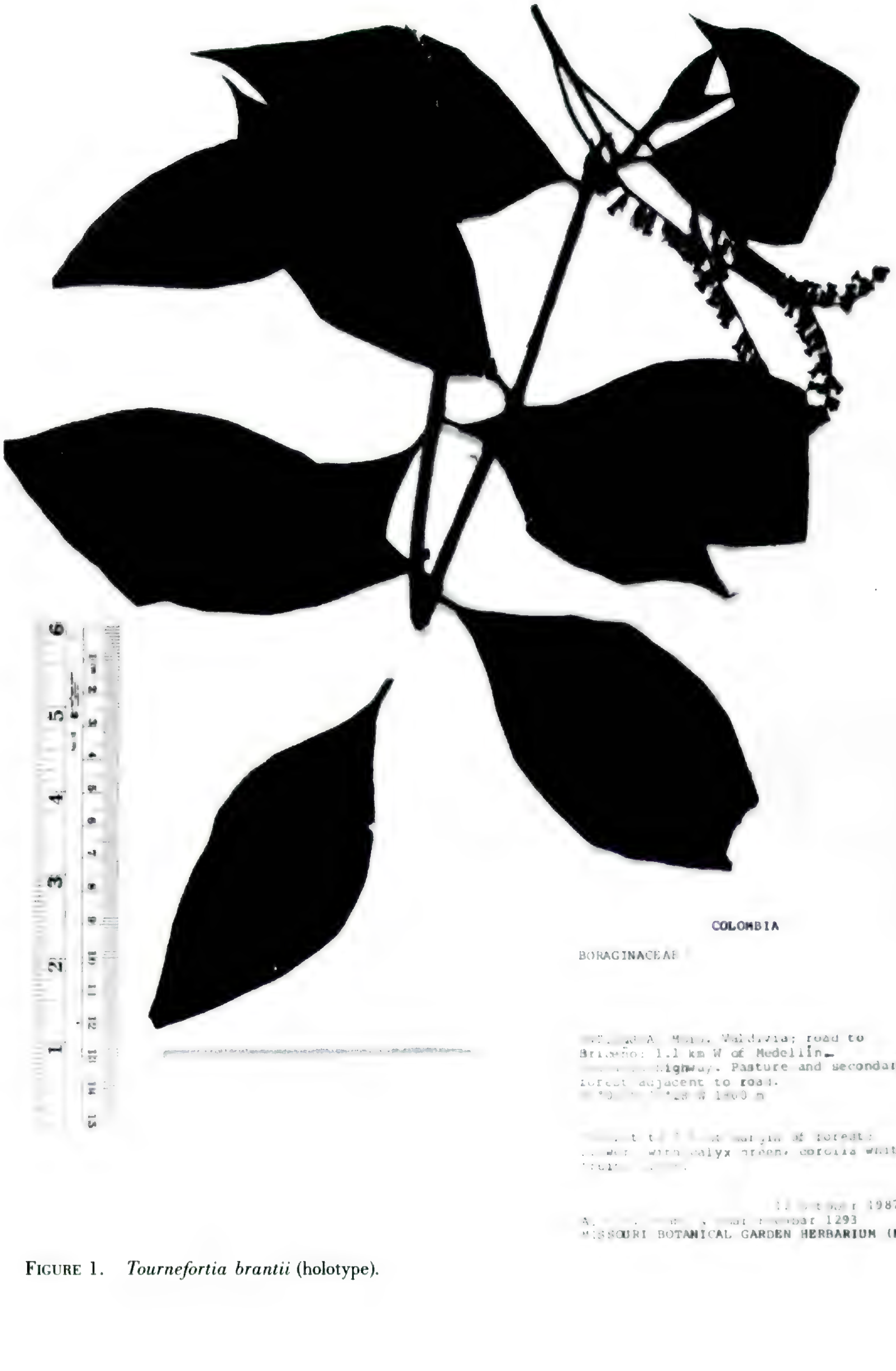

FIGURE 1. *Tournefortia brantii* (holotype).

FIGURE 2. *Tournefortia spicata* (holotype).

Frutex ad 3 m altus, ramunculis veluntinis ad villosis. Folia alterna, ovata, 14.5–21.5 cm longa, 8–10 cm lata, apice acuminato, basi obtusa ad late acuta, supra et infra hirsuta. Inflorescentia dense florifera, clavato-spicata. Sepala lineari-lanceolata, 4–5.5 mm longa; corolla lutea, postea nigra, 8 mm longa, lobis 5, ovatis, 2 mm longis, tubo 4–5 mm longo, hirsuto. Fructus non visi.

Soft-stemmed shrub to 3 m tall, the twigs velutinous to villous with erect golden-brown hairs ca. 1 mm long. Leaves alternate; petioles 11–28 mm long, velutinous, the hairs erect, ca. 1 mm long, golden brown; leaf blade ovate, 14.5–21.5 cm long, 8–10 cm wide, the apex acuminate, the base obtuse to widely acute and decurrent along the petiole for 0.5–1 cm, the margin entire, secondary veins 13–15, arising from the midrib at 70°–80° near the base of the leaf, 35°–40° near the apex, the tertiary and quaternary veins clearly evident, ramifying in a reticulate pattern, the upper surface hirsute, the hairs erect to spreading, arising from the aeroles only giving a slightly bullate appearance to the leaf at maturity, the midrib villous, the lower surface hirsute, villous along the midrib and secondary veins. Inflorescences densely spicate borne in pairs from a dichotomously branched peduncle 9–14 cm long, this velutinous to villous, the hairs erect, ca. 1 mm long, golden-brown, the spikes 5–8 cm long, 1.5–2.5 cm broad, the flowers borne 1 mm or less apart, a few scattered, 3–9 mm apart at the base. Flowers bisexual with the style borne beneath the anthers; sepals 5, free to the base, linear-lanceolate, 4–5.5 mm long, uneven in length, hirsute; corolla yellow, later turning black, tubular with 5 spreading lobes, 8 mm long, the lobes ovate and acuminate at the apex, ca. 2 mm long, the tube 4–5 mm long, hirsute outside; stamens 5, inserted just beneath the mouth of the corolla tube, the anthers nearly sessile, lanceoloid, ca. 1 mm long; ovary ovoid, ca. 0.6 mm tall, the style ca. 5 mm long, the stigma conical with a thickened annular ring at the base. Fruits unknown.

Tournefortia spicata stands apart from the other species of sect. *Tournefortia*, and its relationships are unclear. It is unusual in its soft-stemmed, short growth habit, dense inflorescence, and velutinous to villose peduncle. The flowers are distinctive in having linear-lanceolate sepals 4–5.5 mm long and a corolla tube 8 mm long, It is known only from the area in which the type was collected, and fruits remain unknown.

Additional specimens examined. COLOMBIA. NARIÑO: Mpio. Tumaco, La Guayacana, 20–100 m, *Soejarto 958* (US).

I thank the Department of Botany at the Smithsonian Institution, particularly Joan W. Nowicke, for providing E. P. Killip's unpublished manuscript.

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A NEW SPECIES OF *URGINEA* (LILIACEAE) IN NIGERIA

The genus *Urginea* Stein. is represented in West Tropical Africa by the variable species *U. indica* (Roxb.) Kunth, *U. ensifolia* (Thonn.) Hepper, *U. pauciflora* Bak., and the variable *U. altissima* (L.) Bak., which was recently discovered to resolve into a complex of three species: *U. altissima* (L.) Bak., sensu stricto, *U. gigantea* (Jacq.) Oyewole, and *U. viridula* Bak. (Oyewole, 1975). Samples of wild populations continue to reveal the inadequacy of the existing taxonomy of the genus. For instance, complexes such as in *U. indica* (Oyewole, 1987) or entirely new variants are being discovered. Hence, a revision of the genus is due.

The present report describes a recently discovered wild population of a new species within the main campus site of the University of Ilorin, Kwara State, in west central Nigeria.

Ecology

The flora of a rock outcrop located about 1.5 km to the east of the academic area of the main campus site of the University of Ilorin, about 20 km outside the city of Ilorin, was first sampled in May 1982. The site of the rock was to be part of a proposed botanical garden.

About 100 tiny bulbs of an evidently new representative of *Urginea* were collected between May 1982 and February 1983, from the shallow soils of the outcrop. The soil is brown and lateritic, with occasional dark humus in depressions. The vegetation is low grassland, with few small trees of *Entada africana*, *Erythrina pulcherrima*, and other legumes interspersed with stands of *Butyrospermum paradoxum* and *Lophira lanceolata*, and low stands of *Cochlospermum* sp. Herbaceous species of Commelinaceae and Asteraceae are common among low grasses. Seasonal marshes and ponds support the growth of various Cyperaceae, *Anthericum nigericum*, and many low, herbaceous Acanthaceae and Scrophulariaceae.

Bulbs of *U. nana* occur in an unshaded area with low grass and forb cover. Other bulbous geophytes occurring in the same habitat and interspersed with *U. nana* are *Dipcadi tacazzeanum* (Hochst. ex A. Chev.) Bak. (*D. filamentosa* Morton) and *Pancratium hirtum* A. Chev.

Taxonomy

Urginea nana Oyewole, sp. nov. TYPE: Nigeria. Ilorin: near the academic area, University of Ilorin, *S00/2111* (holotype, IUH; isotype, FHI). Figures 1–3.

Bulbus ovoideo-globosus, circa 3 cm altus, 4 cm diam., collis bulborum 0.5–4 cm, tunicae albae, tunicis exterioribus maroribus; folia tenuia, filiformia appressa aut lineari-lanceolata, erecta, 8–20 cm longa, 1–3 mm lata; pedunculus erectus, 1.5–4 cm longus; racemus compressus umbellatus, floribus 1–6, pedicellis crassis sed non rigidis, postremo in fructu reflexis; tepala subpunicesubflavida, aut subviridula flavida, 6–10 mm longa, 1–2 mm lata; maginibus flavescentibus, antherae 1–2 mm longae; capsula globosa vel ovoidea fulva, apice mucronata, 8–12 mm longa, seminibus nigris vel fusco-fulvis, 7–8 mm longis, usque 4–6 mm longis et usque 6 mm latis. Affinis *Urginea pauciflora* et *Urginea indica* (formae depauperatae) sed pedunculis minoribus, racemo compresso usque umbellato, foliis filiformibus aut lineari-lanceolatis differt.

Bulb small, ovoid-globose, up to 3 cm high and 4 cm diam., usually with bulb neck, 0.5–4 cm long and consisting of rolled bases of old leaves; scales white, outermost tunics membranous; leaves thin, filiform and spreading, or linear-lanceolate and erect to acutely arching, 8–20 cm long, 1–3 mm wide, not borne with the flowers; peduncle stiffly erect, 1.5–4 cm high, naked; inflorescence compressed, 1–6-flowered, all arising from about the same level terminally; pedicel thick but not stiff, reflexed during fruit development; tepal 6, pinkish and tinged yellow at the margin, or greenish yellow with hyaline margin, in 2 whorls of 3 each, alternating and free to the base, 6–10 mm long, 1–2 mm broad, outer segments reflexed at anthesis; filament hyaline, anthers bicelled, dorsally medifixed and versatile, up to 2 mm long, completely fertile; ovary pyramidal, 3–4 mm high at anthesis; style short and stiffly erect, about as long as the ovary. Fruit a 3-chambered capsule, brownish at maturity, ovoid-spherical, with mucronate apex, only slightly trigonal from the exterior, 8–12 mm

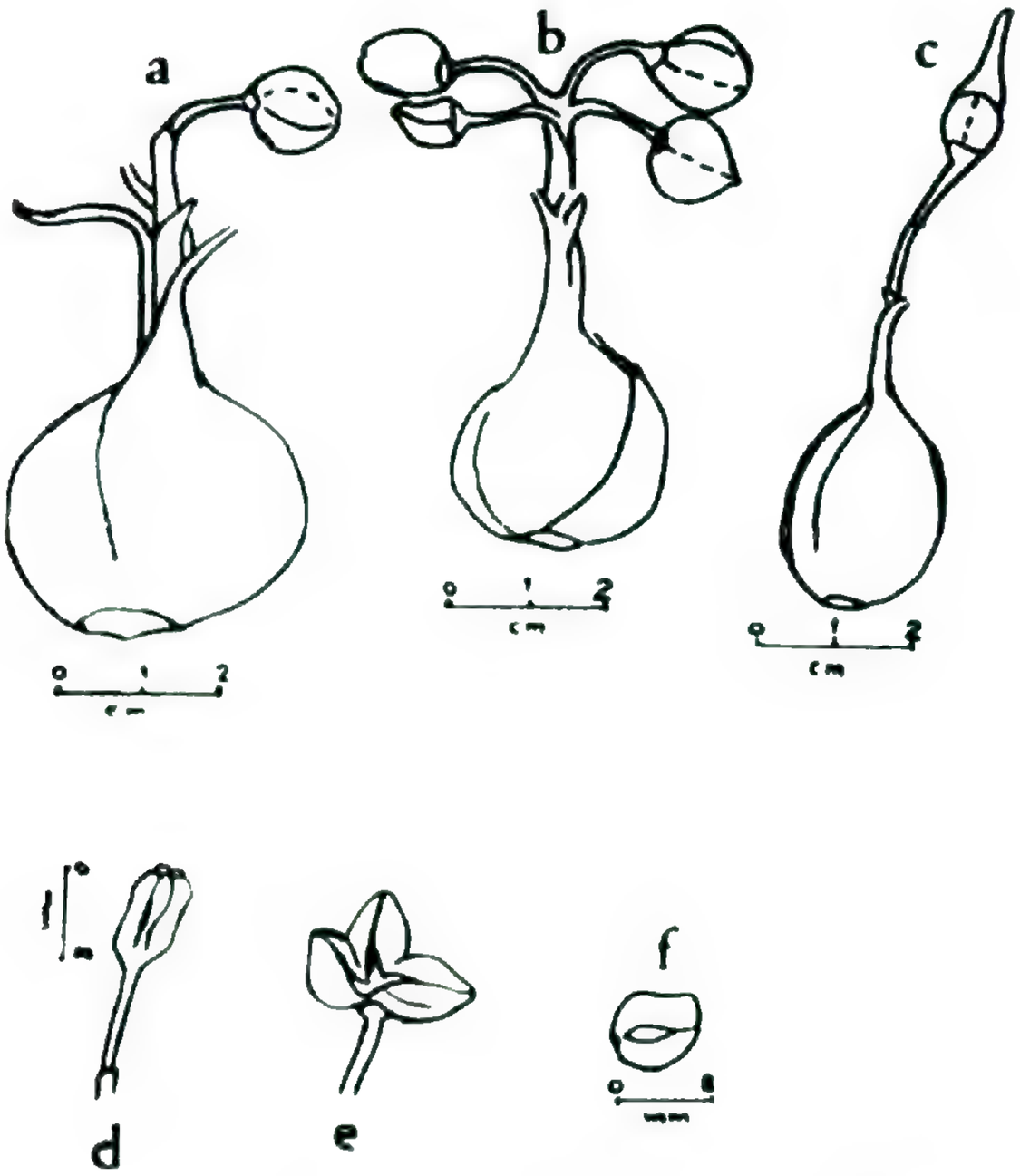

FIGURE 1. Growth habits of *U. nana*.—a, b, c. Fruiting plants of Morphs A, B, and C, respectively.—d. Mature flower before anthesis.—e. Dehisced fruit.—f. Seed.

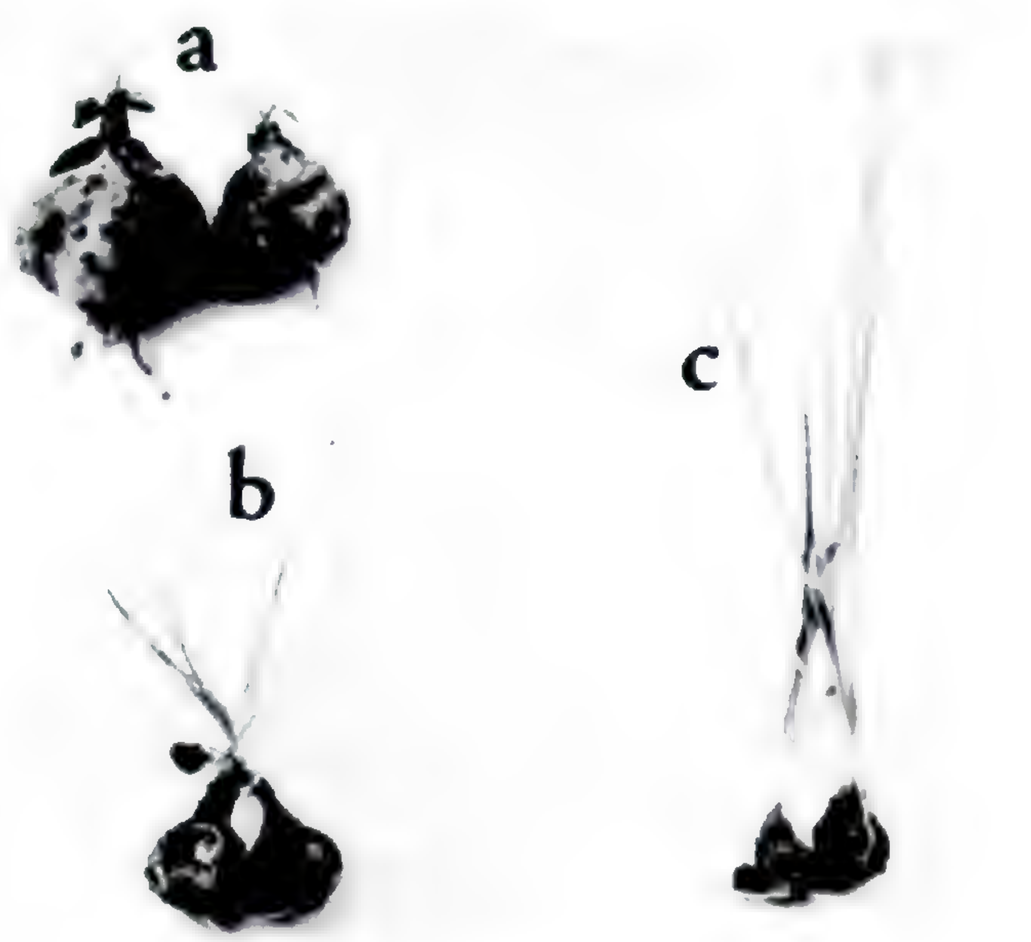

FIGURE 2. Vegetative plants of *U. nana*.—a, b, c from Morphs A, B, and C, respectively.

long as well as in circum.; seeds dark brown to black, 7–8 mm long, 4–6 mm across (including the membranous wing), uniseriate in each loculus.

Paratypes. NIGERIA. ILORIN: about 1.5 km to the northeast of the main buildings of the University of Ilorin, SOO/2121, SOO/2229, SOO/2230, SOO/2231 (IUH, FHI).

These bulbs resemble *U. pauciflora* in being few-flowered, and the depauperate morphs of *U. indica* in having linear-lanceolate, stiffly erect leaves and few-flowered inflorescences. They differ, however, in the form and width of the vegetative leaf, and in the size of the scape and the positioning of the flowers on the inflorescence. Examination of the herbarium specimens at the Herbarium of the Forest Research Institute of Nigeria (FHI), Ibadan, and at the University of Ibadan Herbarium (UIH) revealed that such specimens have not been collected previously in West Tropical Africa. Earlier examination of materials at Kew also showed that specimens of this taxon have not been recorded.

Certain variations were observed in the floral and vegetative morphology, on the basis of which the population was segregated into three morphs designated A, B, and C. This informal categorization was necessary for the purposes of karyotypic examination and eventual cytogenetic studies.

Morph A. Bulbs ovoid-spherical, 3–4 cm diam., 2–3 cm high, usually with relatively short bulb neck. Leaves thin, narrow, coiled (filiform), 10–15 cm long, 1–2 mm broad, dark green, crescent-shaped in transection. Peduncle up to 2.5 cm high outside of the bulb neck, thick and stiffly erect, green, bearing 2–3 flowers terminally. Tepals 8–10 mm long, 2–3 mm broad, yellowish green with hyaline margin.

Morph B. Bulbs ovoid-spherical, 2–3 cm high and diam., with a conspicuous bulb neck as high as 4.5 cm. Leaves thin, narrow, coiled, light green, crescent-shaped in transection, 8–12 cm long, about 1 mm broad. Peduncle stiffly erect, 3–4 cm high outside of the bulb neck, pinkish to purple, usually bearing 3–6 flowers terminally. Tepals pinkish tinted green on the margin, 7–8 mm long and ca. 2 mm broad.

Morph C. Bulbs small, oval-globose, 0.75–1.5 cm diam., 1.5–2.5 cm high, with relatively short bulb neck. Leaves light green, acutely erect, linear-lanceolate with open transcection and shortly apiculate apex, 15–20 cm long, 2–3 mm broad. Peduncle thin, erect but not firm, up to 2.5 cm high outside of the bulb neck, bearing one terminal flower usually. Tepal greenish with hyaline margin, 6–7 mm long, about 1 mm broad.

The floral dimensions of the three morphs overlap so that they are not easily distinguished, but morph C differs distinctly in vegetative morphology. Plants of *U. nana* must have escaped recognition for so long because of their habit of growth: the fruiting shoot is hardly seen above the heap of burnt litter; the inflorescence begins to emerge from the soil less than 36 hours after the first burning. The flower and fruit colors merge with that of the dark brown soil surface once the charred

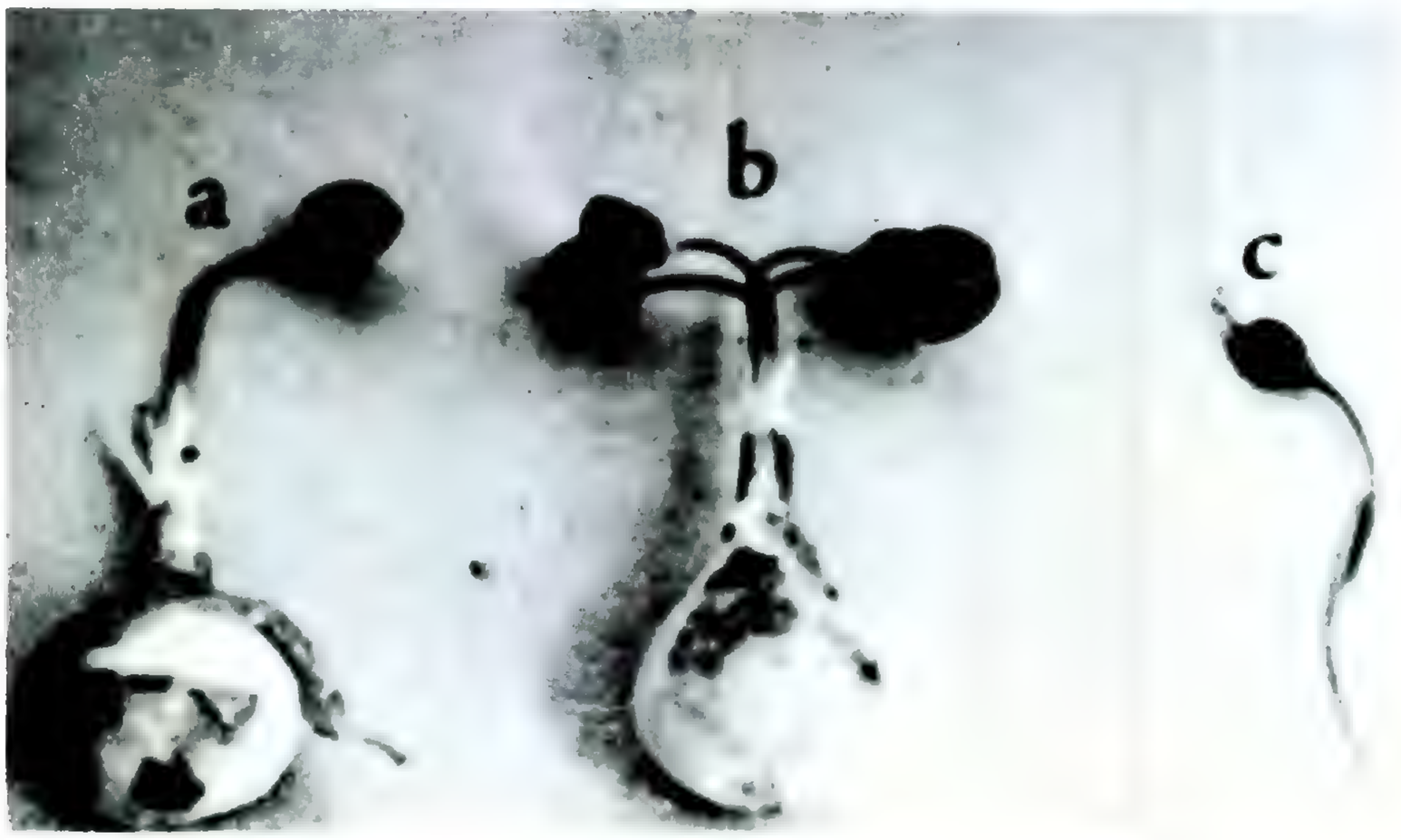

FIGURE 3. Fruiting plants of *U. nana*.—a, b, c from Morphs A, B, and C, respectively.

remains are blown away by the wind, and the vegetative leaves pass easily for the leaves of *Bulbostylis fimbristyloides* and related sedges. The leaves are not evident when the plant flowers but rather are produced when the surrounding vegetation is luxuriant.

Following is a taxonomic key for separating the three morphs and their close relatives within the genus:

1a. Pedicel 3 cm long or longer; inflorescence various in height and number of flowers, but a lax raceme; capsule globose ..... *U. indica*
1b. Pedicel shorter than 2 cm long.
  2a. Scape 6–10 cm tall; inflorescence a raceme of 6–10 flowers; fleshy tunics purplish violet ..... *U. pauciflora*
  2b. Scape less than 5 cm tall; inflorescence of 1–6 flowers borne terminally; fleshy tunics white ..... *U. nana*, morphs A, B & C
    3a. Leaves erect, flat in transection, 15 cm long or longer; inflorescence single-flowered, terminal, or with two flowers, one of which is subterminal ..... *U. nana*, morph C
    3b. Leaves obtusely arching or spreading, coiled, crescent-shaped in transection, up to 12 cm long; inflorescence 2–6-flowered, umbellate.
      4a. Flowers pink, 3–6 per inflorescence ..... *U. nana*, morph B
      4b. Flowers greenish, 2–3 per inflorescence ..... *U. nana*, morph A

DISCUSSION

Urginea is probably of recent origin in West Tropical Africa (Oyewole, 1975), arising probably like its very close relative *Albuca* L. from southern-southeastern Africa and migrating across central Africa into the west (Oyewole, 1971). It is therefore conceivable that, faced with myriads of ecological niches in this region, the number of representative species and infraspecific taxa is likely to be much higher than Hepper (1968) recognized. The distinct morphology of *U. nana*, with its peculiar habitat, sets it apart from previously known species of the genus. However, the existence of different morphs within a seemingly uniform ecological niche suggests that the population of *U. nana* may not entirely represent one genetic system. It is hoped that investigations now in progress on aspects of the biosystematics of this species will resolve this problem before long.

The discovery of *U. nana* in Nigeria underscores the fact that the latest treatment of Liliaceae in West Tropical Africa (Hepper, 1968) is due for revision. It also indicates that *Urginea* may be represented in this subregion by many more taxa than are now known (Oyewole, 1975).

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—S. O. Oyewole, *Department of Biological Sciences, University of Ilorin, Nigeria.*

Julian Alfred Steyermark

This issue of the Annals of the Missouri Botanical Garden *is dedicated with respect and admiration to Julian Alfred Steyermark, who began and ended his astoundingly productive life in St. Louis, Missouri. The following set of recollections will help paint a portrait of one of the world's great botanists and plant explorers. A memorial service for Dr. Steyermark was held at the Missouri Botanical Garden, where he passed the final years of his career. The first contribution, by Dr. Peter H. Raven, Director of the Missouri Botanical Garden, is an overview of Dr. Steyermark's life and accomplishments and was presented at the memorial service. Several remembrances generously contributed by Dr. Steyermark's friends and colleagues follow.*

The frontispiece: Julian Steyermark, 1987, Warren County, Missouri.

Julian Alfred Steyermark

Born, 27 January 1909, St. Louis, MO.

Graduated from Soldan High School, St. Louis, MO, 1925.

Married Cora Shoop, 1 September 1937, no children.

B.A., Washington University, St. Louis, MO, 1929.

M.S., Washington University, St. Louis, MO, 1930.

M.A., Harvard University, Cambridge, MA, 1931.

Ph.D., Washington University, Henry Shaw School of Botany, St. Louis, MO, 1933.

Research Assistant to Robert E. Woodson, Jr., Missouri Botanical Garden, 1934–1935.

Biology Instructor, University City Senior High School, University City, MO, 1935–1937.

Taxonomist-Ecologist, U.S. Forest Service, summers 1936–1937.

Assistant Curator, Field Museum of Natural History, Chicago, IL, 1937–1947.

Associate Curator, Field Museum of Natural History, Chicago, IL, 1947–1950.

Curator, Field Museum of Natural History, Chicago, IL, 1950–1958.

Professor of Botany, Southern Illinois University, Carbondale, IL, April–June 1958.

Professor of Botany, University of Missouri, Columbia, MO, June–August 1958.

Botanist, Instituto Botánico, Ministerio de Agricultura y Cría, Caracas, Venezuela, 1959–1984.

Curator, Instituto Botánico, Caracas, Venezuela, 1975–1981.

Curator, Missouri Botanical Garden, St. Louis, MO, 1984–1988.

Died, 15 October 1988, St. Louis, MO.

132,223 is the last number in Julian Steyermark's collecting book. Julian Steyermark described more than 1,000 new species of plants during his career.

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Carlyle A. Luer with Rodrigo Escobar R. German translations by Fritz Hamer. Illustrations by Stig Dalström.

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Peter Goldblatt & P. P. Lowry, II, Editors

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Cover illustration. *Solanum tolaranaro* D'Arcy & Rakotozafy, by John Myers.

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People were Julian Steyermark's first love, but flowers were his second. He was a passionate man, and some of his passions were shaped by early trips out of a St. Louis that was crowded and smoky into the gentle Missouri countryside, where he and his friends first sought unusual birds. Later he reveled in the autumnal drifts of asters, in enjoying the purple-brown trilliums and delicate orchids of early spring, and in collecting samples from the legions of sedges that he could see only dimly through the torrential cascades of sweat that poured from his brows as he crouched over gravelly riverbars during the torrid Missouri summers. Even the long-exserted anthers of the ribworts that appeared in early summer must have fascinated this unusual young man, who grew in knowledge about the diversity of plants that nurtures all who take the time to stop and appreciate it.

Everywhere he went Julian was recognized for his achievements: the governments of Guatemala, Ecuador, and Venezuela; his alma maters at Washington University and here at the Garden; the Missouri Department of Conservation; and the Sierra Club all soon came to know him as an inspiring and unique individual, and gave him abundantly of their prizes and awards. Everyone knows that Julian collected more plant specimens than anyone else has ever done, an incredible 132,000 specimens, and that he was a prolific writer and herbarium worker. In fact, if we hadn't known him personally, we might think—reading about his accomplishments—that he was some sort of drudge, dreadful, demanding, and uninteresting. Nothing could have been farther from the truth, however; those of us who had the privilege of enjoying his company, whether in the field, listening to his favorite music, or simply exchanging views on some current topic, know far better.

Julian certainly did enjoy hard work, and appreciated all of those wonderful manifestations of recognition that were accorded him for his accomplishments—to be included in the *Guinness Book of World Records* as the world's champion plant collector was for him an absolute delight. In his life, however, he was sustained to a far greater degree by the love of his many friends. Boyhood friends who ranged through the Missouri woods together searching for rare warblers retained the joys of their mutual admiration into the years of maturity. Those who had the privilege of climbing the steep, rocky slopes and breaking through the interlocking branches of the forests of Venezuela with him never forgot the experience, and expressed their deep concern during his final illness. Once you knew Julian, you simply did not forget him.

Returning here to his boyhood home at an age when most have slipped into the relaxation and hazy days of retirement and gentle decline, Julian undertook the preparation of an account of the plants of what is perhaps the least-known part of the world botanically, the interior of Venezuela, where the tepuis and gorges that he loved so deeply make up the spectacular fabric of the fabled Lost World. As he did everywhere he lived and worked, Julian renewed sturdy old friendships, and forged new ones, a process that continued all his life. Bruce and Luther, Gerrit and Jeany, Tamra and Bruno, and so many others—you each gave him much, especially during his final days of great physical discomfort, but you got far more than you gave. Julian's open, happy smile; his sweet, joyous, and dedicated personality; his attentiveness to the task at hand; and his unremitting, dignified friendship will form memories that will be with each of us until our own final days.

For someone who spent his childhood amongst the beauties of bellflowers, gerardias, and desmo-

diums, gumweeds might have seemed a strange choice as the subject of a doctoral dissertation. These sunflower relatives exude a white, sticky sap that fills their unopened flower heads before they expand to reveal the golden-yellow inflorescence hidden within each. Gumweeds are relatively uncommon in Missouri, but range widely over the American West and Mexico. Julian's graduate advisor, Jesse Moore Greenman, who trained an entire generation of American taxonomists here in St. Louis, was determined to complete the great task of John Torrey, George Engelmann, and Asa Gray—to make known the variety and complexity of the plants of our continent, and he assigned doctoral problems accordingly. For this purpose, Dr. Greenman enlisted Julian, who was afire with his love of plants, into his army; and the young man set out along the dirt tracks and across the fields of the West, publishing his work ultimately in the Garden's *Annals*.

For the 28-year-old Julian Steyermark, just married, there followed 21 years in Chicago, where he ultimately became Curator of Botany at the Field Museum. That institution, and his contact with the famous botanist Paul Standley, provided his introduction to the plants of Guatemala and brought home to him just how little we knew about the plants of the American tropics. Missouri's flowers remained his favorites, however, and he cultivated them lovingly, with his wife Cora, in their own wildflower garden near Chicago, a sanctuary now maintained by The Nature Conservancy. For 30 years Cora and Julian crisscrossed Missouri searching for plants, driving thousands of miles back and forth from their home, camping in riverbottoms, by dusty roadsides, or in forests, so that they would come to know more fully the detailed distributions and characteristics of the plants of this state. Their cultivation of many of these plants in their home garden was not merely a scholarly exercise; it was also an act of love, a celebration of their natural beauty and their individual character, as anyone who has turned the pages of Julian's exemplary 1963 *Flora of Missouri* will know. What memories those explorations provided Julian and Cora, and what times they shared together! To know about some of them, read Cora's *Behind the Scenes*, a testimony to the beauties of our state and the joy that is in store for those who take the time to appreciate, understand, and enjoy them. Cora wrote:

> The morning was cold and clear. Pine trees and shrubs, gray and bent with ice and snow, lent variety to the icicled oaks. At the top of the hill we came upon the sunrise. The whole view for miles across the hills was a brilliant blaze of crystalline purity. Against the sun, the tops of trees turned to polished gold, shading to silvered lower limbs rising above a soft setting of snow-covered shrubs.
>
> Julian stopped the car. "I'm stuck with a view," he said. "I'm afraid I'll break something if I move."
>
> "That whole view looks as if it might break if you breathed on it. This is something you see once in a lifetime. I'm glad we stalled last night," I said and really meant it.

From Chicago, Cora and Julian moved on to Caracas, where they traded goldseal, gentians, and puccoon for *Brocchinia*, *Chimantaea*, *Sterigmapetalum*, and *Heliamphora*. The exchange proved a rewarding one, and Julian went on to add more to our knowledge of the plants of Venezuela than anyone had before. A quarter of a century was enough—filled with friends from Venezuela, new friends from the States, wonderful new plants, many of them extravagantly beautiful, and hundreds named in Julian's honor, hundreds of them. After Cora's death, Julian came back here to his hometown and began to write in earnest about the incredible plants of the Lost World. His last work will be completed here, and will stand as a final testament to his industry and to his scholarship. As for any human being, however, what will prove to be even more important to all of us will be our memories, for Julian Steyermark was an inspirational person, one who projected his own values without trumpeting them, and thereby enriched all our lives, as he did the literature of botany.

In concluding her book, Cora wrote:

> It was a long exploration of more than 30 years from which we have related merely a few experiences representing each month of the collecting season. So we see—a book is not only written and rewritten, it is lived through a life of sweat, privations, and joys behind the scenes, before the final word is ever put on paper.
>
> We, X.Y. [that was her affectionate term for Julian in the book] and I, hereby will the state to the next botanist.

Is that not a reflection worthy of us here today? We all toil in a common field, inspired by early memories, contributing to knowledge, doing what we can for one another and regretting what we cannot do. In the plants that support and nurture us, enrich our souls with their beauty, and inspire our actions, we have found a common bond. Here today we have found another: the remarkable and full life of a truly luminous human being, our friend Julian Steyermark, whose fellowship we enjoyed so deeply, and whose life we will remember with gratitude.—*Peter H. Raven, Director, Missouri Botanical Garden; from Julian Steyermark's memorial service.*

During the 1940s in my beginnings as a botanist, I started to understand the importance of Dr. Julian Steyermark's works on the taxonomy of the Venezuelan flora. The National Herbarium already possessed numerous collections made by the remarkable scientist. By the 1950s, our friendship had grown stronger and lasted for more than 30 years. His long and exhaustive research of the Venezuelan geography created a major collection that has contributed in a decisive way to enhance Venezuela's floristic inventory.

His humility and generosity were the most outstanding features of his personality. A few years ago, before departing for Venezuela's Guayana, I asked Julian to inform me on the area I was going to visit, a place he knew and had explored. Among the helpful and valuable facts he supplied was the name of a man who knew the region well and could act as a "baqueano" [guide]. Arriving in the area, I found the person Julian had mentioned. I told him my mission in the area and that Dr. Steyermark had recommended him to me. To my suprise he answered, "Dr. Steyermark? I have never heard such a name." However, I insisted and slowly repeated, "Are you sure you don't know Dr. Julian Steyermark?" His facial expression suddenly changed and he replied smiling, "Oh! you mean Julián, of course I know him and I am ready to help you."

This story helps to illustrate Julian's sense of humility, generosity, and harmony. His legacy as a scientist goes hand in hand with the personal attributes that made him a great human being and a beloved friend to those who knew him.—*Leandro Aristeguieta, Universidad Central de Venezuela, Jardín Botánico de Caracas.*

FIGURE 1. *Fuchsia steyermarkii*, from cloud forest in southern Ecuador.

When I arrived at the Instituto Botánico in Caracas in the summer of 1975 looking for a project to help me learn about tropical plants, I was brought into the office of one very busy, grumpy Dr. Julian Steyermark. Faced with a botanical neophyte, he suggested that I begin collecting plants from the hills surrounding the Instituto—a patch of secondary, deciduous forest in the heart of the city. Years later this project led to a paper we published together on the vegetation of the deciduous forests of Caracas, but only after many journeys in each other's company to the few wooded areas near the city not yet overtaken by apartment buildings or "ranchos." Following up our finding of five species of the coca genus, *Erythroxylum*, growing side by side in the hills above the Botanical Garden, a student of mine at Simón Bolívar University in Caracas completed a wonderful thesis on the comparative reproductive biology of the group. Another result of our study was the recognition of two species new to science, *Eugenia mcvaughii* and *Erythroxylum undulatum*, both based on plants found less than 100 meters from the front door of the Instituto. It was the shortest trip I know of for specimens to be placed in the type collection of the National Herbarium.

Now years later I sit in Julian's former office—sometimes in his chair, picking up where he had left his unfinished project, the *Flora of the Venezuelan Guayana*, more affectionately known as the "Flora of the Lost World." Julian was a "baqueano" (guide, in Venezuela) to me, for he opened up many paths that I was to follow.

My botanical tribute to Julian was the naming of *Fuchsia steyermarkii*. Just after his death, I was to return to the original site where the plant was found, in lush cloud forest on the steep slopes south of the Nudo de Sabanilla, in southernmost

Ecuador. I got there in a rented taxi, a few hours by car from the city of Loja; he got there by foot and mule, on a fortnight trek through endless rains, in October of 1943. His *Fuchsia* is a most unusual species, with needlelike leaves, and if it survives in cultivation it will be highly esteemed.

Many simple folk all over Venezuela knew and remembered Julian. I met some of them, usually in remote places, like "Horacio," a Makiritare Indian who spoke no Spanish but had climbed many a tree for him; and José Mendoza, an Andean homesteader from San Vicente de la Revancha, whose senile father had guided Julian years ago far into the páramos towering over the valley. Both reacted similarly when I mentioned Julian's name: a big, amused grin accompanied by signs of respect for a man so dedicated to his botanical mission.—*Paul E. Berry, Missouri Botanical Garden.*

I had been at the New York Botanical Garden as a doctoral student for all of three weeks in 1980 when I first met Julian Steyermark. He was visiting the New York Botanical Garden to consult our Guayana Highland collections and to collaborate with Bassett Maguire on several taxonomic treatments. Of course, I already knew of him by reputation. I was a novice to tropical botany, so in an attempt to say something intelligent to him I dug back into my M.S. thesis on *Isoëtes* and located the citation of *Steyermark 85179*, which I had identified as *I. melanopoda* Gay & Dur. I reported this to Julian, and to my amazement he immediately told me where in Missouri the specimen had come from and the month during which he collected it 23 years previously! This was not to be the last time over the following eight years years that Julian's prodigious memory would impress me.

I also became aware of Julian's capacity for work as I observed him during his subsequent periodic visits to New York. Occasionally, he would share my office because of our mutual interests in the Guayana Highland flora. He stayed in the Garden's Snuff Mill apartment during his visits. By 7:30 A.M. he would be at the herbarium. With a single-mindedness he worked on specimens until about 6:00 P.M. with only a half-hour break at the lunch table. Julian was not one for idle chat, and he clearly did not like to be disturbed while working. At six, and also with a single-mindedness, he would round up any remaining staff and students and go have a huge dinner, followed always by a stop at the local ice cream establishment. Occasionally, he would take in a movie, but more often than not he would head back to the herbarium for several more hours of work before retiring for the night.

And thus, day after day, he would make his way through huge piles of specimens, writing descriptions of new taxa on the spot in his nearly illegible scrawl. Julian confessed that he "over-described" occasionally, and that perhaps he split excessively. However, he justified it by saying that he viewed his role as one of describing biotic diversity as he saw it. He would leave it to following generations of botanists to determine just how "good" his decisions were. How history will judge his taxonomic decisions does remain to be seen, but there can be no doubt that Julian had an excellent "eye" for seeing differences. I also know that I trust his specimen annotations more than those by just about anybody else. During the first half of this century, when a researcher needed quick, reliable determinations for neotropical specimens, the solution was "send them to Standley." Julian was heir to this role. His magnum opus, *Flora of the Venezuelan Guayana*, will aptly attest to his unparalleled knowledge of the neotropical flora. In an age of few heroes, Julian was one for many of us.—*Brian M. Boom, The New York Botanical Garden.*

Hace cuatro años, el 7 de junio de 1984, tuve el honor de darle con alegría y en nombre de los botánicos de Venezuela, un adiós, un hasta luego, a Julian Steyermark. Esta despedida era transitoria, ya que por su propia decisión, volvía a su tierra natal, Saint Louis, Missouri. A pesar de su ida, Julian no podía resistir la tentación de permanecer mucho tiempo allá, solo en el norte, razón por la cual, con frecuencia hasta principios de este año, regresaba a Venezuela, pues como el decía: "amor a primera vista," fue su reacción al ver por vez primera a este país en 1943. Y, cual enamorado, exclamó: "Mi amor a Venezuela, se debe no solo a sus flores, a su fauna, a sus paisajes, sino también a mis amigos quienes poseen una alta sensibilidad, capacidad, y deseo de trabajar en la botánica y en la conservación de sus recursos naturales. Por eso mi amor por Venezuela fue instantáneo."

Julian Steyermark, nació en Saint Louis, Missouri, el 27 de enero de 1909. Desde muy temprana edad sintió el reto de conocer la naturaleza que lo rodeaba. Allá por el año de 1925, cuando era *Boy Scout* en su ciudad natal, se interesó en la zoología, fijando primeramente su atención en las aves. En ese mismo año ingresa al club de Biología de su colegio y su espíritu naturalista se concentró en el fascinante mundo de las plantas. Desde entonces, sólo vivió en función de ellas. Combinando sus estudios con sus labores de Guía Naturalista en los parques de Saint Louis y sus

FIGURE 2. Julian Steyermark (lower right) at ca. age 20 as counselor at summer camp in Maine.

alrededores, fue formando una buena colección de plantas la cual fue adquirida por el Herbario de Missouri en 1934 por 84 dólares. Este dinero fue la base para comprar su primer vehículo, para poder continuar con mayor facilidad sus trabajos botánicos.

Julian llegó a Venezuela en diciembre de 1943, cuando en misión del gobierno de su patria de origen, vino a buscar la corteza del árbol de la quina, indispensable durante la Segunda Guerra Mundial para combatir el paludismo. Sus primeras incursiones botáncas en el país las efectuó en lo que es hoy el Parque Nacional El Avila, de allí pasó al Oriente de nuestro territorio, regresando a Estados Unidos en 1945 con una colección de 8,000 muestras botánicas.

La belleza escénica de los diferentes ambientes venezolanos, el contacto con las plantas, coló tan hondo en la sencilla humanidad de Julian, que soñaba que Venezuela debería ser su país. Este sueño, cual regalo de navidad, se convirtió en realidad cuando en diciembre de 1959 recibió la invitación de Tobias Lasser, por recomendación de William H. Phelps, para que formara parte del personal del Herbario Nacional de Venezuela, donde permaneció activamente como estudioso de la flora Venezolana. Por su larga trayectoria y aportes al conocimiento florístico del país recibió entre otras las siguientes distinciones: Orden Andrés Bello (1974); Orden al Mérito en el Trabajo, Primera Clase (1974); Orden Henri Pittier (1979); Premio William H. Phelps, otorgado por la Sociedad Venezolana de Ciencias Naturales; Miembro Correspondiente Nacional de la Sociedad de Ciencias Naturales de la Salle; Miembro Titular de la Fundación Terramar; Investigador Emeritus del Jardín Botánico de Caracas, INPARQUES (1986).

Julian Steyermark, después de sesenta y nueve años de búsqueda y trabajo activo en su mayor obra botánica, *Flora of the Venezuelan Guayana*, murió en Saint Louis, Missouri U.S.A, el 15 de octubre de 1988. Por eso hoy siento la necesidad de darle en nombre del personal del Jardín Botánico de Caracas un adiós lastimoso, con dolor y nostalgia.

En este momento recuerdo, que un día en febrero de 1984 Julian me dijo, sentado en la cima del Aratitiyope (Templo Sagrado de Las Guacamayas), Territorio Federal Amazonas, en un momento de descanso y contemplando la majestuosidad reflexiva del paisaje, "Francisco mi mayor deseo es emplear todas mis fuerzas y mi dinero, para seguir explorando este maravilloso país. También, quisiera que al morir, me enterraran en un tepuy." Julian, si bien es cierto, que tu cuerpo no descansará en la arenisca de los tepuyes, tu imagen caracterizada por el pañuelo rojo, con el cual cubría tu cabeza, quedará guardada en estas mesetas y en la memoria de todos los que salimos al campo contigo. Tú estarás presente en cada planta del tepuy, pues quién de nosotros no se reirá de tus ocurrencias cuando nos topemos por ejemplo con una *Steyerbromelia* de Marahuaca; o cuando saboreemos una base foliar tierna de una Rapateaceae,

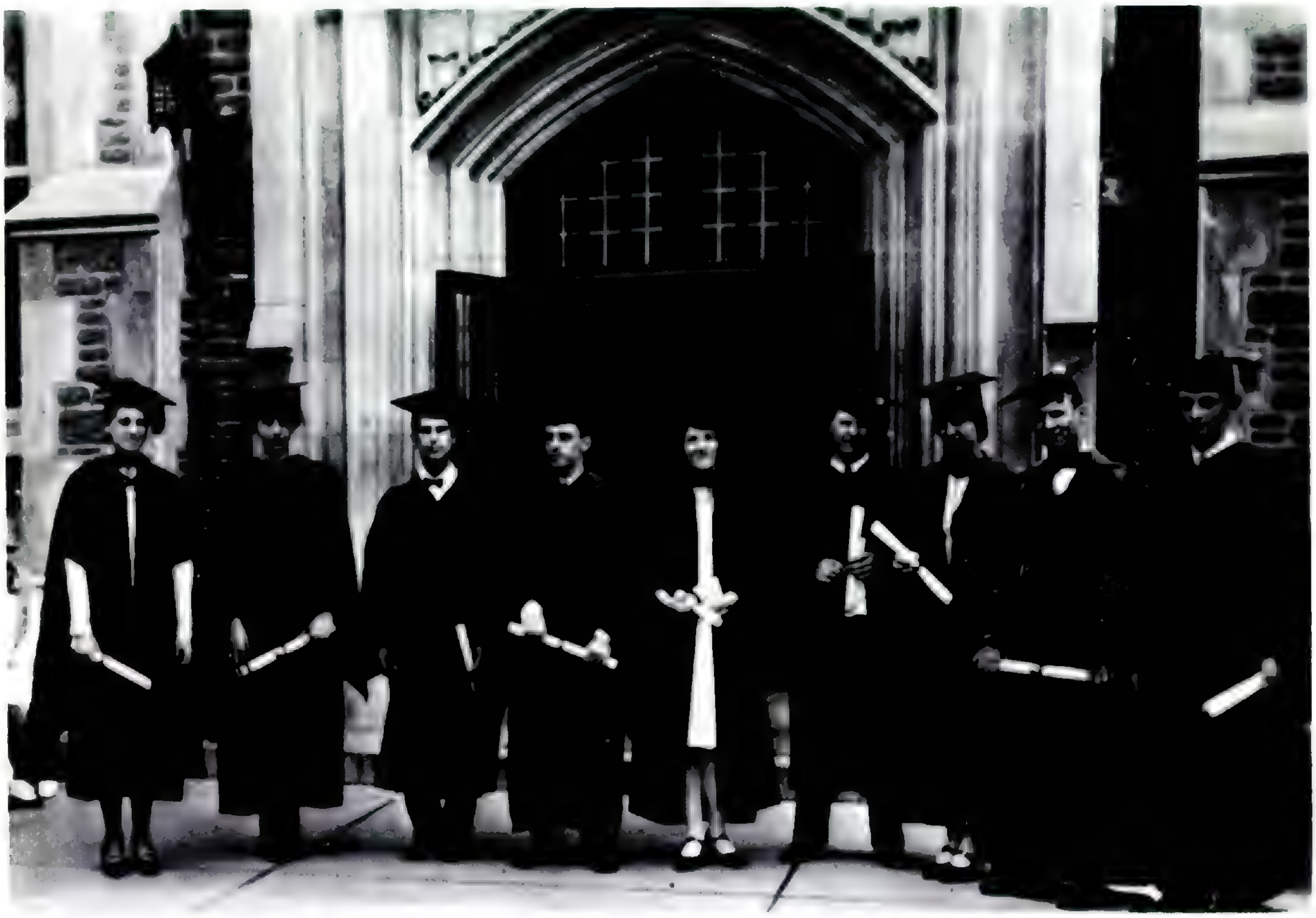

FIGURE 3. Commencement from Washington University, St. Louis, Missouri, June 1929. Graduates in botany, left to right: Marion Child (Moss), Julia Lawrence, Julian Steyermark, Alexander Buchholz, Caroline Allen, Unidentified, Mildred Mathias, Robert E. Woodson, Jr., Harry Fuller. Photo contributed by Mildred Mathias.

bien sea del Roraima, Auyantepuy, Chimantá, o Huachamacari.—*Francisco Delascio Chitty, Director, Jardín Botánico de Caracas, Herbario Nacional de Venezuela; de la Memoria del IX Congreso Venezolano de Botánica, 13–18 Nov. 1988.*

I first met Julian Steyermark 60 years ago. He was painting an orchid in the old Floral Display House of the Missouri Botanical Garden during the annual orchid show. At that time he was an undergraduate student at Washington University.

Later Julian became chairman of the botany group of the Webster Groves Nature Study Society. He wrote articles for *Nature Notes*, which is the monthly publication of the society. He also spoke at the meetings and led botany group field trips to local areas.

Since Julian didn't have the use of an automobile while he was a student at Washington University, he depended on his friends to take him to areas that he couldn't reach by streetcars or trains. He and I went on a field trip to northwestern Missouri to the loess mounds of Atchison and Holt counties during the Labor Day weekend in 1932. This area contains plants that are found only in this part of Missouri. We located most of these species, and Julian took specimens of them for the Missouri Botanical Garden herbarium.

On several occasions Julian and I took streetcars to South Broadway and found many introduced plants along the railroad tracks near the Mississippi River. Some of these plants were very seldom found elsewhere in our area. On the way home from these streetcar trips, Julian identified plants in vacant lots along the city streets.

On one of our field trips to the Ozarks Julian saw a sedge that he wanted to reach on the other side of a stream. We walked through the shoulder-deep water to reach the sedge. He climbed the steepest slopes and descended into the deepest valleys in his search for plants. Julian never seemed to tire, and if he was tired, he continued on anyway.

One of Julian's favorite places was Pickle Springs, where many rare plants were found. This area is now Pickle Springs Natural Area. Another favorite area was near the Meramec River at Pacific, Missouri. This area, which also contains many rare plants, is now known as Pacific Palisades.

Although Julian was so dedicated to collecting

and identifying plants, he did take some time off to play tennis at Tower Grove Park. Also he attended some of the Webster Groves Nature Study Society's parties.

On the day that Julian received his Ph.D. degree from the Henry Shaw School of Botany of Washington University in 1933, I happened to meet him with his parents at the Missouri Botanical Garden. He couldn't stay away from the garden that meant so much to him, even on his graduation day.—*Arthur Christ, St. Louis, Missouri; from Julian Steyermark's memorial service.*

I am very sad with the passing of Julian, a taxonomist extraordinaire and a dear personal friend. I feel very privileged to have known him closely during the last two decades of his life. Julian was truly one of the greats in his field and his contributions to taxonomy, exploration, collecting, and conservation will long be remembered and recognized—and used.

Of all the people I have known personally, he, perhaps as well as anyone, exemplified a person of whom it can be said without any exaggeration that his vocation was also his avocation. I will, above all else, remember him as a person totally devoted to his work and one for whom his work held a never-ending fascination.

I would like to recall several personal experiences and incidents that illustrate some aspects of his personality and career.

I first got to know Julian personally in 1971, when as a graduate student I went to Venezuela to study and collect plants for my thesis. I was already well aware of his many accomplishments and his international reputation. As with almost any other novice going to a foreign country to collect, I was having difficulties in making the necessary arrangements. With some trepidation, I asked for his help, and I was very grateful that he took time to arrange contacts that made my work much easier.

I later learned that he guarded his time very jealously, surely a necessity for someone who received little secretarial help at the time, who published thousands of pages, and who was unrivaled as a plant collector. However, if you were serious about plant collecting, he would often try to help. He was very well aware that the next 20 or 30 years might be the last chance for any of us to study and collect the undisturbed vegetation in many areas of Venezuela that had never been botanically surveyed, and he always felt only a small portion of the country had been adequately surveyed.

After I joined the Missouri Botanical Garden in 1972, a number of other staff members, including Tom Croat and Al Gentry, collected in Venezuela, and we seemed to pass muster as plant collectors since Julian proposed in 1975 that the Garden and the Instituto Botánico organize a cooperative program of joint expeditions to areas in which the vegetation was being severely damaged.

After we secured funds for this work, Julian and I made a number of field trips together, and it was then that I really got to know him well.

Julian was a very goal-oriented person who doggedly pursued his objectives until they were accomplished, whether it concerned writing the *Flora of Missouri* during his free time or whether it concerned collecting plants from a tepui never before explored.

When he went to the Field Museum in 1937, he had already collected over 25,000 plants. There he worked under and was greatly influenced by another of the great plant collectors, Paul Standley, who was to collect well over 100,000 numbers by the end of his own career. Julian early on, as he told me early during our association, determined in his own mind that he would eventually surpass Standley's numbers, and he did.

Even on a daily basis, he—as had Standley before him—would set a goal of a certain number of collections to be made that day, and he would challenge his companions to do the same. He would invariably have a very precise recall of what he collected each day, and he loved to challenge you to guess the totals gained by each person, spicing the proceedings by betting a milkshake on who could guess the closest. I soon learned to keep closer track of what I was collecting!

Although Julian was a modest person who lived a quiet, simple life, he, like all of us, appreciated recognition. After several years of working together, I knew that he was proud of the large number of plants he had collected, and I began to think of ways in which this collecting record might become more widely recognized.

I finally hit upon the idea of nominating him as a champion plant collector to the *Guinness Book of World Records*. Because I was a bit uneasy that he might consider this a trivialization of his accomplishments, I checked out the idea with him beforehand, and he approved. Unfortunately, it took the editors of *Guinness* several years to decide what plant collecting was all about and whether it really had a place in their book. In the meantime, Julian would ask me every time I came to Venezuela what had happened to this proposal, and I had to tell him to be patient, that it was still in the

works. The record was finally included in the 1986 edition, and Julian seemed to enjoy the additional attention it brought him from the popular media.

I earlier mentioned that I'll always remember Julian as a person totally devoted to his work. This perception comes from watching him put in long hours of fiercely concentrated work each day, seven days per week, and 52 weeks per year, but it was also brought home to me in a much more amusing way on our first trip together in 1978.

Our objective on that trip was to collect in a small range of mountains known as the Cerros de Bachiller in the Coastal Cordillera of northern Venezuela, where new agricultural developments seemed certain to destroy much of the virgin vegetation in the near future. Close to a small mountain stream at the foot of the mountains, we had constructed a nice base camp, from which we collected every day. As was customary, we slept in hammocks strung beneath a plastic sheet to keep out the rain. Julian would always wake just before dawn, and as we were getting ready for the day's collecting, he would tell me his dreams of the night before. Every morning during the two weeks of that trip, the dream he recalled would be enjoyable and botanical. Their setting would often be in the "Lost World," and he would discover the most amazing new plants, which often combined bizarre characters from several families, so that he would be very puzzled and strongly challenged on how to interpret these strange plants. After a couple of days of this, I began to think to myself, here is an even more devoted man than I had realized, not only does he devote most of his working hours to botany, but even his sleeping hours are devoted to it.

So these are some of the ways I'll always remember Julian, a valued friend, a man of great accomplishments, a man truly devoted to the good things of this world, and one who leaves an enormous legacy to us all.—*Gerrit Davidse, Missouri Botanical Garden; from Julian Steyermark's memorial service.*

Omnia fluerit. Everything flows. Fifty-five years ago Julian Steyermark, then 24, and taking his Ph.D. here, wrote to me in the spring of 1933—I was at UCLA at the time—asking for the loan of *Grindelia* collections that I had made, gumweeds of the Compositae (as we called them then). On June 21st he wrote again, that the loan was being returned and added that he was tending a ¾-acre plot of grindelias, and rushing his getting a Ph.D. He wrote, "I shall be starting off soon on a 2 or 3 weeks botanical expedition into unexplored parts botanically of Missouri, getting into many remote sections." Some readers may wonder when Julian really began botanizing: on October 13th, 1930, he collected *Grindelia lanceolata* along the railroad tracks bordering the Washington University campus. That collection was numbered *1506*. By September 11, 1932 he had numbered to *7164*, or 5,658 field numbers in less than two years.

Now and then I encountered Julian at the Gray Herbarium or the New York Botanical Garden. Then, with deep pleasure, I came here in 1986 to work in the library, as Julian before me had come to forage in the *hortus siccus*, the dry garden. In researching the vismias and the shrubby gentians, I came to know Julian's detailed collections and his keen interest in plant geography and those "unexplored parts botanically" of Venezuela. By their specimens you shall know them!—so true of botanists. Let me return to Julian's letter of 1933: "One derives the chief or almost the chief pleasure from studying plants in their natural habitat, exploring for them in remote places which add to the zest and thrill of discovery. At least I have always felt that way and most field naturalists hold similar opinions." The tepuis used to be called the "Lost World" but that was before Julian. *Omnia fleurit.—Joseph Ewan, Missouri Botanical Garden; from Julian Steyermark's memorial service.*

My introduction to Julian Steyermark was through the *Flora of Guatemala* while working as a Peace Corps volunteer in Honduras on a floristic survey of one of the central valleys. Honduras does not have any written flora, so the next best thing was the *Flora of Guatemala* of which many volumes were written by Standley and Steyermark. Filled with useful information, excellent keys, and descriptions, it taught me a great deal about tropical botany. When I was finally preparing to leave Honduras with some of my more interesting collections, I was directed here to the Missouri Botanical Garden as the best place to have them identified.

When I finally made it here some months later and luckily was able to get a job, I was told that Julian Steyermark had just come up from Venezuela and was on the staff! One of the first things that I wanted to do was meet him, and you can imagine my surprise and pleasure upon learning that I was going to be working for him, and how much even more surprised I was when three months later I was in Venezuela on a major expedition to the Lost World!

It was a real thrill and a tremendous learning experience to work in the field with Julian. He had

FIGURE 4. Field trip, 1929–1930. Left to right: Charles Leo Hitchcock, Caroline Allen, Julian Steyermark, Josephine Darlington, Mildred Mathias, Dorothy Francis, George Goodman. Photo contributed by Mildred Mathias.

an "eagle eye" for spotting plants and if you didn't see something that he did, he would let you know it. When I first went out on my own to collect some specimens I found a beautiful plant that I thought was very unusual; it had large bright red bracts surrounding a dense cluster of flowers. When I returned to camp, I pulled it out of my collecting bag with pride to show him. But when he saw it, he took it from me in disgust and threw it to the ground, saying sternly "this is *Psychotria poeppigiana* subsp. *barcellana*, one of the most common and weedy plants of South America, don't ever collect it again." I was a little bit embarrassed, so the next day I made even more of an effort and risked my neck to get up on some difficult sandstone bluffs. When I got back to camp, I sheepishly pulled another member of the same family out of the bag to show him. This time, however, he looked at it with a great deal more interest, a puzzled look came over his face, and he admitted that he didn't know what it was, and that it was very likely something new. From then on I learned that whenever he gave that look at a plant, it meant something interesting had turned up. In this particular case it was a genus of the coffee family new for science.

Fieldwork was very special for Julian—rather than "vacations," he went on field trips. It was impossible not to be caught up by his enthusiasm for collecting plants. He always likened collecting to a "treasure hunt." Even with his two artificial hips, he would plow through brush, crawl over and under logs, fall down, laugh about it, and push on. He truly liked collecting all kinds of plants, but I think that the Bromeliaceae were his favorite family.

Julian was involved in the first helicopter expedition in Venezuela, which took place in 1967 to the isolated Cerro Jaua. He quickly realized the advantages of that mode of transportation and found that it would increase even his amazing productivity. He would use it frequently in the following years to get to some of the most inaccessible of the Lost World summits. To think that in all the years prior, when he made so many of his famous expeditions to some of the most remote areas in the country, that everything was by foot, including long and hazardous climbs to the tops of several of the more prominent tepuis, such as Chimantá and Auyan-tepui. Once I understood the complexities involved in these huge expeditions back then, my admiration for him increased even more.

He was a great friend to the Indians of the region. They enjoyed his sense of humor and spirit of adventure. He is somewhat famous in certain Indian tribes. Two years ago, when we were planning a trip to a series of unexplored mountains in the heart of the Lost World, we were surprised to be met by the son and grandsons of an Indian who had worked with Julian back in the 1940s. They

had heard that "Hulian Esteyermark" was to be back in the area, and were eager to volunteer their help.

On a personal side, it took a while to get to know him, and he did have some unusual ways.

—I thought that he was kidding when he told me about his liking for rock & roll music until he showed me his more than 800 records ranging from Elvis Presley to the Rolling Stones. He also loved Venezuelan and Andean folk music.

—He loved to bet milkshakes on whether his friends could identify a plant or not. I paid out my fair share to him and to Ron Liesner (an expert at plant family identifications).

—He would eat sparingly for breakfast or lunch, but there were few who could match him at the dinner table. Buffets at nice restaurants were his favorite, and he would go back time after time before he was ready for dessert.

—Other than fancy buffets, he thrived on fruits, vegetables, and ice cream and was a great experimenter with native edibles. Flower fragrances were irresistible to him; we would have contests in the field to see who could find the most fragrant flower, and he smelled every one with great pleasure.

—Swimming was a favorite pastime of his. The only time that he would take off from the herbarium or field (or let any of his assistants do so) was to go to the beach. He loved floating in the waves and would do so for hours at a time.

Julian was a most ardent and effective conservationist. He worked hard in Venezuela through the National Park Service to protect the forests in the North that were, and still are, rapidly being destroyed, and was instrumental in identifying many areas in the South worthy of protection. In late 1988, we were told that the President of Venezuela was signing into legislation a new National Park in the delta of the Orinoco River. It was planned with Julian's help.

Finally, I would like to share some parts of a letter that was sent to Julian a few weeks ago that illustrates his impact upon others around him, not just as a botanist, but as a person who could inspire others:

> I was a student of your Biology Class at University City High School during the *1937–38* period at the time just prior to your leaving for the Field Museum in Chicago. My memories of you are very strong and positive as a teacher and as a person. You provided a great role model for a youngster interested in science. And I remember how impressed I was with the fact that *my teacher* was leaving to become Curator of a portion of the famous Field Museum. You and several of the other faculty members at U. City High provided great inspiration to accomplish at that point in my life. Thanks.

Fifty years later, another student of his feels the same way.

I am deeply saddened to lose a great friend and a teacher. I will never forget him and what he has done for botany, for conservation, and for me.—*Bruce K. Holst, Missouri Botanical Garden; from Julian Steyermark's memorial service.*

The expression on his face was rather eloquent when Julian saw the pile of newspapers that I had put in front of him on his desk. He knew that I was an ecologist starting to do research in the cloud forests of Rancho Grande, in National Park Henri Pittier some 100 km west of Caracas. My "botanical collections" consisted mainly of large, unlabeled leaves pressed between five or even ten sheets of newspaper in order to assure their drying. "What am I supposed to do with this?" Julian asked me impatiently. "Well, I think that you can identify them," I answered a little bit scared. After a few silent minutes, during which Julian glanced through the "specimens," he returned the pile to me and said, shaking his head, "These specimens are unidentifiable, they are all sterile; there is nothing I can do with them." And with these words he continued typing labels on his old OLIVETTI typewriter, and I suspected that I had done something wrong.

After this episode, which occurred sometime in early 1974 in Julian's office at the Instituto Botánico in Caracas, I realized that plant collecting in a tropical cloud forest was rather different from what I had done before on a very limited scale in the Mediterranean macchia of southern Italy or the island of Sardinia. Under Dr. Steyermark's guidance I learned how to make proper plant collections and how to identify them to family, genus, or even species. I soon realized, too, how fortunate I was to have such an outstanding teacher: every passing day I was increasingly impressed by the astonishing taxonomic knowledge of this man, who seemed to be omniscient and blessed with a remarkable memory of the most complicated plant names!

After having been invited to my first chili con carne at Julian's home (his favorite dish expertly prepared by his wife Cora), our relationship strengthened, partly because in the meantime I had improved the quality of my botanical specimens. A couple of years later, we engaged in a joint venture, resulting in the publication of the

Flora del Avila. Julian wrote most of the keys of that book at home while recovering from his two hip operations and while I was in Austria concluding my Ph.D. thesis. At my return to Venezuela in September 1976, we then had a rather hard time finishing the rest of the manuscript (some 1,600 pages), since my Tyrolean stubbornness was not less persistent than Julian's Missouri stubbornness! This book, however, constituted a tremendous experience for me, and since then we had become colleagues, working together very closely in the Instituto Botánico. From then on, Julian was always anxious to be the first to see my collections from the Venezuelan Amazonas and later from the many tepuis of the Guayana Highlands.

In 1982 we decided to start another new project titled *Flora and Vegetation of the Venezuelan Guayana*. We realized that such an enterprise would take years of most intensive work, but we both decided to dedicate all our efforts and resources to that project. Although destiny later divided our paths, Julian and his collaborators have advanced relentlessly towards completion of that flora, whereas I have continued to contribute by collecting interesting plants from the many places visited during my ecological and phytogeographical fieldwork in that region.

It was a great satisfaction for me to invite Julian to an expedition into the Chimantá massif, one of the richest Guayana mountains, where he and John Wurdack had done such pioneering botanical exploration in 1953 and 1958. When we established camp near a huge colony of *Chimantaea mirabilis*, a most striking member of the Compositae discovered by him in 1953, Julian could not hide the emotion caused by this reencounter after 25 years! And then, there he was, the "classic" Julian Steyermark, sitting at his camping table describing and pressing plants . . . and plants . . . and plants, amazingly numerous plants every night (at that time he was at his number 128,000). And every two minutes he would call me and exhibit another exciting find, or explain another variation or another novelty. One year later we would be again on the same mountain and discover a new genus (*Acopanea* in the Theaceae), and then get flooded at our camp at 2 o'clock in the morning with icy water half a meter deep from the nearby caño!

Julian Alfred Steyermark, the great botanical explorer of the Guayana and many other places of the Venezuelan country, has now left us, but his memories, as numerous as his botanical collections, will always accompany us from tepui to tepui, together with the gratitude of having had the privilege to be one of his students!—*Otto Huber, Caracas, Venezuela.*

I first heard of Julian Steyermark when I was a student at the University of Wisconsin. Dr. Hugh Iltis said he wanted to prepare a flora of Wisconsin that was as good as Steyermark's *Flora of Missouri*. Julian enjoyed hearing that.

I first met Julian when I went to Venezuela in 1977 as part of the joint Missouri Botanical Garden and Herbario Nacional de Venezuela project sponsored by NSF and CONOCIT. When I arrived, Julian was skeptical and concerned and told me about the difficult conditions: rain, heat, insects, snakes, and other perils. Julian, Francisco Delascio, and I went to the Delta Amacuro (delta of the Orinoco River) for a month. The collecting and the trip were exciting and one was able to ignore the difficult conditions. I quickly learned Julian was very good at spotting plants to collect. He first started using clippers when he saw me using them and we sometimes joked that he learned to collect plants from me (he had 114,000 collections when we met).

Numerous field trips with Julian were a privilege. I learned many plants from him and how to find specimens to collect. We frequently bet a milkshake if we thought we could catch the other person not knowing a plant to family. Even a sterile plant was game if that person collected it. Usually I could catch him only if it was a genus that was unusual for the family and the genus was new for Venezuela. We also bet milkshakes for guessing how many plants we had collected before we pressed and numbered them. I, also he, sometimes would collect numerous extra mosses so the competitor's guess would be too low. Once, after Julian had guessed right three days in a row, he stated his guess aiming at a fourth win, then I guessed one lower, and Ángel González guessed one higher. Julian had to do something else. Ángel and I pressed the plants and wrote the field notes. It came out to Julian's number! Ángel and I decided to trick him. One species of herb had both flowering and fruiting individuals. We split them into different collection numbers. But Julian had the last laugh. Not only were they different species, they were different genera! We also guessed at arrival times for a milkshake. Cora, Julian's wife, said they had bet ice-cream cones when they did fieldwork in Missouri.

Julian loved to try different restaurants and go to the movies, and many of his friends enjoyed going with him. For a long time, Julian was my closest friend. Julian had a good sense of humor and it was fun to tease him. But it did annoy him when I said I was from Missouri and to show me. Gerrit Davidse did the same. For a long time he didn't consider us Missourians.

He often corrected my Spanish. I sometimes joked that Julian taught me Spanish. He vehemently denied it, but everyone else liked it.

When he came to Missouri, he had to get his driver's license, and I had to teach him to drive my car. Later, I joked I had taught him how to drive. He would mention the first two things the driving examiner asked were the lights and horn, and I hadn't shown him those.

Julian claimed that he had shaved every morning since the thirties. We could be short of water and he would still shave. He, Bruce Holst, and I were almost stranded on top of a tepui without our things. Bruce and I kidded him that we would see him unshaved. But then we decided he would shave with his machete. The helicopter came so we didn't find out.

Julian and I were in some very risky, potentially dangerous places in collecting. But the most worried and most concerned I ever saw him was when we arrived back in Caracas and he couldn't find his hairpiece. It frustrated him when women saw him without his hairpiece the first time in the field and told him they thought he looked better without it.

When we were stranded on Cerro Duida, wet, with no shelter or supplies, in a potentially fatal situation, Julian joked about dying on a tepui. We assured him that was fine as long as it was some other tepui.

In the field Julian often remembered collecting the same rare species 30 years previously. An amazing number of species were either described by him or named after him. I wonder what level Venezuelan botany would be at if it were not for Julian. He worked fast, long hours, and accurately.

One could go many places in Venezuela and local people would remember Julian when he was there 20 to 40 years previously.

Identifying specimens, I worked on many different plant groups. Julian was a good friend because I could talk about many different groups and he had worked on them also.

For quite a while when I ran into a problem with a plant group or if I had a plant I couldn't identify to family, my first reaction was still to go ask Julian, only to remember Julian was no longer here.—*Ronald Liesner, Missouri Botanical Garden.*

I first met Julian Steyermark in October, 1963, at a difficult time in my life, and I am proud to say that since that time, he has helped me more than anyone else.

At that time I was an unemployed and completely frustrated young man 24 years old; and just "to kill time," I decided to draw flowers. So I began to go around with some paper and a box of color pencils, and devoted myself to drawing flowers in Caracas near where I lived in a student dormitory. After a month or so, I had checked all the gardens, houses, and whatever natural vegetation there was around and had exhausted interesting subjects for drawing and so expanded into surrounding neighborhoods, eventually reaching the Botanical Garden of Caracas, where there was a large variety of exotic and beautiful flowers.

I remember that one day, while concentrating on trying to reproduce the colors of a "bird of paradise" flower (*Strelitzia reginae*), a man came up to look at my work. I had seen him occasionally on previous days, but we never had spoken to each other. He was August Braun, the head gardener. After exchanging some comments, he told me that there was no artist at the Botanical Garden, since the former artist (the late Mr. Ebersteins) had retired four months earlier; and he suggested that I show my drawings to Dr. Lasser, the director.

The following day I took some of my best drawings and showed them to Dr. Lasser. He liked them but said that drawings needed for scientific publications had to be more "objective" and made with black india ink. As I had no experience with that kind of drawing, he introduced me to Dr. Julian Steyermark and asked him to give me some orientation. So I met the man, and got the job!

After I had gained some confidence, in 1963 Julian asked me to draw a new species that he was describing, *Palicourea chimo*, and I complained that I had only herbarium specimens, not live plants. Julian, who also began his botanical career as an artist, understood and helped me look for a solution and invited me along on a trip to Naiguatá, on the northern side of the coastal mountain range of Venezuela, where he had not been before. The *Palicourea* was encountered and drawn fresh.

On the two-day expedition we found a new species, which Julian named *Heisteria olivae* (later placed into the synonymy of *H. latifolia*) to honor our guide, the young architect Francisco Oliva Esteva [see recollections in this volume].

Julian was so impressed by the rich vegetation there that two weeks later we went back to explore further. As Julian had begun his botanical activity in Venezuela in search of quinine plants and was an adviser to a large drug company in the U.S., he was always interested in potentially useful plants as suppliers of drugs. On our second expedition to

the coastal range, we found a big *Lacmellea* tree, called "vaco negro" (black cow) by our guide, who stated that its sweet, milky sap was used as a remedy for asthma. Since we found only flowers and fruits on the ground, Julian felt frustrated, but I returned a few weeks later, climbed the tree using a liana "rope," and collected several complete specimens. I illustrated these, and Julian named *Lacmellea costanensis* as a new species.

So delighted was Julian with the scenery of those slopes facing the sea, completely carpeted by virgin cloud forests, that he soon made yet another expedition there. On this third trip, we went with Mr. G. C. K. Dunsterville, the great orchid artist, and his wife, Nora. Cora Steyermark also came with us, but, as she was suffering from some bad health and could not match our pace, Julian went ahead with a bunch of yellow and red woolen threads, dropping them from time to time along the trail for her to follow. So, late in the afternoon, Cora reached us bright with joy and carrying all the threads she picked up along the trail.

On this same trip, Victoriano Carreño Espinoza joined us. Julian had met him a month earlier on a previous expedition to Cerro Humo in the eastern peninsula of Paria. He was so satisfied with Victor's knowledge of plants, skill, and enthusiasm, that Julian brought him to Caracas and helped him get a job in horticulture at the Central University. Victor continued to work with Julian and quickly became his faithful and efficient assistant on many expeditions throughout Venezuela during a fifteen-year period.

When I met Julian, he was living in an apartment complex called "Residencias Magnolia" located in Los Palos Grandes, Caracas. The apartment had a terrace where he kept plants that he brought back from his botanical expeditions. He would lead visitors on a ritual tour around the garden to give an explanation of the plant names and the regions they came from, with considerations about their color, shape, or scent. But, Julian's expeditions were so frequent and fruitful that the apartment's terrace became too crowded, and about 1971 he moved to the suburb of Santa Eduvigis. There he had more room to display his plants and on the back side of the house he created a miniature jungle under a mango tree. In some cases Julian collected sterile plants, which he brought home until they flowered and then made herbarium specimens from them.

Besides the small garden space, noise from traffic, and the fact that their house was broken into bothered Julian and Cora, so in mid-1975 they found a new house in the neighborhood of Santa Fe Sur. They were particularly pleased with it, because from it they enjoyed a complete view of Avila National Park across the Caracas Valley, and it was close to a place officially listed as a "green area," where supposedly no other buildings could be built. But several months later, in spite of all the official statements, construction began on a huge apartment complex whose wall reached right up to the Steyermark's garden. He felt very frustrated, and in his field book he remarked sadly, "Nov. 20, 1975. Destruction of green area back of our home."

Yet the new house still had room for gardening, and the Steyermarks displayed the beautiful collection of bromeliads on the porch and put the aroids, orchids, begonias, peperomias, and ferns under a plastic net. In the center, there was a planter of red roses, surrounded by several *Hippeastrum* lilies, and another plant of rosemary surrounded by the thorny *Euphorbia splendens.* In back, towards the new apartment complex's wall, there was a *Chrysalidocarpus lutescens* palm, a *Tibouchina semidecandra* with big purple flowers, a *Mussaenda erythrophylla*, a healthy *Clusia minor* with waxy rose flowers, a terrestrial *Cyrtopodium* orchid, and other miscellaneous herbs. On the right side, climbing on the fence was *Aristolochia ringens, Heliconia caribaea, Nicolaia elatior*, and *Lafoensia* with white flowers pollinated by bats. In a pot, there was also a "lily of the valley" with very fragrant white flowers that Julian especially enjoyed. On the side of the garden close to the porch grew a row of *Iris confusa* that never bloomed. Once a month, Victor went to the house to cut the grass and clean the garden.

Cora, a member of the Audubon Society, enjoyed observing birds, and every day would put bananas and oranges in a feeder to attract them to the garden, and sugar water for the hummingbirds. She kept a diary of the garden and recorded the exact date of blooming for every plant, days of rain and sun, and other data for the garden's management. She was also one of the founders of a garden club, which in 1973 created a scented garden for the blind along the avenue Rómulo Gallegos in Caracas.

On many occasions Julian would honor me with an invitation to dine in his house, where I thoroughly enjoyed Cora's excellent cooking, especially the pies and brownies. Sometimes when we came back late at night from some expedition, he invited me to sleep in their house in the guest room. The following day, of course, I would get a delicious

breakfast. I remember that when we sat at the breakfast table, Julian and Cora would recount the dreams they had the night before.

On a trip to Puerto Cabello in 1973 with Julian and Victor, I found out that Julian had a love for snakes. We walked along an old canal breached in areas and useless due to many rocks and earth that had fallen into it; but in a corner, under a little waterfall, it was full of clear and fresh water. Julian, who loved to drink from sparkling streams, put his right hand on the edge of the water and bent over to take a drink (with the left he was holding the plant press). When he finished drinking, and before he stood up, he spotted a poisonous snake out of the corner of his eye, a fer-de-lance (*Bothrops atrox*), just between his hand and his cheek. Victor hurried there with the machete to kill it, but Julian didn't let him; instead, he pushed and chased the snake away into the high vegetation.

In 1983, Julian returned to that area again with Paul Berry and me to gather specimens of *Selaginella gigantea*, but the old trail was completely lost. Paul and I managed to reach the *Selaginella* site, but just as we arrived, a heavy thunderstorm came up. Paul hurried to make a collection of the rare *Selaginella*, and then we headed straight down the mountain, since we lost our trail very quickly. When at last we reached Julian half an hour later, the rain still falling, we found him sitting on his press, trying to protect himself with a completely wet piece of paper but he regained his spirits as soon as he saw Paul's collection. All that area where the *Selaginella* is found now belongs to the San Estaban National Park, created in 1986 thanks to Julian's enthusiastic report.

In October 1970, Julian joined the Venezuelan Brazilian Frontier Commission in a survey of the Cerro de la Neblina, the highest mountain in the Guayana, and he collected as intensely as ever. While participating in that trip, the expeditionaries were sent supplies from San Carlos de Río Negro (Venezuela) and Cocui (Brazil) by helicopter, so Julian decided to send his first lot of collections ahead to San Carlos, preserved in formol in plastic bags; but, due to confusion, the plants were unloaded in Cocui. When Julian returned to Caracas, he realized that a lot of his plants were missing, so in March of the following year he sent me down to San Carlos and Cocui to see if I could find the lost collections and bring them back. When I met the Brazilian officer in charge at Cocui, he told me that he had been there only since January, and that the soldiers, cleaning the warehouse, found a lot of very bad-smelling plants and threw them into the Rio Negro.

At that time Julian was preparing a monograph of the Rubiaceae for the *Flora of Venezuela* to which I contributed as an artist, and in 1973, when I received my degree at the Central University, I resigned my job at the Botanical Garden and turned to teaching. Julian complained about my decision and told me that he had a lifelong dream to write a flora of the Guayana, for which he would like to employ me as the artist; but at that time I didn't see how it would be possible. Anyway, I kept in contact with him, and from time to time, on the weekends or during vacation, he would invite me to join him on some botanical expeditions, even though at that time he was plagued by arthritis of the hips. As Julian could not walk like he used to, he needed extra help on his collecting trips.

In 1973 Julian was asked by a governmental agency to make botanical surveys of several coastal areas recently designated as national parks, and he invited Victor and me along. We would rent a boat for the day, and Victor and I would go out with a bag and a machete and collect samples from every plant we saw. Then, we would go back to the boat, where Julian cleaned the specimens and put them in his press. In the evening, we returned to the hotel with the plants, and Julian, keeping with his usual routine, worked for hours to number the specimens and to make notes on habit, habitat, and other peculiarities that he observed about the living plants. On the following day when the employees went to clean the apartment, they would complain loudly about the mess.

In February 1974, Julian joined the great expedition directed by Charles Brewer-Carias to explore the biggest sinkhole on top of Cerro Sarisariñama in southern Venezuela. Victor went with him since he was having difficulty walking at that time. Even with the problems getting around, he managed to collect more than 1,000 plants in 20 days, many of them rare, including 50 new to science. From the bottom of the sinkhole, Charles sent up a pretty little melastome with white flowers and a shaded rose-colored ring around the calyx. It turned out to be a new species that John Wurdack of the Smithsonian Institution named *Phainantha steyermarkii*. For his part, Julian felt so satisfied and grateful with Victor's work, that he named three new species for him: *Psychotria carrenoi*, *Phyllanthus carrenoi*, and *Sloanea carrenoi*.

During the several months before the expedition to Sarisariñama, Julian had been corresponding with people who had had hip operations to correct arthritis problems. They told him that they had felt much better after the surgery, so at last he decided

to undergo the operation. Since he had to be operated on one side first, and then six months later on the other side, he had to stay at home for a whole year. But how was anybody going to convince Julian to rest? That word was unknown to him, and in fact I suspect he was afraid to rest. For that reason, it did not surprise me that he soon found a way to keep busy at home.

His good friend Otto Huber had been preparing a list of all of the plants in the national herbarium ever collected on the south slopes of Avila National Park, the mountain that rises above the valley of Caracas to the north. Since Otto was an ecologist, he proposed to Julian that they coauthor a book to be called the *Flora of Avila*. Julian was fascinated with the idea, but he insisted that the value of such a flora would increase if it also covered the less-explored northern slopes.

As he was recovering in a hospital room that had a view of Avila high in front, he was inspired to write the following phrase in the introduction to the flora in reference to the fantastic view of the mountain from the city: "We see this beautiful green panorama as we look through the windows of our houses, offices, colleges, *hospitals* or factories."

Surely when Julian planned the *Flora of Avila* he had in mind the style of his huge and successful work, *Flora of Missouri*. Since that was lavishly illustrated, he wanted me to draw as many species as possible in every plate, just like in his previous work. He didn't want to prepare a strictly scientific work, but one that was usable by many different people. One of the ways that he did this was to insist that the publisher include a metric scale on the back cover, with the hope that the flora would be carried along up the mountain and used on the spot to identify plants. A hopeful assumption, indeed, but one that demonstrated Julian's interest in making plants known and loved.

So, we began work on the *Flora of Avila*! I had to make drawings from live material, and then bring them back to Julian to be identified. As the work progressed, he began to complain that I had too many drawings of orchids and other showy plants but few or nothing of several families; and as time passed, we reached a serious impasse. Luckily for us, there was Otto Huber, who could throw water on the flames, and the work went on. It was hard for Julian to type, due to the semireclined position in which he had to remain, so he would turn his manuscripts over to Cora, who was the only person able to read and interpret his thick scratches. Thus she also was a member of the flora team. Julian was later awarded the prestigious "Order of Henry Pittier" by the Ministry of the Environment for the flora.

One peculiarity that I observed in Julian's character was that during his fieldwork, he never dared to identify a plant to species, only to genus. For example, once I asked him, "Julian, how do you like that nice *Palicourea fendleri*?" Immediately he criticized my confidence, which he termed as an expression of ignorance and presumption, and pointed out that *P. fendleri* was known only from the coastal range of Venezuela, and now we were in the Andes . . . . Only later, at the Botanical Garden in Caracas, would he make a decision on the identity of a plant by checking it against herbarium specimens or sending it to one of his colleagues. Once, I told him that I felt that he was too insecure about identifying plants. He answered sharply that he was a scientist and I was only a rank amateur, that ignorance is petulant, and that I should be more careful in my opinions.

In those years, Julian also devoted his weekends to a survey of the plants of the wild areas around his neighborhood of Santa Fe, which at that time was being encroached upon by housing developments. That work was later included in a paper by Paul Berry and Julian entitled "Florula of the deciduous forests of Caracas."

As a scientist, Julian was absolutely objective, and he made no statement without proof to back it up; but sometimes, I thought him to be too objective. For example, when we were working on the *Flora of Avila*, I was fascinated with a beautiful orchid, *Oncidium papilio*, growing in Julian's garden, which in the thirties had been collected "close to Caracas" according to the label. I argued to him that "close to Caracas" might mean "in Avila," but Julian cut me short and said that he, as a native of Missouri, was a "show-me-man," and therefore, he wouldn't include any species in his treatment if not supported by a more precise collecting locality. But, if I were to make a collection of that orchid from the mountain itself, he would include it in the flora . . . . I did look for it indeed, but I couldn't find a specimen; that is, until 1985 in the northern side of the national park, seven years after the flora was published.

In September 1979, Julian went back to Missouri for a couple of weeks for the dedication of the Steyermark Woods. Cora stayed in Venezuela alone in their house, and an American lady who lived close by kept in contact with her and took her to the market whenever she needed to go. Cora felt very uneasy and alone in Venezuela, and Julian was making plans to bring or send her back to Missouri. In fact, since some time earlier, he had

been in contact with Dr. Peter Raven, Director of the Missouri Botanical Garden, and had told him of his desire to write a *Flora of the Venezuelan Guayana*. Dr. Raven was interested, and they began to consider ways to produce it. Although Julian had become a Venezuelan citizen, he realized that the only way to obtain the help that he needed was to return to the large herbarium in Missouri, and so he made final plans to leave Venezuela with Cora in the spring of 1984.

All of his careful plans changed abruptly in October of 1983. One night, when he arrived home from the botanical garden, he found Cora tied to a chair, very scared. What had happened? That afternoon, somebody rang the bell at the entrance and when she opened the door, there were two young men at the gate. One of them pointed a gun at Cora and ordered her to open up. She did as they said, and when they entered, they tied her to a chair with a blanket and searched the house. They found very few things of interest and soon left, leaving Cora tied to the chair, where she stayed until Julian found her hours later. He called the police immediately, and when the officers arrived, and as a matter of routine, they asked Cora to show them her passport. She went upstairs, still very upset, and on her way back down lost her footing and fell, breaking a bone in her right leg. Her leg was set in a cast, and she was released from the hospital, but a couple of weeks later she contracted pneumonia, and a week later, on November 4, 1983, she passed away at age 92. Her last wish to return and see her country again was unfulfilled.

I visited Julian frequently in the following weeks. He spoke very little about what had happened, perhaps trying to forget as quickly as possible. He kept busy working and asked me seriously about contributing the drawings for the flora of Guayana that he had planned. In order to motivate me, he placed at my disposition the thousands of color slides he had taken during many years of exploration. I started by choosing close-ups of flowers, which would be the most useful for my work; but as I went on, I was impressed by the many beautiful slides of landscapes, and an idea came to my mind: to write a book on the Guayana using many of Julian's slides. So, without telling him anything, I wrote an essay on the history of the search for El Dorado, entitled "En la Tierra del Oro," and added to it 100 of the slides. When I had the manuscript completed, I showed it to Julian, who was at first confused, because he didn't understand that I had tricked him a little bit. Anyway, after he read the manuscript and made some corrections, he agreed that I should carry out the plan and went along with me to an editor, who promised to publish it as soon as possible, though it was not completed until December of 1988, too late for Julian to see it.

In December 1983, I began the drawings for the *Flora of the Venezuelan Guayana* using the provisional survey of the herbarium in Caracas that Julian made to find out which families were known from the area. In April of 1984, he moved back to his hometown of St. Louis, but only a few months later he came back to Caracas for two or three months to begin checking the herbarium systematically to record all of the plants collected in the area covered by the intended flora. And in February of 1985, Julian was in Caracas again. This time, he had with him a young man, his efficient assistant Bruce Holst, who helped in the general inventory of the herbarium; he was admired for his ability and correct Spanish.

Until then, except for the short trip in 1971 in search of Julian's lost plants in San Carlos and Cocui, I had never been on any expedition south of the Orinoco River. Julian wanted to give me an opportunity to see as much of the Guayana as possible now, to help me in preparing the drawings for the Flora by taking pictures, or making drawings from live plants, as I preferred. So, in Easter week of 1985, Julian, Bruce, and I headed for the Gran Sabana, in Bolívar State, with the intention of going as far as possible in the ten days that we had.

On that trip, we rented a car called a "Zephyr," a clumsy, two-wheel drive that, when weighed down with all of our gear, barely cleared the ground. Because of the busy vacation week, all of the four-wheel drive vehicles were already rented. On the rough roads of the south, everybody looked at us in astonishment since it was the *only* two-wheel drive in the whole Gran Sabana, but Bruce managed to sort out the numerous ruts in the road and cross the streams to make it all the way to Kamá Falls. Along the way, we collected mostly along the road since Julian didn't want Bruce or me to go too far into the woods and use up too much time, but we managed to find numerous plants to sketch and photograph that would be valuable for my illustrations.

On our way back down to the lowlands, we had a funny incident with a group of university students camped by the side of the road who were in charge of checking the cars returning to the north and helping the tourists with information. As we slowed

down to pass them, the guard on watch blew his whistle for us to stop, and when he saw some plants that we had in the back of the car, he called for the leader to come out of his tent. He asked for our identification and told us that it was forbidden to remove plants from the Canaima National Park. Julian answered that he was Dr. Julian Steyermark, working for the Ministry of the Environment and . . .

"Are you Dr. Steyermark, the author of the *Flora of Avila*?" he asked in delight. "I have wanted to meet you for many years to congratulate you on such a beautiful book!"

Immediately he called all of his helpers to come out and insisted that all of us line up for a picture to be taken with our arms around each other. When the photographer apologized for a delay in taking the picture, Bruce mentioned that there was no hurry since he was standing next to the most beautiful girl of the group.

In August of the same year, Julian and Bruce were in Caracas once more. On this visit, Julian received his retirement payment and immediately purchased a Toyota Land-Cruiser for use on expeditions by both the Caracas Garden and Missouri Botanical Garden. We took it on its maiden voyage to Puerto Ayacucho in the Federal Territory of Amazonas (1–13 September 1985). We had some trouble at the crossing of the Orinoco since a fierce storm was coming up that made the pilot of the ferry think twice about crossing the wide river. But there was a long line of cars waiting, and at last, some people convinced him to make the trip, hoping to beat the storm. As soon as we were well out into the river, it started to rain, and big waves splashed over the floor of the ferry, obliging us to take refuge under the covered area. Many passengers began regretting having started the trip, and we were beginning to think that we might not make it to the other side. Apparently Julian was not at all concerned, even though his new car was perched on the front of the ferry, since he sat quietly under the overhang seemingly enjoying the roller coaster. But after one hour or so of being tossed around and getting soaked by the waves, we reached the town of Caicara on the other side. Bruce overheard one of the ferry attendants say that our trip was the roughest that he ever made.

On that expedition, I was fascinated by the many strange flowers that we found, especially with a half-dozen species of *Mandevilla*, a vining genus of the Apocynaceae family with showy yellow flowers (a couple of new species would be described later from those collections), and different species of purple morning glories and mallows. Of course, when I saw a pretty flower, I asked Bruce to stop to take a picture; but Julian started getting bothered with so many stops, and he ordered Bruce to follow his instructions, not mine, and to go ahead without stopping any more to make better time. Julian looked very bothered when he said that, and we went on a short time without speaking, all of us feeling tense. I knew Julian as a mild-mannered man, who only on a few occasions would lose his patience, and usually for just a short time. So, I began to tell him in a humble voice: "Julian, suppose we see a donkey on a bicycle. Shouldn't that be a reason to stop and take a picture? . . ." (No answer). Again, a bit later: "Julian, and if we saw a mammoth flying over that boulder over there, wouldn't it be a good reason to stop and take a picture? . . ." No answer! I understood that maybe I went too far with my stupidities, and I decided to shut up and resign myself to his wishes . . . . Suddenly, Julian cried:

"Bruce, stop! . . . Bruno, did you see those big yellow flowers in that bush over there? . . . Have you already taken a picture of them?"

On the way back to Caicara a few days later, Bruce was driving slowly on the muddy road to avoid the many potholes, but Julian asked him to speed up, thinking that when we arrived in Caicara at the hotel, he had to record in his field book all the plants he collected that day. Bruce tried to obey, but when he came across any rut, he would slow down again. At last Julian lost his patience and ordered him to turn over the wheel; and the Land-Cruiser started away at full speed, jumping, splashing, and shaking us up. We arrived at Caicara early that evening, and we were the first customers in the restaurant, as was usual with Julian.

The following day, early in the morning, we crossed the Orinoco River again, this time with a nice sun and good weather, and by evening we were in Caracas.

As a man who loved nature, not only to enjoy it but also to make it known and be loved, he supported with his own money several expensive expeditions to Guayana. He also paid for some botanists from Venezuela to visit herbaria in the United States and for some U.S. botanists to go to Venezuela to work on treatments for his flora. As he was demanding with himself, he used the same standard for others. I was in the office one night when Luis Marcano Berti, a Venezuelan botanist whose trip to the New York Botanical Garden was funded by Julian, called. "Are you also working at

night and on the weekends?" Julian asked. "Yes!" "Oh, very good," answered Julian contentedly.

In my case, although he wanted me to work hard on the drawings, he wished too that I would be able to see and enjoy from time to time the natural beauty of Missouri and especially of the Ozarks. To help me out, he asked Bruce to take me camping some weekend, which we did several times. So, with their help, I was able to get to know some of that wonderful country of Missouri, and also gaze at the stars through Bruce's telescope. Bruce, for his part, would tell me that in late October, when Julian was better, we would all go out again together to see the fall colors, which delighted Julian so much.

The weekend after Julian passed away, Bruce took me out to the Ozarks. The sun was bright that afternoon, and the many colors of the falling leaves were spectacular. We regretted that Julian was not with us to enjoy one of his favorite shows of nature.

That night, Bruce and I sat a long time looking at the fire. The words came out with difficulty, and several times I had to bite my lips not to weep. Both had lost a great friend, and I missed a man who for me was like a father. At that moment we felt closer than ever before, feeling the responsibility we now had to bear of completing Julian's great dream, but glad to have been with Julian in his last hours.

A few days later, while writing down these memories, a letter came from Victoriano Carreño, dated Caracas, October 4, 1988. It said: "Dear friend, I heard that you were sick, and I am praying to God for your quick recovery. All of us remember you, and we hope that you can visit us again . . . ."

Surely, Julian would have enjoyed receiving this letter with the sincere wishes of Victor, the faithful field assistant who during many years helped him get a bit closer to his dearest dream.—*Bruno Manara, Caracas, Venezuela.*

The return of Dr. Julian A. Steyermark to Missouri during the last week in September [ca. 1978] provided me with a chance to talk again to my esteemed friend and to reminisce about my first experiences with him over two decades ago.

I had grown up on Steyermark's *Spring Flora of Missouri*, which I found very useful in adjacent southern Illinois. While I was doing research at the Missouri Botanical Garden 1954–56, working on my Ph.D. at Washington University, I was constantly reminded of Dr. Steyermark because of his vast collections in the MBG herbarium, because of his prodigious writings, and because of the stories retold about him by Edgar Anderson, Bob Woodson, and others.

Following my Ph.D., I began my professional career in the Department of Botany at Southern Illinois University in January 1957. It was my great fortune that during the three-month spring quarter in 1958, Julian Steyermark was offered a Visiting Professorship in the Department of Botany at SIU. The impact that those three months had on my professional career cannot be overstated.

Our department at that time was in cramped quarters. I already was sharing a 16 by 8-foot office with Professor John Voigt, the departmental ecologist. Since Dr. Voigt's interests and mine were more closely aligned to Dr. Steyermark's interests, the three of us were crowded into this small office.

Steyermark and I spent every day and partway into nearly every evening working side by side. He was putting the finishing touches on his *Flora of Missouri* and I, along with my wife, Beverly, was revising Jones's *Flora of Illinois*. Often Steyermark would quiz me on some specimen he was working on or sketching. Many species previously unknown by me were quickly and eagerly learned.

While much of the three months was devoted to serious botany, Dr. Steyermark would take a little time off now and then to come to our home for dinner. On one occasion he took my wife and me to the local movie theater to see *War and Peace*. I recall the incident vividly because Julian insisted on picking us up in his vehicle, an International Scout built high to enable him to negotiate Missouri's back roads. The Scout was so high that I had to climb awkwardly. My poor wife stood helplessly at the door until Dr. Steyermark boosted her up into her seat!

One of my most pleasant recollections was an overnight visit to Steyermark's estate near Barrington, Illinois, north of Chicago. Julian had talked so often about the wildflower preserve he had built that my wife and I were thrilled to be invited to see it. We arrived early one afternoon. Julian guided us over about half of the property, pointing out with great enthusiasm the many species transplanted from the Ozarks. That evening we talked of plants, browsed through his extensive library, and listened to classical music.

We awoke the next morning to the delightful smell of bacon frying. Cora, Julian's wife, had prepared a feast, including the most delicious baked eggs my wife and I had ever eaten. The rest of the morning was spent walking over the remainder of the grounds before we all began the long drive back to Carbondale.

From mid-March to late April 1958, Steyer-

mark enthralled me with stories of his experiences. I was particularly excited about his rediscovery in 1957 of the very rare and little-known *Geocarpon minimum*. This species had been found originally in Jasper County [Missouri] in 1913. This remained the only known station until Steyermark had rediscovered it in St. Clair County [Missouri] in 1957. My nagging at Dr. Steyermark to show me *Geocarpon* paid off. He agreed to take Dr. Voigt and me with him on a three-day excursion to see if we could discover additional stations for this dwarf rarity.

We left Carbondale on May 2, heading in the general direction of Springfield, Missouri. Leaving Cape Girardeau, we stopped briefly at the Bollinger Mill and then headed into the Ozarks. Up and down lettered and double-lettered county highways, past shortleaf pine woods, over clear, rock-bottomed streams we went, Steyermark pointing out species right and left. We made frequent stops, usually after an enthusiastic comment such as "Wait! There's a county record." I tried to absorb all the species as fast as I could, but Steyermark never relented. We screeched to a halt in Bollinger County, pulling off the road next to a steep, wooded cherty slope. Julian asked if any of us had ever seen the little sedge *Scirpus verecundus*. We replied in the negative, and off we went down the slope. *Scirpus verecundus* was not known from Bollinger County, but Julian was optimistic, saying that this slope looked just right for the little plant. In what could not have been more than five minutes, the woods echoed Steyermark's voice: "Whee! Over here. I've found it!" Scrambling over the treacherous chert, Dr. Voigt and I made it to the kneeling botanist who crouched over a four-inch-tall tuff of green. I had seen my first *Scirpus verecundus*, and I was never to forget the habitat. Some 15 years later, while exploring in Alexander County, Illinois, I camp upon a similar steep, cherty slope. Recalling my earlier experience, I began to comb the woods and was rewarded by making the first discovery of *Scirpus verecundus* in Illinois.

By late afternoon we had reached Dallas County and were heading along Route 43 when Steyermark observed that the little chickweed on the road shoulder looked peculiar. On closer look, the plant indeed was different from anything we had ever seen. We learned later that the plant was *Cerastium pumilum*, a new record for Missouri.

We persisted beyond supper and into the duskiness of twilight. By dark, we were still on the road. I began to understand how Steyermark had been able to canvass every square foot of Missouri in 30 years—he never stopped to rest. I saw my first

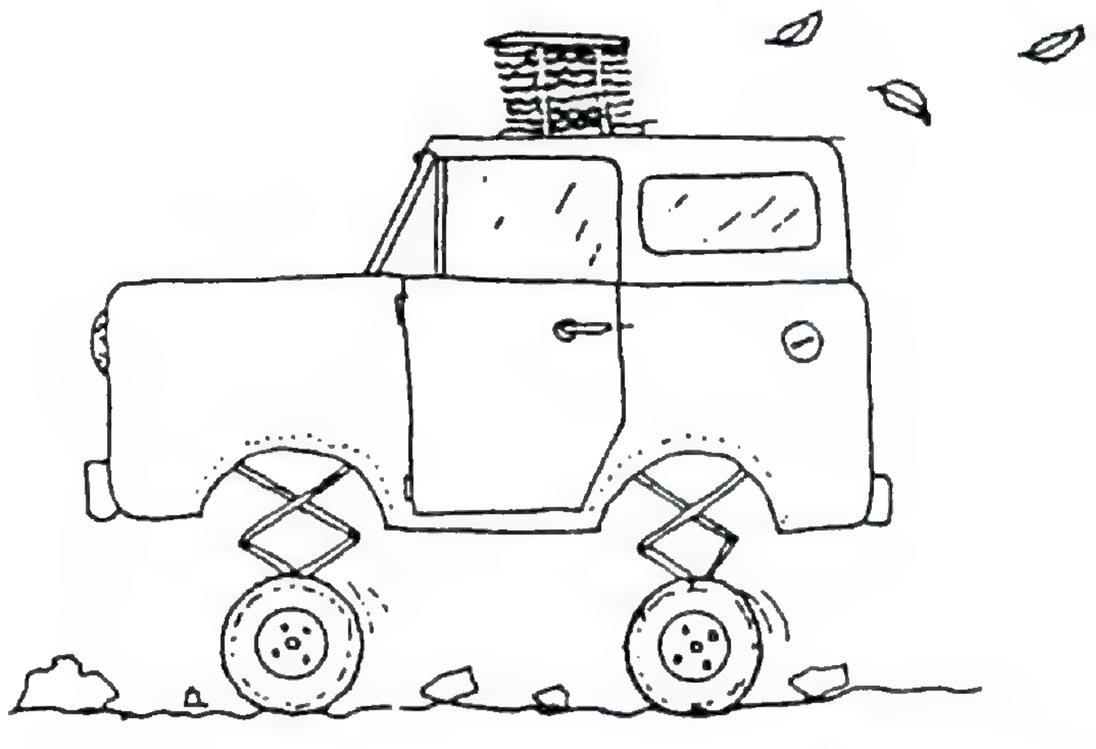

FIGURE 5. Steyermarkmobile. Contributed by Robert Mohlenbrock.

Ozark tarantula, scurrying aross the road in the glow of our headlights. Finally we stopped for camp at about 9:30, reeling from the vast amount of information imparted by Dr. Steyermark.

We arose early on May 3 in anticipation of seeing *Geocarpon*. We had entered Polk County [Missouri] near Graydon Springs when Dr. Steyermark announced that we had arrived at a likely looking spot for *Geocarpon*. It was a glade on a west-facing sandstone escarpment next to Coates Branch, a tributary of the Little Sac River. We quickly found *Isoëtes butleri*, *Talinum parviflorum*, and *Arenaria patula*, species known to be associated with *Geocarpon* at its other stations. Then, in a small, moist depression on the glade, we spotted it—dwarf, two inches tall, semi-succulent. At this stage, the plants were wine-purple. Once we knew what we were looking for, we began to spot another, and another and yet another. Our discovery marked the third known location for *Geocarpon* in the world! On the same glade, I also saw for the first time in my life *Selenia aurea*, *Saxifraga texana*, and *Collinsia violacea*.

Our spirits were buoyed by these discoveries. We hastened into Green County and stopped at a likely looking sandstone glade near Pearl. We noticed *Selenia aurea* and *Saxifraga texana* from a distance and, more closely, *Isoëtes butleri*. It certainly would be just a matter of time. Sure enough, the wine-purple plants of *Geocarpon minimum* became evident after we had wandered into an adjacent glade. I don't recall how many specimens there were but I would think there were dozens of them.

As we were hopping over the glade in our crouched positions, we happened upon a small plant previously unknown from Missouri. It was *Scleranthus annuus*, the awlwort of the Caryophyllaceae.

FIGURE 6. Julian Steyermark. Date unknown.

With our success in finding *Geocarpon*, we headed into Dade and Cedar counties, stopping at several glades. Much to our consternation, we couldn't find *Geocarpon* at any of them. By late afternoon, we started back to the east where we had planned to camp at beautiful Alley Springs. Darkness caught us again while still on the rolling hills of the Ozarks. The night scarcely slowed Dr. Steyermark as he continued to name roadside plants as our headlights struck them. "*Andropogon elliottii*," he shouted once, as we whizzed by a clump of two-foot tall grasses. Most people have trouble identifying this species in the daylight with the specimen in front of them, but Steyermark's identification was right on the money.

We got to Alley Springs at last. The long, eventful day was conducive to good sleeping, and I scarcely noted that I was spending the first night of my life atop a hard, slatted picnic table!

Next morning we were soon on the road, finding more goodies. About two miles west of Piedmont along Highway 34, we found *Cerastium brachypetalum*, the third collection of it in Missouri. Near Cape Girardeau, we discovered our second station for *Cerastium pumilum*. Since the afternoon was young, Dr. Steyermark expressed a desire to go into Perry County to a deep ravine he had had his eyes on for years. The ravine was new collecting ground for Julian, and he took his plant press with him. He is the only botanist I have ever been in the field with in the United States who carries his press with him. Most of us use plastic bags or tin cans (vascula), and our semiwilted specimens are proof of it. Steyermark had custom-made his own press with a hinged back that opens like a giant book. Our visit to the ravine netted nearly a dozen records for Perry County.

We got back to Carbondale early in the evening, finishing a three-day red-letter trip I will never forget.—*Robert Mohlenbrock, Dept. of Botany, Southern Illinois University; reprinted with permission from* Missouriensis 1(3): 1979.

My first meeting with Julian Steyermark was at the Caracas Botanical Garden in 1960, after returning from landscape architecture studies at the Rhode Island School of Design. At that time, there were very few books in Spanish about local ornamental plants. As a landscape architect, I felt it would be interesting to write a book about tropical trees that would be useful for landscape projects. Gradually, my visits to the Botanical Garden became more frequent. Julian was always ready to answer my many questions about trees and other plants, as well as to identify living material that I brought in.

In 1963, we made a three-day expedition to the mountains above the coastal town of Naiguatá in a very rich rainforest at 1,000 m elevation and only about 60 km by road from Caracas. We found many new species there including huge trees, and we collected the bromeliad *Guzmania sanguinea* for the first time in Venezuela. At later dates we went on other trips, and even met at the top of different tepuis with a group from the Terramar Foundation.

In 1962, when I began to write and illustrate a color edition of ornamental trees in Spanish, Julian kindly supervised my work. We also maintained close contact over the next eight years as I worked on my second book called *Garden Plants of the Tropics* (printed in English and Spanish). Julian wrote the introduction for me.

Despite his intensive work in families such as the Rubiaceae, Julian was always intrigued with the beauty and wonderful colors of the Bromeliaceae. The enchanting forms and the extravagance of the flowers fascinated him, something we certainly shared. I began to fancy the idea of making a book on Bromeliaceae along with him. The first step was to compile photographs, including ones

Julian occasionally took of the Bromeliaceae on the tepuis. Because of the difficulties of getting to the Guayana, his pictures were particularly valuable. Soon he agreed to write the text for the book on *Bromeliaceae of Venezuela* with me. It took about five or six years to organize the text and pictures. From 1980 to 1983, Julian was already very involved with the *Flora of the Venezuelan Guayana* project, so I decided to do most of the text in order to facilitate his work. I would generally give him eight to ten pages of text to check and translate; he would review these and return them to me after a few days. He was very adept at translating text from Spanish to English and vice versa. Once, Julian became upset with me because, according to him, I was including too many species, and he had no more time to keep reading, correcting, and translating. Although there were about 230 species prepared, I went on against his wishes to include a few more that I had collected at the last minute. I insisted that he go over these too. He always wanted to please people, so he did the final effort to finish the last translation and corrections for our work. I can still remember hearing him along the corridors of the Botanical Institute saying, "I am very busy with the *Flora of the Guayana* and have no time to do anything else. Please can you stop adding new data to the book?" Our manuscript was handed to the printer just days before Julian left Caracas to move to St. Louis, but then the book took about two years to be printed.

Before leaving his post at the Caracas Botanical Garden, Julian was awarded diplomas and medals together with a reception and a farewell party, by the National Parks Institute in recognition for his tremendous work accomplished in Venezuela. He was most happy and pleased by these honors. After Julian's departure from Venezuela, we kept in touch by mail about the last details and corrections of the proofs of our book. He returned many times to Caracas with his assistant Bruce Holst to work and collect for his monumental *Flora of the Venezuelan Guayana*. Although he was expecting to finish this project, destiny had other plans.—*Francisco Oliva-Esteva, Caracas, Venezuela.*

Libro de la Sabiduría de Salomón:

> Mas las almas de los justos están en la mano de Dios, y no llegará a ellos el tormento de la muerte eterna. A los ojos de los insensatos pareció que morían, y su tránsito, o salida del mundo, se miró como una desgracia, y como un aniquilamiento su partida de entre nosotros: mas ellos, a la verdad, reposan en paz.

Julián Steyermark no está hoy entre nosotros, pero no podemos decir que está muerto, no podemos decir que ha desaparecido; no existe la muerte para un hombre que hizo tantos caminos. Su obra como su bondad son imperecederas.

Su alma se separa de su cuerpo ya inmóvil el sábado 15 de octubre, allá lejos, en tierras norteñas, en la ciudad de Saint Louis. Allá mismo donde nació. Pero la mayor parte de su vida, los mejores años, los pasa con nosotros.

No ha habido hombre que haya estudiado más nuestra flora. La pasión máxima de Julián Steyermark fue la Guayana, con sus imponentes tepuyes, pero también recorrió con sus ojos bien abiertos a toda Venezuela, viendo y colectando muestras botánicas.

Deja una valiosa obra. Era infatigable. Fueron múltiples sus contribuciones: las Rubiáceas, las Piperáceas, exploraciones botánicas de las regiones orientales, nuestra vegetación, la Sierra Imataca y altiplanicie Nuria, la flora de la Sierra de San Luis en Falcón, el Cerro Autana, Cima del Macizo Jaua, Cerro Patao en Paria, el Roraima, el Auyantepuy, la flora del Avila.

Julián Steyermark fue un excelente botánico. Un incansable admirador de nuestra naturaleza. Coleccionó miles de muestras para herbario. Clasificó una cantidad igual. Atendió centenares de consultas. Pero lo más importante es que fue un hombre bueno. Honesto, noble, muy sencillo, extremadamente sencillo, cordial, amable, siempre dispuesto a responder cualquier pregunta. El gran complemento de su erudición era la sencillez.

No podemos decir que Julián Steyermark ha muerto. Tal como está escrito en la Biblia: las almas de los justos están en la mano de Dios, y no llegará a ellos el tormento de la muerte eterna. Ellos a la verdad, reposan en paz.—*Mauricio Ramia, Universidad Central de Venezuela; palabras pronunciadas en el acto de apertura del IX Congreso Venezolano de Botánica, el día 13 de noviembre de 1988 en Caracas.*

Julian took my wife and me for our first look at the Grand Savanna in the Guayana Highland, and with us the Dunstervilles looking for orchids and to whom the place was an old story. As we entered the Grand Savanna, Julian and I stopped on an area of dry open sand and discovered a tiny sundew with one or two sessile flowers in the center of the rosette. Julian named it *Drosera felix* because of the happy event of our visit.

Later on our trip we were camping one night by a small stream, and while Julian was preparing supper, I went out exploring and found an aquatic aroid in a deep pool that the stream had hollowed out of the solid rock. Julian came when he was

free and with his longer arm was able to collect it. It proved to be a new genus, and George Bunting named it *Jasarum*, compounding it with Julian's initials and *Arum* because Julian had discovered so many new genera that such tactics were necessary. Later I contributed with the bromeliad *Steyerbromelia*.—*Lyman B. Smith, Smithsonian Institution.*

I participated in a number of field trips to Missouri when Dr. Steyermark was accumulating vouchers for his flora. The average trip down [from Chicago] was about six hours, and he would continuously quiz me on botanical questions.

Typical questions would be: "What type of placentation occurs in the Caryophyllaceae?" or "What monotypic genus in the Cruciferae is endemic to the Kerguelen Archipelago?" or "Name all of the phanerogamic genera native to Antarctica." In many cases he was actually thinking about the second question while I was working on the answer to the first one. So you get some idea how many questions were involved on a given trip.

I would say that he, perhaps more than any other person, stimulated my interest in taxonomic botany.—*Floyd Swink, Morton Arboretum.*

Julian knew Missouri as did few others, and he had a remarkable memory of people, sites, and plants. The Department of Conservation bought the land where Julian found pondberry [*Lindera melissifolia*] from a man called O. K. Hamlett. We were discussing this site one day and Julian not only remembered O.K.'s name but he described in detail where several of the rare species were located on the property. I had been on the property a week earlier and Julian talked as if he had—not 25 years before.

When the Natural History Section first started to locate and buy significant sites (often with rare or endangered species) we used a list Julian had prepared 20 years before. The same list went into the Natural Heritage Database prepared by The Nature Conservancy and the Department of Conservation.

Thanks to Julian, a number of these areas are now State Natural Areas and protected for those who will come after us. Sand Ponds (the pondberry site), Pickle Springs, and Barn Hollow are examples.

Every time we walk in these places Julian's shade will be there too.—*John Wylie, Retired Natural History Officer, Jefferson City, Missouri.*

Members and friends of the Garden were saddened by the death of Dr. Julian Steyermark on Saturday, October 15, 1988. Steyermark was one of the Garden's best-known research botanists, famous locally and around the world for his botanical collections and publications, and for his strong support for conservation of the environment.

Born in St. Louis on January 27, 1909, Julian Alfred Steyermark enrolled in 1925 in the Henry Shaw School of Botany, a cooperative program between the Garden and Washington University, where he received A.B. (1929), M.S. (1930), and Ph.D. (1933) degrees. He also earned an M.A. degree (1931) from Harvard University. During his early years at the Garden, Julian indulged his other great love, painting watercolors of native flora and plants in the Garden's orchid collection. At that time he began collecting herbarium specimens in Missouri and other states, and by graduation in 1933 he had already surpassed the quantity most botanists collect in a lifetime.

After college, Steyermark assisted Robert Woodson, a research botanist at the Garden. This led to his first tropical expedition, a collecting trip to Panama in 1934. He then taught high school in the St. Louis area for two years before moving to the Field Museum of Natural History in Chicago as an Assistant Curator. For the next 21 years Steyermark worked on the *Flora of Guatemala* and other tropical projects during the week, but continued his Missouri studies in his spare time. A revealing and delightful look at those weekend expeditions from Chicago to the wilds of Missouri was provided by his wife, Cora, in her book, *Behind the Scenes*, published by the Garden in 1984 (and still available in the Garden Gate Shop). These efforts culminated in the massive *Flora of Missouri* (1963). This widely acclaimed manual is often referred to as the state's "botanical bible" and has sold out six printings.

During World War II, Steyermark was sent to South America as part of the government's program to locate new botanical sources for quinine. At that time he first visited the Venezuelan Guayana region, which he lovingly referred to as "The Lost World." (See the Missouri Botanical Garden's *Bulletin*, November/December 1986 and July/August 1987.) His interest in this picturesque area was so great that in 1958 he left the Field Museum to take a position at Instituto Botánico in Caracas, Venezuela. In 1984, Julian returned to the Missouri Botanical Garden, where he strove to complete his last major project, a flora of the more than 9,000 plant species in the Venezuelan Guay-

FIGURE 7. Cora and Julian Steyermark in front of their home at Santa Eduvigis, Caracas, Venezuela, 1965–1970.

ana. This task remains for his friends and colleagues to complete.

Bruce Holst, project coordinator for the *Flora of the Venezuelan Guayana*, said, "It was a real thrill and a tremendous learning experience to work in the field with Julian. He really had an 'eagle eye' for spotting plants, and if you didn't see something that he did, he would let you know it . . . . Fieldwork was very special for Julian. He never took any 'vacation,' he went on field trips instead. He was just *so* excited about collecting plants, it was impossible not to be caught up by his enthusiasm. He always likened collecting to a 'treasure hunt'! Even with his two artificial hips, he would

FIGURE 8. Julian Steyermark on El Avila, outside of Caracas, Venezuela. Date unknown.

plow through brush, crawl over and under logs, fall down, laugh about it and push on . . . ."

Steyermark received numerous honors during his eventful life, including awards and citations from the governments of Guatamala and Venezuela, and the Garden's Henry Shaw Medal in 1979. That same year, the Ozark Chapter of the Sierra Club awarded him a special citation for his conservation efforts, and the Missouri Department of Conservation named the 73-acre Julian A. Steyermark Woods, near Hannibal, in his honor.

To commemorate Steyermark's achievements, the Garden has established a fund to promote botanical research and expeditions in Latin America, particularly in the Venezuelan Guayana region, and to support research on the natural history of Missouri. In addition, the Missouri Department of Conservation and the Garden are revising Julian's best-known book, which will be retitled *Steyermark's Flora of Missouri*, a lasting memorial to a giant among botanists.

A memorial service was held for Julian Steyermark at the Garden on October 25, 1988. In the eulogy, Dr. Raven said, ". . . His last work will be completed here, and will stand as a final testament to his industry and to his scholarship. As for any human being, however, what will prove to be even more important to all of us will be our memories, for Julian Steyermark was an inspirational person, one who projected his own values without trumpeting them, and thereby enriched all our lives, as he did the literature of botany."—*George Yatskievych heads the Garden's joint project with the Missouri Department of Conservation to revise Steyermark's* Flora of Missouri.—*Luther Raechal assisted Dr. Steyermark on the* Flora of the Venezuelan Guayana *and is continuing his work on the staff of this ongoing project; reprinted with permission from the* Bulletin of the Missouri Botanical Garden *77(1): 5. 1989.*

FIGURE 9. Geoffrey C. K. Dunsterville (fourth from left); Nora Dunsterville (sitting in front); Julian Steyermark (holding papers).

FIGURE 10. Cora and Julian Steyermark on their wedding day, 1 September 1937, in Hannibal, Missouri. Photo contributed by Coralie Lippold.

FIGURE 11. "A dream come true, but Mr. Peterson is responsible for picking it. The rain had broken the stem, and it was no crime, therefore, for Mr. Peterson to take the flower to paint," Steyermark wrote on the back of this photograph, dated 5 May 1929.

FIGURE 12. Julian Steyermark.

PLANT TAXA DESCRIBED BY JULIAN A. STEYERMARK[1]

Mary Susan Taylor[2]

ABSTRACT

In his 62 years of actively collecting plants (1925–1987), Julian Steyermark described 2,392 taxa, including 1 family, 38 genera, and 1,864 species. He named plants from 26 countries and from 16 states in the U.S.A. Types of taxa that he named are listed alphabetically by family, with author, literature citation, collector, collection number, date of collection, locality, elevation, and depository. Comments are supplied, where pertinent, on never-published names, illegitimate names, and some current nomenclature (which are not referenced in the bibliography). Appendices include eponymy, collectors index, and family index. The bibliography includes 395 references. Statistical summaries are provided.

Julian Steyermark collected his first plant in 1925, his last in 1987, both in Missouri. He collected so many plants, over 130,000 collections, that he received recognition from the unusual source of the *Guinness Book of World Records*. Julian was most known for his *Flora of Missouri*, and his work in Guatemala and Venezuela, yet he described plants from 26 countries and from 16 states in the U.S.A.

His statistical record is astonishing. Julian Steyermark described a single family, 38 genera, and 1,864 species. Including other ranks, he named at least 2,392 taxa. *Taxonomic Literature* (*second edition*) cites an as yet unobtainable reference edited by H. Villanueva, 1977 (Bibl. Alfredo Jahn, Bol. Inf. 9: 9–12) which purports to contain the 'most important of over 350 publications' by Julian Steyermark. It is estimated by the present author that this compilation lacks about 80 references, although the exact number is unknown.

In the list of types families are arranged alphabetically, and species alphabetically within families, then by descending rank within species. Data include the name, author(s), place of publication, collector, collection number, date of collection, locality, elevation, and depository. Current nomenclature (which are not referenced in the bibliography) and accession number of the Missouri Botanical Garden sheet are indicated when found serendipitously. New combinations are not included. A few never-published names are included and correct nomenclature given for sheets known to have been distributed bearing the unpublished name. Author abbreviations follow *Draft Index of Author Abbreviations Compiled at The Herbarium, Royal Botanic Gardens, Kew* and *Taxonomic Literature* (*second edition*). Publication abbreviations are standardized according to *Botanicum-Periodicum-Huntianum*.

STEYERMARK TYPES

ACANTHACEAE

Aphelandra gigantiflora Lindl. f. *lutea* Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(5): 237. 1947. *P. C. Standley 89560*; 16 Mar. 1941; Guatemala, Dept. Escuintla, Río Gavilán, NE of Escuintla; 720 m; F (holo) = *A. gigantiflora* Lindl. var. *gigantiflora*, 1974.

Bravaisia integerrima (Spreng.) Standl. var. *pilosa* Steyerm., Ernstia 23: 36. 1984. *J. A. Steyermark et al. 124622*; 28 Feb. 1981; Venezuela, Yaracuy, Dept. Urachiche, Quebrada Higueronal; 50 m; VEN (holo).

Jacobinia umbrosa (Benth.) S. F. Blake f. *erythrantha* Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(5): 241. 1947. *P. C. Standley 60082*; 15 Dec. 1938; Guatemala, Dept. Chimaltenango, above Las

[1] Julian never kept a list of what he described or maintained a complete bibliography. He was always helpful with suggestions on where to look for more of his work, and soon I didn't have to prompt him with questions, he would seek me out to ask if I had looked at certain journals. I shall always remember his generous gift of time in talking with me about his life and his work. He was always encouraging, and gracious with advice when I had a thorny taxonomic problem of my own. I am deeply grateful to Bruce Holst, Doug Stevens, Robbin Moran, and George Yatskievych for making valuable suggestions on the manuscript. Dolly Dorigo spent many hours double-checking the indices. Thanks are due to Bruce Holst, Paul Berry, and Luther Raechal for allowing me temporary office space. My friends Roy Gereau, Myra Guzman-Teare, and Amy Pool gave me support and encouragement during the two years I spent working on the list.

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TABLE 1. *Statistics.* Numbers of Steyermark taxa named within each rank, and within each country and state.

TAXA			
Families:	1	Genera:	38
Tribes:	1	Species:	1,864
Sections:	10	Subspecies:	54
Subsections:	4	Varieties:	241
Series:	5	Forms:	175
Subgenera:	3	New names:	33
Hybrids:	4		
Total taxa: 2,392 known to date			
Publications: 379 known to date			
Eponymy: 229 known to date			

COUNTRIES FROM WHICH TAXA WERE NAMED			
Argentina:	1	Belize:	6
Bolivia:	2	Brazil:	109
Canada:	2	Colombia:	49
Costa Rica:	1	Cuba:	2
Dominica:	1	Dominican Republic:	1
Ecuador:	23	El Salvador:	2
French Guiana:	19	Guatemala:	391
Guyana:	67	Honduras:	5
Mexico:	27	Panama:	11
Paraguay:	1	Perú:	22
Puerto Rico:	1	South Africa:	1
Suriname:	13	Trinidad:	4
U.S.A.:	124	Venezuela:	1,420

STATES IN THE U.S.A. FROM WHICH TAXA WERE NAMED			
Alabama:	1	Arkansas:	2
Arizona:	2	Colorado:	3
California:	28	Illinois:	3
Idaho:	2	Missouri:	62
Indiana:	1	Ohio:	1
New Mexico:	2	Tennessee:	1
Oregon:	2	Utah:	1
Texas:	13	Washington:	1

TABLE 2. Family and genera described by Julian Steyermark.

FAMILY	Tepuianthaceae
GENERA	
Achnopogon	Asteraceae
Acopanea	Theaceae
Adenanthe	Ochnaceae
Ahozolia* = *Sechium	Cucurbitaceae
Aphanocarpus	Rubiaceae
Aratitiyopea	Xyridaceae
Bartholomaea	Flacourtiaceae
Bonifazia* = *Disocactus	Cactaceae
Brewcaria	Bromeliaceae
Cardonaea	Asteraceae
Cephalodendron	Rubiaceae
Chimantaea	Asteraceae
Chondrococcus* = *Coccochondra	Rubiaceae
Coryphothamnus	Rubiaceae
Croizatia	Euphorbiaceae
Cuatrecasasiodendron	Rubiaceae
Dahlgrenia	Arecaceae
Dioicodendron	Rubiaceae
Holstianthus	Rubiaceae
Itzaea	Convolvulaceae
Maguireocharis	Rubiaceae
Maguireothamnus	Rubiaceae
Meruma	Rubiaceae
Mortoniodendron	Tiliaceae
Neblinathamnus	Rubiaceae
Orthion	Violaceae
Pachecoa	Fabaceae
Pagameopsis	Rubiaceae
Perissocarpa	Ochnaceae
Pittierothamnus* = *Amphidasya	Rubiaceae
Rojasianthe	Asteraceae
Rutaneblina* = *Rutaneblinaria	Rutaceae
Senefelderopsis	Euphorbiaceae
Sipaneopsis	Rubiaceae
Tecunumania	Cucurbitaceae
Tepuianthus	Tepuianthaceae
Thymocarpus	Marantaceae
Vesicarex	Cyperaceae
Yutajea	Rubiaceae

Calderas; 1,800–2,100 m; F (holo) = *Justicia aurea* Schlecht. f. *erythrantha* (Standl. & Steyerm.) D. Gibson, 1973.

Poikilacanthus setiferus Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 246. 1947. *H. Johnson 523*; 15 Aug. 1920; Guatemala, Dept. Alta Verapaz, between Chamá and Cobán; 900 m; F (holo).

Ruellia caroliniensis (Walt.) Steudel f. *alba* Steyerm., Rhodora 41: 585. 1939. *J. A. Steyermark 6058*; 23 June 1938; U.S.A., Missouri, Caldwell Co., along Long Creek, 1.5 mi. S of Kingston; F (holo), MO (1174668) = *R. humilis* Nutt. var. *longifolia* (A. Gray) Fern. f. *alba* (Steyerm.) Steyerm., 1960.

Ruellia pedunculata Torr. f. *baueri* Steyerm., Rhodora 51: 118. 1949. *B. Bauer s.n.*; 20 June 1948; U.S.A., Missouri, St. Francois Co., Koester; F (holo).

Ruellia strepens L. f. *alba* Steyerm., Rhodora 54: 258. 1952. *J. A. Steyermark 70292*; 26 Aug. 1950; U.S.A., Missouri, Schuyler Co., tributary to Chariton River, NE of Livonia, 6 mi. SW of Glenwood; F (holo), MO (1703638).

Siphonoglossa hondurensis Standl. & Steyerm., Ceiba 3: 131. 1952. *P. C. Standley 12459*; 18 Sep. 1948; Honduras, Dept. Morazán, región de La Travesía, cerca de Suyapa; F (holo) = *Siphonoglossa sessilis* (Jacq.) D. Gibson, 1973.

ACTINIDIACEAE

Saurauia cuchumatanensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 215. 1947. *J. A. Steyermark 49810*; 31 July 1942; Guatemala, Dept. Huehuetenango, Cruz de Limón, Sierra de los Cuchumatanes; 2,600–3,000 m; F (holo).

Saurauia meridensis Steyerm., Fieldiana Bot. 28(2): 368. 1952. *J. A. Steyermark 56344*; 6 May 1944; Venezuela, Mérida, Río Canagua, near Canagua; 1,065–1,820 m; F (holo).

Saurauia "perseifolia" Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 216. 1947. *J. A. Steyermark 41748*; 24 Dec. 1941; Guatemala, Dept. Izabal, along Río Tamejá, Cerro San Gil; 50 m; F (holo). Note: *S. persifolia* is the correct spelling.

Saurauia veneficorum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 217. 1947. *J. A. Steyermark 31081*; 2 Nov. 1939; Guatemala, Dept. Chiquimula, Montaña Norte to El Jutal, Cerro Brujo; 1,700–2,000 m; F (holo).

AGAVACEAE

Agave huehueteca Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 4. 1943. *P. C. Standley 82039*; 2 Jan. 1941; Guatemala, Dept. Huehuetenango, along Aguacatán road E of Huehuetenango; 1,950 m; F (holo).

ALBOLBODACEAE = Xyridaceae

AMARANTHACEAE

Cladothrix lanuginosa Nutt. var. *caruosa* Steyerm., Ann. Missouri Bot. Gard. 19: 389. 1932. *J. A. Moore & J. A. Steyermark 3795*; 26 June 1931; U.S.A., Texas, Brewster Co., 3 mi. E of Study Butte; 762 m; GH (holo), MO (1012577) = *Tidestromia lanuginosa* var. *caruosa* (Steyerm.) Cory.

AMARYLLIDACEAE

Pancratium guatemalense Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 38. 1944. *J. A. Steyermark 39288*; 13 Apr. 1940; Guatemala, Dept. Izabal, between Escobas and Montaña Escobas, across bay from Puerto Barrios; sea level; F (holo).

ANACARDIACEAE

Tapirira dunstervilleorum Steyerm., Aristeq. & Wurd., Bol. Soc. Venez. Ci. Nat. 26: 159. 1965. *J. A. Steyermark 90883*; 4 June 1962; Venezuela, Miranda, Oritopo, above Los Guayabitos and Baruta; 1,500 m; VEN (holo).

ANNONACEAE

Annona primigenia Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 7. 1943. *C. L. Lundell 2213*; Mar. 1933; Guatemala, Dept. Petén, Gavilán, Fallabón–Yaxhá road; F (holo).

Desmopsis guatemalensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 156. 1944. *J. A. Steyermark 34304*; 17 Jan. 1940; Guatemala, Dept. Quezaltenango, Montaña Chícharro, Volcán Santa María; 1,500 m; F (holo).

Desmopsis izabalensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 157. 1944. *J. A. Steyermark 41543*; 18 Dec. 1941; Guatemala, Dept. Izabal, Río Frío, Cerro San Gil; 75–150 m; F (holo).

Sapranthus megistanthus Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 7. 1943. *P. C. Standley 59219*; 8 Dec. 1938; Guatemala, Dept. Guatemala, Estancia Grande; 600 m; F (holo).

APOCYNACEAE

Aspidosperma decussatum Woodson subsp. *jauaensis* Steyerm. & Maguire, Mem. New York Bot. Gard. 23: 881. 1972. *J. A. Steyermark 98086*; 22–27 Mar. 1967; Venezuela, Bolívar, Cerro Jaua; 1,922–2,100 m; VEN (holo).

Lacmellea costanensis Steyerm., Bol. Soc. Venez. Ci. Nat. 25: 240. 1964. *J. A. Steyermark 92131*; 15–19 Nov. 1963; Venezuela, Distr. Federal, Cerro Naiguata; 1,000–1,300 m; NY, US, VEN (holo).

Mandevilla subcarnosa (Benth.) Woodson var. *angustata* Steyerm., Acta Bot. Venez. 2: 318. 1967. *J. A. Steyermark 93737*; 11 May 1964; Venezuela, Bolívar, Auyan-tepui; 1,660 m; VEN (holo).

Peltastes manarae Steyerm., Acta Bot. Venez. 3: 206. 1968. *B. J. Manara s.n.*; 11 July 1966; Venezuela, Distr. Federal, Quebrada Guayoyo, Cerro Naiguata; 1,000 m; VEN (holo).

AQUIFOLIACEAE

Ilex abscondita Steyerm., Ann. Missouri Bot. Gard. 75: 320. 1988. *T. Croat 59478*; 30 Nov. 1984; Venezuela, T.F. Amazonas, Cerro de la Neblina, Camp 7; 1,900 m; MO (holo—59478), NY, VEN.

Ilex acutidenticulata Steyerm., Ann. Missouri Bot. Gard 75: 321. 1988. *R. L. Liesner 18595*; 12 Mar. 1985; Venezuela; T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca; 1,500–1,650 m; MO (holo—3446418), VEN.

Ilex altiplana Steyerm., Ann. Missouri Bot. Gard. 75: 321. 1988. *J. A. Steyermark 111402*; 4 Jan. 1975; Venezuela, Bolívar, between San Ignacio de Yuruani and San Francisco de Yuruani; 1,200 m; VEN (holo).

Ilex anodonta Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 245. 1940. *J. A. Steyermark 36381*; 22 Feb. 1940; Guatemala, Dept. San Marcos, Río Tonana, between Canjula and La Unión Juárez, near SE portion of Volcán Tacaná; 2,000–3,000 m; F (holo).

Ilex aracamuniana Steyerm., Ann. Missouri Bot. Gard.: in press. 1989. *R. L. Liesner & G. Carnevali 22473*; 26 Oct. 1987; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro Aracamuni, summit, Proa Camp; 1,400 m; MO (holo), VEN.

Ilex attenuata Steyerm., Ann. Missouri Bot. Gard. 75: 322. 1988. *N. T. Silva & U. Brazao 60873*; 24 Jan. 1966; Brazil, Amazonas, Sierra Pirapucú, Comissão de Limites BR-1; 1,250 m; G, INPA, MO (holo—3283928), NY, VEN.

Ilex brevipedicellata Steyerm., Ann. Missouri Bot. Gard. 75: 322. 1988. *J. A. Steyermark & B. Holst 130531*; 21–22, 24 Feb. 1985; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca, Sima Camp; MO (holo—3446417), VEN.

Ilex brevipetiolata Steyerm. & Wurd., Mem. New York Bot. Gard. 9: 479. 1957. *J. A. Steyermark & J. J. Wurdack 347*; 27 Jan. 1948; Venezuela, Bolívar, Uaipán-tepui; 1,400 m; NY (holo) = *I. subrotundifolia* Steyerm., 1952.

Ilex cardonae Steyerm., Ann. Missouri Bot. Gard. 75: 323. 1988. *F. Cardona 1480*; 16–24 Feb. 1946; Venezuela, T.F. Amazonas, orillas del Río Castanho, afluente del Padauiri que del Río Negro y éste último al Amazonas; 100–140 m; VEN (holo).

Ilex ciliolata Steyerm., Ann. Missouri Bot. Gard. 75: 323. 1988. *R. L. Liesner 19479*; 4 Nov. 1985; Ven-

ezuela, Bolívar, 0.4 km N of El Pauji on trail to Uaiparú; 800–900 m; MO (holo—3446424), VEN.

Ilex culmenicola Steyerm., Fieldiana Bot. 28(2): 322. 1952. *G. H. H. Tate 424*; 26 Nov.–16 Dec. 1928; Venezuela, T.F. Amazonas, Mt. Duida; 1,830–2,000 m; F, NY (holo).

Ilex davidsei Steyerm., Ann. Missouri Bot. Gard 75: 324. 1988. *G. Davidse 22719*; 23 July 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, lower part of the Río Baria; 80 m; MO (holo—3524657), VEN.

Ilex glabella Steyerm., Ann. Missouri Bot. Gard. 75: 324. 1988. *R. L. Liesner 16688*; 15–16 Mar. 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro de la Neblina, Camp 4; 780 m; MO (holo—3524663), VEN.

Ilex glaucophylla Steyerm., Bol. Soc. Venez. 15: 176. 1954. *L. Aristeguieta 2295*; June 1954; Venezuela, Miranda, Los Guayabitos; 1,200 m; F (holo), VEN.

Ilex gleasoniana Steyerm., Fieldiana Bot. 28(2): 322. 1952. *G. H. H. Tate 526*; 26 Nov.–16 Dec. 1928; Venezuela, T.F. Amazonas, Ridge 25, Mt. Duida; 2,000 m; F, NY (holo).

Ilex gransabanensis Steyerm., Ann. Missouri Bot. Gard. 75: 325. 1988. *T. Croat 54158a*; 26 July 1982; Venezuela, Bolívar, rd. from Ikabarú to Santa Elena, 16 mi. N of Ikabarú; 750 m; MO (holo—3524662), VEN.

Ilex guaiquinimae Steyerm., Ann. Missouri Bot. Gard. 75: 325. 1988. *J. A. Steyermark et al. 117276*; 24 May 1978; Venezuela, Bolívar, Cerro Guaiquiníma; 900 m; MO, VEN (holo).

Ilex holstii Steyerm., Ann. Missouri Bot. Gard. 75: 326. 1988. *J. A. Steyermark & B. Holst 130481*; 21–22, 24 Feb. 1985; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca, Sima Camp; 1,140 m; MO (holo—3446423), VEN.

Ilex ignicola Steyerm., Ann. Missouri Bot. Gard. 75: 326. 1988. *J. A. Steyermark et al. 130112*; 24–28 Feb. 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro Aratitiyope, 70 km SSW of Ocamo; 990–1,100 m; MO (holo—3226838), VEN.

Ilex jauaensis Steyerm., Ann. Missouri Bot. Gard. 75: 327. 1988. *J. A. Steyermark et al. 109294*; 22–28 Feb. 1974; Venezuela, Bolívar, Meseta de Jaua, Cerro Jaua, SW summit; 1,750–1,800 m; VEN (holo), MO (2582368).

Ilex karuaiana Steyerm., Fieldiana Bot. 28(2): 323. 1952. *J. A. Steyermark 60660*; 27 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,220 m; F (holo), NY.

Ilex liesneri Steyerm., Ann. Missouri Bot. Gard. 74: 94. 1987. *R. L. Liesner 18469*; 8–9 Mar. 1985; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca, 1–2 km N of Sima Camp; 1,100 m; MO (holo—3462076), VEN.

Ilex longipilosa Steyerm., Ann. Missouri Bot. Gard. 75: 327. 1988. *R. L. Liesner 19878*; 11 Nov. 1985; Venezuela, Bolívar, 3 km S of El Pauji, S slope and summit of El Abismo; 800–1,050 m; MO (holo—3446416), VEN.

Ilex magnifructa Edwin var. *minor* Steyerm., Ann. Missouri Bot. Gard. 75: 328. 1988. *F. Cardona 2943*; Feb. 1962; Venezuela, T.F. Amazonas, Cerro Ualipano; 1,760 m; MO, US (holo).

Ilex marahuacae Steyerm., Ann. Missouri Bot. Gard. 75: 328. 1988. *J. A. Steyermark & B. K. Holst 130425*; 21–22, 24 Feb. 1985; Venezuela, T.F. Amazonas, Cerro Marahuaca, Sima Camp; 1,140 m; MO (holo—3524661), VEN.

Ilex nervosa Triana var. *glabrata* Steyerm., Fieldiana Bot. 28(2): 324. 1952. *J. A. Steyermark 56653*; Venezuela, Mérida, above Tabay; 2,285–2,745 m; F (holo).

Ilex paruensis Steyerm., Ann. Missouri Bot. Gard. 75: 330. 1988. *O. Huber 4437*; 7 Oct. 1979; Venezuela, T.F. Amazonas, Dept. Atabapo, Serranía del Parú (Aroko); 1,100 m; VEN (holo).

Ilex paujiensis Steyerm., Ann. Missouri Bot. Gard. 75: 330. 1988. *R. Liesner & B. Holst 18796*; 19 Oct. 1985; Venezuela, Estado Bolívar, 3 km S of El Pauji; 900 m; MO (holo—3524660), VEN.

Ilex polita Steyerm., Ann. Missouri Bot. Gard. 75: 331. 1988. *G. Davidse & O. Huber 22679*; 25–27 Nov. 1982; Venezuela, Bolívar, Guayaraca, southern base, Auyán-tepui; 950 m; MO (holo—3524659), VEN.

Ilex ptariana Steyerm., Fieldiana Bot. 28(2): 324. 1952. *J. A. Steyermark 59574*; 30 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 2,285–2,405 m; F (holo), NY.

Ilex retusa Klotzsch f. *glabra* Steyerm., Fieldiana Bot. 28(4): 959. 1957. *J. A. Steyermark 58123*; 31 Aug. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,675 m; F (holo).

Ilex retusa Klotzsch f. *glaucescens* Steyerm., Fieldiana Bot. 28(4): 959. 1957. *J. A. Steyermark 58349*; 4 Sep. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,820–2,075 m; F (holo).

Ilex retusa Klotzsch f. *major* Steyerm., Fieldiana Bot. 28(4): 960. 1957. *J. A. Steyermark 58127*; 31 Aug. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,675 m; F (holo).

Ilex spathulata Steyerm., Ann. Missouri Bot. Gard. 75: 331. 1988. *R. L. Liesner 17599*; 17–18 Feb. 1985; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca; 12,250 m; MO (holo—3446415), VEN.

Ilex stenophylla Steyerm., Fieldiana Bot. 28(2): 325. 1952. *J. A. Steyermark 58038*; 26 Aug. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,095–1,520 m; F (holo), NY = *I. retusa* Klotzsch.

Ilex subrotundifolia Steyerm., Fieldiana Bot. 28(2): 328. 1952. *J. A. Steyermark 59394*; 26 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,220 m; F (holo).

Ilex summa Steyerm., Ann. Missouri Bot. Gard. 75: 332. 1988. *B. K. Holst 3617*; 26 Mar. 1987; Venezuela, Bolívar, Dist. Piar, Camarcaibarai-tepui, summit; 2,400 m; MO (holo—3446422), VEN.

Ilex tateana Steyerm., Fieldiana Bot. 28(2): 330. 1952. *J. A. Steyermark 58022*; 26 Aug. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,095–1,520 m; F (holo).

Ilex tepuiana Steyerm. ex Edwin, Mem. New York Bot. Gard. 12(3): 138. 1965. *J. A. Steyermark 60290*; 15–17 Nov. 1944; Venezuela, Bolívar, mesa between Ptari-tepui and Sororopan-tepui; 1,600 m; F (holo), NY.

Ilex venezuelensis Steyerm., Fieldiana Bot. 28(2): 330. 1952. *J. A. Steyermark 58340*; 4 Sep. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,820–2,075 m; F (holo).

Ilex vesparum Steyerm., Fieldiana Bot. 28(2): 332. 1952. *J. A. Steyermark 61659*; 21 Mar. 1945; Venezuela, Anzoátegui, above Santa Cruz; 2,000–2,300 m; F (holo).

Ilex wurdackiana Steyerm., Ann. Missouri Bot. Gard. 75: 332. 1988. *J. A. Steyermark & S. Nilsson 449*; 21 Apr. 1960; Venezuela, Bolívar, Cerro Venamo, NW slopes; 1,100–1,140 m; VEN (holo).

ARACEAE

Anthurium coibionii Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 209. 1947. *J. A. Steyermark 42212*; 9 Jan. 1942; Guatemala, Dept. Zacapa, Río Sitio Nuevo, Sierra de las Minas; 1,200–1,500 m; F (holo) = *A. subcordatum* Schott, 1958.

Anthurium duidae Steyerm., Fieldiana Bot. 28(1): 92. 1951. *J. A. Steyermark 58099*; 31 Aug. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,675 m; F (holo) = *A. ptarianum* Steyerm., 1979.

Anthurium krauseanum Steyerm., Fieldiana Bot. 28(1): 93. 1951. *J. A. Steyermark 60847*; 4–5 Dec. 1944; Venezuela, Bolívar, SE base of Carrao-tepui; 1,460–1,615 m; F (holo).

Anthurium monsterioides Steyerm., Fieldiana Bot. 28(1): 93. 1951. *J. A. Steyermark 56727*; 23 May 1944; Venezuela, Bolívar, N of Mesa Bolívar, along Río Onia; 545–915 m; F (holo) = *A. clavigerum* Poepp. & Endl., 1979.

Anthurium ptarianum Steyerm., Fieldiana Bot. 28(1): 94. 1951. *J. A. Steyermark 59509*; 29 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 1,810 m; F (holo).

Anthurium radicosum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 210. 1947. *J. A. Steyermark 44776*; 6 Mar. 1942; Guatemala, Dept. Alta Verapaz, along Río Icvolay, N and NW of Finca Cubilquitz to Quebrada Diablo; 300–350 m; F (holo) = *A. pittieri* Engler, 1958.

Anthurium retiferum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 211. 1947. *J. A. Steyermark 48621*; 14 July 1942; Guatemala, Dept. Huehuetenango, Sierra de los Cuchumatanes, Cerro Huitz; 1,500–2,600 m; F (holo).

Anthurium titanium Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 211. 1947. *J. A. Steyermark 37963*; 16 Mar. 1940; Guatemala, Dept. San Marcos, Volcán Tajumulco along Río Cabús; 1,300–1,500 m; F (holo).

Monstera grandifolia Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 212. 1947. *J. A. Steyermark 45423*; 28 Mar. 1942; Guatemala, Dept. Petén, between Finca Yalpemech and Chinajá; 50–100 m; F (holo).

Philodendron duidae Steyerm., Fieldiana Bot. 28(1): 96. 1951. *J. A. Steyermark 58225*; 2 Sep. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,025–1,200 m; F (holo) = *P. englerianum* Steyerm. subsp. *duidae* (Steyerm.) Bunting, 1988.

Philodendron englerianum Steyerm., Fieldiana Bot. 28(1): 96. 1951. *J. A. Steyermark 60863*; 5–6 Dec. 1944; Venezuela, Bolívar, Carrao-tepui; F (holo).

Philodendron krauseanum Steyerm., Fieldiana Bot. 28(1): 98. 1951. *J. A. Steyermark 60567*; 25 Nov. 1944; Venezuela, Bolívar, Quebrada O-paru-ma; 915–1,065 m; F (holo).

Philodendron ptarianum Steyerm., Fieldiana Bot. 28(1): 99. 1951. *J. A. Steyermark 59682*; 1 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,600 m; F (holo) = *P. callosum* subsp. *ptarianum* (Steyerm.) Bunting, 1988.

Philodendron rojasianum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 3. 1940. *J. A. Steyermark 33244*; Dec. 1939; Guatemala, Dept. Quezaltenango, Finca Pirineos, Volcán Santa María; 1,300–1,500 m; F (holo) = *P. guatemalense* Engler, 1958.

Philonotion williamsii Steyerm., Fieldiana Bot. 28(1): 99. 1951. *L. Williams 13922*; 23 Jan. 1942. Venezuela, T.F. Amazonas, Yavita; 128 m; F (holo) = *Schismatoglottis spruceana* (Schott) Bunting var. *williamsii* (Steyerm.) Bunting, 1988.

Schismatoglottis bolivariana Bunting & Steyerm., Brittonia 21(2): 187. 1969. *J. A. Steyermark 97811*; 17–29 Mar. 1967; Venezuela, Bolívar, del Río Kanarakuni, N and NE of Mision de Campamento Sanidad del Río Kanarakuni; 400 m; NY, VEN (holo).

Spathicarpa duidae Steyerm., Fieldiana Bot. 28(1): 101. 1951. *J. A. Steyermark 57994*; 25–26 Aug. 1944; Venezuela, T.F. Amazonas, Caño Negro, Cerro Duida; F (holo).

Stenospermation ammiticum Bunting, Bol. Soc. Venez. Ci. Nat. 25: 42. 1963. *J. A. Steyermark 89543*; 27 Aug. 1961; Venezuela, Bolívar, cabeceras de Río Chicanan; 500 m; BH, VEN (holo). Note: This is the accepted spelling of the genus.

Stenospermatium pittieri Steyerm., Fieldiana Bot. 28(1): 101. 1951. *J. A. Steyermark 57455*; 18 July 1944; Venezuela, Táchira, Alto de Lirio, between Bramon and Las Delicias; F (holo). Note: *Stenospermation* is the correct spelling for the genus.

Urospatha savannarum Steyerm., Fieldiana Bot. 28(1): 102. 1951. *J. A. Steyermark 57853*; 23 Aug. 1944; Venezuela, T.F. Amazonas, base of Cerro Duida, Sabana Grande; 200 m; F (holo) = *U. angustiloba* Engl., 1988.

ARALIACEAE

Dendropanax larensis Steyerm., Fieldiana Bot. 28(2): 441. 1952. *J. A. Steyermark 55434*; 11 Feb. 1944; Venezuela, Lara, between Buenos Aires and Páramo de las Rosas; 2,285–3,290 m; F (holo).

Dendropanax neblinae Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 82. 1984. *B. Maguire et al. 42062*; 14–16 Nov. 1957; Venezuela, T.F. Amazonas, just S of Camp 3, Cerro de la Neblina; 700 m; MO (3401817), NY (holo).

Dendropanax veillonii Steyerm., Pittieria 4: 9. 1972. *J.-P. Veillon 7*; 1971; Venezuela, Mérida, San Eusebio, La Carbonera; 2,350 m; VEN (holo).

Didymopanax auyantepuiensis Steyerm., Acta Bot. Venez. 2: 271. 1967. *J. A. Steyermark 93974*; 15 May 1964; Venezuela, Bolívar, Auyan-tepui; 2,050–2,300 m; VEN (holo) = *Schefflera auyantepuiensis* (Steyerm.) Maguire, Steyerm. & Frodin, 1984.

Didymopanax chimantensis Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 456. 1967. *J. A. Steyermark 75788*; 20 June 1953; Venezuela, Bolívar, Apacara-tepui, Chimantá Massif; 2,000–2,150 m; NY (holo) = *Schefflera chimantensis* (Steyerm. & Maguire) Maguire, Steyerm. & Frodin, 1984.

Didymopanax multiramosus Steyerm., Acta Bot. Venez. 2: 273. 1967. *J. A. Steyermark 93926*; 15 May 1964; Venezuela, Bolívar, Auyan-tepui; 2,050–2,300 m; VEN (holo) = *Schefflera chimantensis* (Steyerm. & Maguire) Maguire, Steyerm. & Frodin, 1984.

Oreopanax capitatus (Jacq.) Decne. & Planch. var. *minor* Steyerm., Fieldiana Bot. 28(2): 442. 1952. *J. A. Steyermark 56242*; 3 May 1944; Venezuela, Mérida, between La Cumbre, San Jose and Mucutuy; 1,820–2,590 m; F (holo).

Oreopanax venezuelense Steyerm., Fieldiana Bot. 28(2): 442. 1952. *J. A. Steyermark 62017*; 11 Apr. 1945; Venezuela, Monagas, Cerro Guacharo; 1,100–1,300 m; F (holo).

Schefflera ayangannensis Maguire, Steyerm. & Frodin,

Mem. New York Bot. Gard. 38: 63. 1984. *S. S. Tillett et al. 45178*; 7 Aug. 1960; Guyana, Mt. Ayanganna; 900–1,100 m; NY (holo), VEN.

Schefflera coriacea subsp. *neblinae* Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 79. 1984. *N. T. Silva & U. Brazao 60903*; 26 Jan. 1966; Venezuela, Pirapucu, Serra da Neblina, Río Negro, Río Cauaburi, Río Maturaca; 1,300 m; NY (holo).

Schefflera cuatrecasasiana Steyerm., Fieldiana Bot. 28(2): 443. 1952. *J. A. Steyermark 57336*; 15 July 1944; Venezuela, Táchira, base of Páramo de Tamá, 4–10 km above Betania; 2,500–2,895 m; F (holo).

Schefflera duidae Steyerm., Fieldiana Bot. 28(2): 444. 1952. *J. A. Steyermark 57989*; 25–26 Aug. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 305–1,095 m; F (holo).

Schefflera globulifera Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 69. 1984. *B. Maguire et al. 37354*; 23 Jan. 1954; Venezuela, T.F. Amazonas, Cerro de la Neblina, Cumbre Camp; 1,700–2,000 m; NY (holo).

Schefflera gracillima Steyerm. & Maguire, Bol. Soc. Venez. Ci. Nat. 32: 371. 1976. *J. A. Steyermark et al. 109373*; 22–28 Feb. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Jaua; 1,750–1,800 m; NY, VEN (holo).

Schefflera guanayensis Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 66–67. 1984. *B. Maguire et al. 31740*; 2 Feb. 1951; Venezuela, T.F. Amazonas, Cerro Guanay; 1,800 m; NY (holo).

Schefflera guanayensis Maguire, Steyerm. & Frodin subsp. *paruensis* Maguire, Steyerm. & Frodin, New York Bot. Gard. 38: 67. 1984. *R. S. Cowan & J. J. Wurdack 31405*; 12 Feb. 1951; Venezuela, T.F. Amazonas, Cerro Parú, Serranía Parú; NY (holo).

Schefflera guanayensis Maguire, Steyerm. & Frodin subsp. *sipapoensis* Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 67. 1984. *B. Maguire & L. Politi 27756*; 17 Dec. 1948; Venezuela, T.F. Amazonas, Cerro Sipapo (Paraque), Phelps Camp to N Savanna; 1,400 m; MO (3401819), NY (holo).

Schefflera huachamacarii Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard 38: 76. 1984. *B. Maguire et al. 30253*; 15 Dec. 1950; Venezuela, T.F. Amazonas, Cerro Huachamacari, vicinity of Summit Camp; 1,620 m; NY (holo).

Schefflera monosperma Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 51. 1984. *I. Thurn 162*; Venezuela, Roraima; K (holo).

Schefflera pallens Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 72. 1984. *B. Maguire et al. 60503*; 3 Dec. 1965; Brazil, Amazonas, trail to Pico Phelps, Serra de Neblina; 2,425 m; NY (holo).

Schefflera pauciradiata Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 74. 1984. *B. Maguire & L. Politi 28454*; Venezuela, T.F. Amazonas, Cerro Sipapo, Upper E Basin; 1,900 m; NY (holo).

Schefflera pedicelligera Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 63. 1984. *B. Maguire et al. 29546*; 19 Nov. 1950; Venezuela, T.F. Amazonas, Culebra Creek drainage, Río Cununcunuma, Cerro Duida; 1,500 m; NY (holo).

Schefflera pimichinensis Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 55. 1984. *B. Maguire & J. J. Wurdack 35635*; 14 Apr. 1953; Venezuela, T.F. Amazonas, Sabana El Venado, left bank of Caño Pimichin, above Puerto Pimichin; 140 m; NY (holo), VEN.

Schefflera plurispicata Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 52. 1984. *N. T. Silva & U. Brazao 60941*; 29 Jan. 1966; Brazil, Amazonas, Serra Pirapucu, Serra da Neblina; MG, NY (holo).

Schefflera quinquecarinata Steyerm., Bol. Soc. Venez. Ci. Nat. 25: 44. 1963. *J. A. Steyermark & S. Nilsson 483*; 23 Apr. 1960; Venezuela, Bolívar, headwaters of Río Cuyuni; 1,300 m; VEN (holo).

Schefflera quinquestylorum Steyerm., Bol. Soc. Venez. Ci. Nat. 25: 46. 1963. *J. A. Steyermark & S. Nilsson 429*; 21 Apr. 1960; Venezuela, Bolívar, Cerro Venamo; 1,100–1,140 m; VEN (holo) = *S. duidae* Steyerm. subsp. *quinquestylorum* (Steyerm.) Maguire, Steyerm. & Frodin, 1984.

Schefflera reticulata (Gleason) Maguire, Steyerm. & Frodin subsp. *jauaensis* Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 59. 1984. *J. A. Steyermark 98078*; 22–27 Mar. 1967; Venezuela, Estado Bolívar, Meseta de Jaua; 1,922–2,100 m; NY (holo), VEN.

Schefflera reticulata (Gleason) Maguire, Steyerm. & Frodin subsp. *yutajensis* Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 59. 1984. *B. Maguire & C. K. Maguire 35154*; 11 Feb. 1953; Venezuela, T.F. Amazonas, Serranía Yutaje, Río Manapiare; NY (holo).

Schefflera rugosifolia Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 71. 1984. *McConnell & Quelch 663*; Venezuela, Bolívar, Mt. Roraima; K (holo).

Schefflera simplex Steyerm. & Holst, Ann. Missouri Bot. Gard. 75: 1082. 1988. *A. Gentry & B. Stein 46694*; 17 Apr. 1984; Venezuela, T.F. Amazonas, Cerro de la Neblina; 1,900–2,100 m; MO (holo—348100), VEN.

Schefflera sipapoensis Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 59. 1984. *B. Maguire & L. Politi 28471*; 20 Jan. 1949; Venezuela, T.F. Amazonas, Cerro Sipapo (Paraque), Upper E Basin; 1,500–1,650 m; NY (holo).

Schefflera tamana Steyerm., Fieldiana Bot. 28(2): 444. 1952. *J. A. Steyermark 57321*; 15 July 1944; Venezuela, Táchira, base of Páramo de Tamá, 4–10 km above Betania; 2,500–2,895 m; F (holo).

Schefflera tamatamaensis Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 55. 1984. *J. J. Wurdack & L. S. Adderley 43148*; 23 June 1959; Venezuela, T.F. Amazonas, Caño Tama Tama, just above Tama—Tama, right bank Río Orinoco; 150 m; K, MG, NY (holo), US, VEN.

Schefflera tremuloidea Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 61. 1984. *B. Maguire et al. 42379*; 13 Dec. 1957; Venezuela, T.F. Amazonas, Summit, Cerro Neblina, E escarpment of upper Cañon Grande Basin; 2,000 m; NY (holo), MO (2911090, 3401829), VEN.

Schefflera tremuloidea Maguire, Steyerm. & Frodin var. *marahuacensis* Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 63. 1984. *J. A. Steyermark et al. 124406*; 16 Feb. 1981; Venezuela, T.F. Amazonas, Cerro Marahuaca; 2,500 m; MO, NY (holo), US, VEN.

Schefflera umbellata (N.E. Br.) Viguier subsp. *duidana* Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 74. 1984. *G. H. H. Tate 431*; 16 Dec. 1928; Venezuela, T.F. Amazonas, Cerro Duida, summit, slopes of ridge; 1,650–1,800 m; NY (holo).

Schefflera yutajensis Steyerm. & Holst, Ann. Missouri Bot. Gard. 75: 1082. 1988. *B. K. Holst & R. L. Liesner 3426*; 11 Mar. 1987; Venezuela, T.F. Amazonas, Dept. Atures, valley of Río Coro-Coro, W of

Serranía de Yutaje; 1,100 m; MO (holo—3485098), MO.

ARECACEAE

Asterogyne yaracuyense Henderson & Steyerm., Brittonia 38: 309. 1986. *J. A. Steyermark et al. 100311*; 9–10 Nov. 1967; Venezuela, Yaracuy, Cerro de Chapa; 1,200–1,400 m; BH (holo), VEN.

Bactris bergantina Steyerm., Fieldiana Bot. 28(1): 71. 1951. *J. A. Steyermark 61039*; 20 Feb. 1945; Venezuela, Anzoátegui, NE of Bergantin, tributary to Río Neveri, along Río Leon by Quebrada Danta; 500 m; F (holo).

Bactris duidae Steyerm., Fieldiana Bot. 28(1): 73.1951. *J. A. Steyermark 57908*; 23 Aug. 1944; Venezuela, T.F. Amazonas, near Base River (Caño Negro) at SE base of Cerro Duida; 215 m; F (holo).

Bactris kamarupa Steyerm., Fieldiana Bot. 28(1): 75. 1951. *J. A. Steyermark 60542*; 25 Nov. 1944; Venezuela, Bolívar, Quebrada O-paru-ma, tributary of Río Pacairao, below Santa Teresita de Kavanayen; 915–1,065 m; F (holo).

Bactris ptariana Steyerm., Fieldiana Bot. 28(1): 77. 1951. *J. A. Steyermark 60046*; 10–11 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,585–1,600 m; F (holo).

Bactris sororopanae Steyerm., Fieldiana Bot. 28(1): 78. 1951. *J. A. Steyermark 60781*; 29 Nov. 1944; Venezuela, Bolívar, along Río Karuai, base of Sororopan-tepui, W of La Laja; 1,220 m; F (holo).

Bactris venezuelensis Steyerm., Fieldiana Bot. 28(1): 80. 1951. *J. A. Steyermark 57933*; 23 Aug. 1944; Venezuela, T.F. Amazonas, SE base of Cerro Duida, along Base River (Caño Negro); 225 m; F (holo).

Chamaedorea aequalis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(50): 196. 1947. *J. A. Steyermark 51666*; 31 Aug. 1942; Guatemala, Dept. Huehuetenango, Cerro Negro; 1,600–2,080 m; F (holo).

Chamaedorea aguilariana Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 197. 1947. *P. C. Standley 86890*; 9 Feb. 1941; Guatemala, Dept. Quezaltenango, between Finca Pirineos and Patzulín; 1,200–1,400 m; F (holo).

Chamaedorea brachypoda Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 198. 1947. *J. A. Steyermark 39185*; 9 Apr. 1940; Guatemala, Dept. Izabal, between Bananera and La Presa, base of Sierra del Mico; 150 m; F (holo).

Chamaedorea carchensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 199. 1947. *P. C. Standley 90160*; Mar. 1941; Guatemala, Dept. Verapaz, along Río Carchá, between Cobán and San Pedro Carchá; 1,350 m; F (holo).

Chamaedorea digitata Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 200. 1947. *J. A. Steyermark 51683*; 31 Aug. 1942; Guatemala, Dept. Huehuetenango, Cerro Negro; 1,600–2,000 m; F (holo).

Chamaedorea fusca Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 201. 1947. *J. A. Steyermark 38123*; 28 Mar. 1940; Guatemala, Dept. Izabal, Sierra del Mico; 300 m; F (holo).

Chamaedorea nubicum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 202. 1947. *J. A. Steyermark 43583a*; 5 Feb. 1942; Guatemala, Dept. El Progreso, Sierra de las Minas; 2,900 m; F (holo).

Chamaedorea pachecoana Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 203. 1947. *P. C. Standley 63104*; 20 Jan. 1939; Guatemala, Dept. Guatemala, cultivated, said to come from Dept. Totonicapan, but probably from some other part of the Occidente; F (holo).

Chamaedorea quezalteca Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 204. 1947. *P. C. Standley 87159*; 9 Feb. 1941; Guatemala, Dept. Quezaltenango, between Finca Pirineos and Patzulín; 1,200–1,400 m; F (holo).

Chamaedorea rojasiana Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 205. 1947. *J. A. Steyermark 33479*; 1–2 Jan. 1940; Guatemala, Dept. Quezaltenango, Quebrada San Gerónimo, Finca Pirineos, Volcán Santa María; 1,300–2,000 m; F (holo).

Chamaedorea skutchii Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 206. 1947. *A. F. Skutch 935*; 4 Aug. 1934; Guatemala, Dept. Quezaltenango, Volcán Zunil; 2,400 m; F (holo).

Chamaedorea stenocarpa Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 206. 1947. *J. A. Steyermark 41893*; 25 Dec. 1941; Guatemala, Dept. Izabal, Cerro San Gil; 650–900 m; F (holo).

Chamaedorea stricta Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 207. 1947. *J. A. Steyermark 37381*; 9 Mar. 1940; Guatemala, Dept. San Marcos, Volcán Tajumulco, up Cerro de Mono; 1,400–1,700 m; F (holo).

Chamaedorea vulgata Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 208. 1947. *J. A. Steyermark 37735*; 14 Mar. 1940; Guatemala, Dept. San Marcos, Volcán Tajumulco, 9 mi. NW of El Porvenir; 1,300–2,000 m; F (holo).

Dahlgrenia Steyerm., Fieldiana Bot. 28(1): 82. 1951, gen. nov.

Dahlgrenia ptariana Steyerm., Fieldiana Bot. 28(1): 82. 1951. *J. A. Steyermark 60044*; 10–11 Nov. 1944; Venezuela, Bolívar, SE facing slopes of Ptari-tepui; 1,585–1,600 m; F (holo) = *Dictyocaryum ptariense* (Steyerm.) Moore & Steyerm., 1967.

Desmoncus duidensis Steyerm., Fieldiana Bot. 28(1): 85. 1951. *J. A. Steyermark 57944*; 23 Aug. 1944; Venezuela, T.F. Amazonas, SE base of Cerro Duida, along Base River (Caño Negro); 225 m; F (holo).

Desmoncus multijugus Steyerm., Fieldiana Bot. 28(1): 85. 1951. *J. A. Steyermark 60968*; 18 Dec. 1944; Venezuela, Bolívar, Tumeremo; 305 m; F (holo).

Euterpe ptariana Steyerm., Fieldiana Bot. 28(1): 87. 1951. *J. A. Steyermark 60045*; 10–11 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,585–1,600 m; F (holo).

Geonoma karuaiana Steyerm., Fieldiana Bot. 28(1): 88. 1951. *J. A. Steyermark 60789*; 29 Nov. 1944; Venezuela, Bolívar, W of La Laja, base of Sororopan-tepui, along Río Karuai; 1,220 m; F (holo).

Hyospathe maculata Steyerm., Fieldiana Bot. 28(1): 89. 1951. *J. A. Steyermark 60406*; 20–21 Nov. 1944; Venezuela, Bolívar, Quebrada O-paru-ma, between Santa Teresita de Kavanayen and Río Pacairao (tributary of Río Mouak); 1,065–1,220 m; F (holo).

Mauritia flexuosa L. var. *venezuelana* Steyerm., Fieldiana Bot. 28(1): 90. 1951. *J. A. Steyermark 57649*; 2 Aug. 1944; Venezuela, Bolívar, between Río Caroni and Ciudad Bolívar; 200 m; F (holo).

Prestoea humilis Henderson & Steyerm., Brittonia 38: 311. 1986. *A. Henderson 501*; 12 Nov. 1985; Venezuela, Yaracuy, Cerro la Chapa; 1,200–1,400 m; K, MYF, NY, VEN (holo).

Socratea albolineata Steyerm., Fieldiana Bot. 28(1): 91.

1951. *J. A. Steyermark 60541*; 25 Nov. 1944; Venezuela, Bolívar, Quebrada O-paru-ma, tributary Río Pacairao, below Santa Teresita de Kavanayen; 915–1,065 m; F (holo).

ARISTOLOCHIACEAE

Aristolochia mollis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 155. 1944. *J. A. Steyermark 51269*; 24 Aug. 1942; Guatemala, Dept. Huehuetenango, canyon tributary to Río Trapichillo, between Democracia and canyon of Chamushú; 1,000 m; F (holo) = *A. paracleta* Pfeiffer, nom. nov.

ASCLEPIADACEAE

Asclepias woodsoniana Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 224. 1947. *J. A. Steyermark 31781*; 15 Nov. 1939; Guatemala, Dept. Jutiapa, between Trapiche Vargas and Asunción Mita; 500 m; F (holo).

Blepharodon auyantepuiense Steyerm., Acta Bot. Venez. 2: 319. 1967. *J. A. Steyermark 93889*; 14 May 1964; Venezuela, Bolívar, Auyan-tepui; 2,000–2,200 m; VEN (holo).

Cynanchum auyantepuiense Steyerm., Acta Bot. Venez. 2: 320. 1967. *J. A. Steyermark 93892*; 14 May 1964; Venezuela, Bolívar, Auyan-tepui; 2,050 m; VEN (holo).

Cynanchum stenomeres Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 224. 1947. *W. A. Schipp 674*; 5 Feb. *s.n.*; Belize, All Pines; sea level; F (holo).

Marsdenia blepharodes Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 226. 1947. *J. A. Steyermark 33615*; 6 Jan. 1940; Guatemala, Dept. Quezaltenango, San Juan Patzulín 1,500 m; F (holo).

ASTERACEAE

Achnopogon Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 437. 1957, gen. nov.

Achnopogon virgatus Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 438. 1957. *J. A. Steyermark & J. J. Wurdack 681*; 9 Feb. 1955; Venezuela, Bolívar, Chimantá Massif, Torono-tepui; 2,090 m; F (holo), NY.

Ageratum chortianum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 98. 1944. *J. A. Steyermark 31269*; Nov. 1939; Guatemala, Dept. Chiquimula, Montaña Castilla, near Montaña Cebollas, along Río Santa Lucía Saso; 1,200–1,500 m; F (holo).

Alomia ballotifolia Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 425. 1957. *J. A. Steyermark 75520*; 21 May 1953; Venezuela, Bolívar, Chimantá Massif, Chimantá-tepui (Torono-tepui); 1,700 m; F (holo), NY.

Aphanactis standleyi Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 390. 1940. *P. C. Standley 58674*; 4 Dec. 1938; Guatemala, Dept. Chimaltenango, Cerro Tecpán, Santa Elena; 2,700 m; F (holo).

Aplopappus gymnocephalus DC. f. *albus* Steyerm. & Moore, Ann. Missouri Bot. Gard. 20: 797. 1933. *J. A. Moore & J. A. Steyermark 3488*; 17 July 1931; U.S.A., Texas, Culberson Co., Guadalupe Mountains, ridge above McKittrick Canyon; MO (holo) = *Haplopappus gymnocephalus* DC.

Archibaccharis blakeana Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 296. 1940. *P. C. Standley 58597*; 1938–1939; Guatemala, Dept. Sacatepéquez, near Antigua; 1,500–1,600 m; F (holo).

Aspilia avilensis Aristeg. & Steyerm., Fl. Venez. 10(2): 552. 1964. *C. Vogl 41*; Aug. 1937; Venezuela, Distr. Federal, Caracas, Serranías del Avila; depository not indicated.

Aster anomalus Engelm. f. *albidus* Steyerm., Rhodora 51: 119. 1949. *J. A. Steyermark 65135*; 23 Sep. 1947; U.S.A., Missouri, Barry Co., Natural Bridge Hollow, 8–9 mi. SE of Cassville; F (holo).

Aster bimater Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 141. 1944. *C. A. Purpus 12091*; May 1927; Mexico, Chiapas, Hacienda Monserratee; F (holo) = *Aster moranensis* H.B.K., 1976.

Baccharis erectifolia Steyerm., Fieldiana Bot. 28(3): 620. 1953. *J. A. Steyermark 62583*; 6 May 1945; Venezuela, Sucre, Cerro Turumiquire; 2,360–2,500 m; F (holo).

Baccharis meridensis Steyerm., Fieldiana Bot. 28(3): 622. 1953. *J. A. Steyermark 56537*; 14 May 1944; Venezuela, Mérida, Páramo de Los Colorados; 2,745–2,955 m; F (holo) = *Psila brachylaenoides* DC. var. *brachylaenoides* (DC.) Aristeg., 1964.

Baccharis ptariensis Steyerm., Fieldiana Bot. 28(3): 623. 1953. *J. A. Steyermark 59928*; 7 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 2,410–2,450 m; F (holo) = *Psila brachylaenoides* DC. var. *ligustrina* (DC.) Aristeg., 1964.

Baccharis schomburgkii Baker subsp. *occidentalis* Steyerm. & Maguire, Acta Bot. Venez. 14(3): 25. 1984. *B. Maguire et al. 65567*; 15 Jan. 1981; Venezuela, Dept. Atabapo, Cerra Marahuaca; 2,685 m; VEN (holo), NY.

Baccharis venulosa DC. var. *cuspidibracteata* Steyerm., Fieldiana Bot. 28(3): 624. 1953. *J. A. Steyermark 57298*; 15 July 1944; Venezuela, Táchira, base of Páramo de Tamá; 2,500–2,895 m; F (holo).

Cacalia guatemalensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 99. 1944. *J. A. Steyermark 32823*; Dec. 1939; Guatemala, Dept. Jalapa, summit of Buena Vista, Montaña Miramundo; 2,000–2,200 m; F (holo) = *Psacalium guatemalensis* (Standl. & Steyerm.) Cuatr., 1955, 1976.

Cacalia pinetorum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 142. 1944. *J. A. Steyermark 34933*; 22 Jan. 1940; Guatemala, Dept. Quezaltenango, Volcán Santo Tomás; 3,000–3,200 m; F (holo) = *Psacalium pinetorum* (Standl. & Steyerm.) Cuatr., 1955, 1976.

Cacalia pudica Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 255. 1947. *J. A. Steyermark 48344*; 7 July 1942; Guatemala, Dept. Huehuetenango, Sierra de los Cuchumatanes; 3,400–3,500 m; F (holo) = *Senecio nubivagus* L. Williams, 1975.

Calea clematidifolia Steyerm., Fieldiana Bot. 28(3): 627. 1953. *J. A. Steyermark 59072*; 1 Oct. 1944; Venezuela, Bolívar, Gran Sabana, 1,065–1,220 m; F (holo).

Calea crassifolia Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 256. 1947. *J. A. Steyermark 45627*; 1–2 Apr. 1942; Guatemala, Dept. Alta Verapaz, Cerro Chinajá; 150–700 m; F (holo) = *C. deltophylla* Cowan, 1964.

Calea lucidivenia Gleason & S. F. Blake f. *lanceolata* Steyerm., Fieldiana Bot. 28(3): 628. 1953. *J. A. Steyermark 59408*; 26 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,220 m; F (holo).

Calea oliveri Robinson & Greenman var. *taeniotricha* Steyerm., Fieldiana Bot. 28(3): 628. 1953. *J. A. Steyermark 59403*; 26 Oct. 1944; Venezuela, Bolívar, near

Río Karuai, NW of Mission of Santa Teresita de Kavanayen; 1,220 m; F (holo).

Calea savannarum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 257. 1947. *J. A. Steyermark 38658*; 3 Apr. 1940; Guatemala, Dept. Izabal, between Milla 49.5 and Cristina; 70 m; F (holo) = *Spilanthes uliginosa* Sw., 1976.

Calea standleyi Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 299. 1940. *J. A. Steyermark 37004*; 1 Mar. 1940; Guatemala, Dept. San Marcos, Volcán Tajumulco; 1,300–3,000 m; F (holo) = *Verbesina standleyi* (Steyerm.) D. Nash, 1975.

Cardonaea Aristeg., Maguire & Steyerm., Mem. New York Bot. Gard. 23: 892. 1972, gen. nov.

Cardonaea jauaensis Aristeg., Maguire & Steyerm., Mem. New York Bot. Gard. 23: 892. 1972. *J. A. Steyermark 97945*; 22–27 Mar. 1967; Venezuela, Bolívar, Meseta de Jaua, Cerro Jaua; 1,922–2,100 m; VEN (holo), NY.

Chimantaea Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 428. 1957, gen. nov.

Chimantaea sect. *Cinerea* Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 429. 1957, sect. nov.

Chimantaea acopanensis Steyerm., Ann. Missouri Bot. Gard. 71: 335. 1984. *J. A. Steyermark et al. 129932*; 14–16 Feb. 1984; Venezuela, Bolívar, Piar, Macizo de Chimantá; 1,920 m; VEN (holo).

Chimantaea cinerea (Gleason & S. F. Blake) Maguire, Steyerm. & Wurd. f. *glabra* Steyerm., Ann. Missouri Bot. Gard. 71: 337. 1984. *E. Foldats 7100*; 15 Aug. 1968; Venezuela, Bolívar, Auyan-tepui, lado derecho del Salto Angel; VEN (holo).

Chimantaea eriocephala Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 431. 1957. *J. J. Wurdack 34225*; 26 Jan. 1953; Venezuela, Bolívar, Chimantá Massif, Churi-tepui (Muru-tepui); NY (holo).

Chimantaea espeletoidea Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 433. 1957. *J. A. Steyermark & J. J. Wurdack 574*; 7 Feb. 1955; Venezuela, Bolívar, Chimantá Massif; 1,940 m; F (holo), NY.

Chimantaea huberi Steyerm., Ann. Missouri Bot. Gard. 71: 335. 1984. *J. A. Steyermark et al. 128815*; 2–5 Feb. 1983; Venezuela, Bolívar, Piar, Macizo del Chimantá; 1,850 m; VEN (holo), K, MO (3223158), NY, U, US.

Chimantaea humilis Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 432. 1957. *J. A. Steyermark & J. J. Wurdack 747*; 11 Feb. 1955; Venezuela, Bolívar, Chimantá Massif; 2,120–2,210 m; NY (holo), F.

Chimantea lanocaulis Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 430. 1957. *J. A. Steyermark 75912*; 21–22 June 1953; Venezuela, Bolívar, Chimantá Massif, summit of Apacara-tepui; F (holo), NY.

Chimantaea mirabilis Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 432. 1957. *J. A. Steyermark & J. J. Wurdack 821*; 13 Feb. 1955; Venezuela, Bolívar, Chimantá Massif; 2,120 m; F (holo), NY.

Chimantaea rupicola Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 431. 1957. *J. A. Steyermark & J. J. Wurdack 748*; 11 Feb. 1955; Venezuela, Bolívar, Chimantá Massif; 2,120–2,210 m; F, NY (holo).

Chimantaea similis Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 429. 1957. *J. A. Steyermark & J. J. Wurdack 511*; 5 Feb. 1955; Venezuela, Bolívar, Chimantá Massif; 1,925 m; F, NY (holo).

Chionolaena breweri Steyerm. & Maguire, Acta Bot. Venez. 14(3): 26. 1984. *B. Maguire et al. 65587*; 15 Jan. 1981; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca; 2,685 m; NY, VEN (holo).

Cirsium altissimum (L.) Spreng. f. *moorei* Steyerm., Rhodora 41: 585. 1939. *G. Moore s.n.*; 25 Aug. 1939; U.S.A., Missouri, Laclede Co., Mill Creek; F (holo), MO.

Cirsium nigriceps Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 258. 1947. *J. A. Steyermark 50157*; 6 Aug. 1942; Guatemala, Dept. Huehuetenango, between Tojquiá and Caxin, Sierra de los Cuchumatanes; 3,700 m; F (holo).

Clibadium surinamense L. var. *macrophyllum* Steyerm., Fieldiana Bot. 28(3): 629. 1953. *J. A. Steyermark 62437*; 3 May 1945; Venezuela, Sucre, Cerro Turumiquire; 1,700–1,840 m; F (holo) = *C. surinamense* L., 1964.

Duidaea marahuacensis Steyerm., Brittonia 30: 50. 1978. *S. S. Tillett et al. 752-348*; 2 Feb. 1975; Venezuela, T.F. Amazonas, Cerro Marahuaca; 2,750 m; VEN (holo).

Echinacea pallida Nutt. f. *albida* Steyerm., Rhodora 44: 150. 1942. *J. A. Steyermark 28797*; 4 June 1941; U.S.A., Missouri, St. Francois Co., Koester Springs, limestone glade on top of bluffs along Plattin Creek; F (holo).

Echinacea purpurea (L.) Moench. var. *arkansana* Steyerm., Rhodora 40: 71. 1938. *Brinkley 250*; 19 July 1937; U.S.A., Arkansas, Sevier Co., Boggy Springs; F (holo).

Echinacea purpurea (L.) Moench. f. *liggettii* Steyerm., Rhodora 44: 150. 1942. *W. E. Liggett 1*; 9 July 1940; U.S.A., Missouri, Dallas Co., Hwy. 54, W of Niangua River; F (holo).

Erigeron aquarius Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 301. 1940. *P. C. Standley 65053*; 11 Feb. 1939; Guatemala, Dept. Sacatepéquez, Volcán de Agua, above Santa María de Jesús; 2,250–3,000 m; F (holo).

Erigeron venezuelensis Steyerm., Fieldiana Bot. 28(3): 629. 1953, nom. nov. = *Oritrophium venezuelense* (Steyerm.) Cuatr., 1964

Eupatorium antiquorum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 302. 1940. *P. C. Standley 60304*; 18 Dec. 1938; Guatemala, Dept. Sacatepéquez, near Antiqua; 1,500–1,600 m; F (holo).

Eupatorium benjamin-lincolnii Steyerm., Fieldiana Bot. 28(3): 635. 1953, nom. nov.

Eupatorium carmonis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 303. 1940. *P. C. Standley 63743*; 27 Jan. 1939; Guatemala, Dept. Sacatepéquez, Finca Carmona, hills SE of Antiqua; 1,600–1,800 m; F (holo).

Eupatorium crassicaule Steyerm., Fieldiana Bot. 28(3): 629. 1953. *J. A. Steyermark 57749*; 21 Aug. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 150 m; F (holo).

Eupatorium crocodilium Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 182. 1944. *J. A. Steyermark 51498*; 29 Aug. 1942; Guatemala, Dept. Huehuetenango, Ciénaga de Lagartero, below Miramar; 300 m; F (holo).

Eupatorium cupressorum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 183. 1944. *P. C. Standley 84001*; 19 Jan. 1941; Guatemala, Dept. Totonicapán, along road between San Francisco El Alto and Momostenango; 2,220–3,000 m; F (holo).

Eupatorium harvardianum Steyerm., Fieldiana Bot. 28(3): 636. 1953, nom. nov.

Eupatorium hastiferum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 303. 1940. *P. C. Standley 71125*; 9 Apr. 1939; Guatemala, Dept. Alta Verapaz, E of Tactic, on road to Tamahu; 1,500–1,650 m; F (holo).

Eupatorium huehuetecum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 304. 1940. *P. C. Standley 65798*; 20 Feb. 1939; Guatemala, Dept. Huehuetenango, Río Pucal; 1,775 m; F (holo).

Eupatorium ibaguense Schultz-Bip. var. *indiscretum* Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 425. 1957. *J. J. Wurdack 34112*; 13 Jan. 1953; Venezuela, Bolívar, Chimantá Massif, Sarven-tepui; 1,900–2,050 m; F, NY (holo).

Eupatorium jejunum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 183. 1944. *P. C. Standley 75788*; 30 Oct. 1940; Guatemala, Dept. Jutiapa, El Barrial, E of Jutiapa; 800 m; F (holo).

Eupatorium macram Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 184. 1944. *J. A. Steyermark 31534*; 9 Nov. 1939; Guatemala, Dept. Chiquimula, base of Cerro Colorado along Río Jocotán, near Jocotán; 400 m; F (holo).

Eupatorium mendax Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 185. 1944. *J. A. Steyermark 36341*; 21 Feb. 1940; Guatemala, Dept. San Marcos, along Río Vega, between San Rafael and Mexican border, Volcán Tacaná; 2,500–3,000 m; F (holo) = *E. leucocephalum* Benth., 1976.

Eupatorium mimicum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 186. 1944. *P. C. Standley 85146*; 27 Jan. 1941; Guatemala, Dept. Quezaltenango, region of Las Nubes, S of San Martín Chile Verde; 2,250 m; F (holo).

Eupatorium montigenum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 258. 1947. *J. A. Steyermark 43532*; 5 Feb. 1942; Guatemala, Dept. El Progreso, N of Finca Piamonte, Volcán Santa Luisa; 2,400–3,000 m; F (holo).

Eupatorium ovillum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 305. 1940. *P. C. Standley 65862*; 20 Feb. 1939; Guatemala, Dept. Totonicapán, Cumbre del Aire, on road between Sija and Huehuetenango; 3,000–3,450 m; F (holo).

Eupatorium pharcidodes Robinson var. *sororopanensis* Steyerm., Fieldiana Bot. 28(3): 632. 1953. *J. A. Steyermark 60090*; 13 Nov. 1944; Venezuela, Sororopan-tepui; 2,225–2,255 m; F (holo).

Eupatorium plethadenium Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 186. 1944. *P. C. Standley 61100*; 26 Dec. 1938; Guatemala, Dept. Chimaltenango, region of Santa Elena, Cerro Tecpán; 2,400–2,700 m; F (holo) = *E. semialatum* Benth.

Eupatorium rojasianum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 188. 1944. *P. C. Standley 67221*; 1 Mar. 1939; Guatemala, Dept. Quezaltenango, near El Muro, below Santa María de Jesús; 1,200 m; F (holo).

Eupatorium roupalifolium Robinson f. *latifolium* Steyerm., Fieldiana Bot. 28(3): 633. 1953. *J. A. Steyermark 59505*; 28 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 1,810 m; F (holo) = *E. roupalifolium* Robinson var. *roupalifolium*, 1976.

Eupatorium roupalifolium Robinson var. *subintegrifolium* Steyerm., Fieldiana Bot. 28(3): 636. 1943. *J. A. Steyermark 59865*; 4 Nov. 1944; Venezuela, Bolívar, Ptari-tepui, 2130 m; F (holo) = *E. roupalifolium* Robinson var. *roupalifolium*, 1976.

Eupatorium salinum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 188. 1944. *J. A. Steyermark 31775*; 13 Nov. 1939; Guatemala, Dept. Jutiapa, between RR station of Mita and town of Asunción Mita; 650 m; F (holo) = *E. prunellifolium* H.B.K., 1976.

Eupatorium saxorum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 189. 1944. *J. A. Steyermark 36075*; 19 Feb. 1940; Guatemala, Dept. San Marcos, between Sibinal and summit of Volcán Tacaná; 2,500–4,000 m; F (holo).

Eupatorium stevioides Steyerm., Fieldiana Bot. 28(3): 637. 1953. *J. A. Steyermark 57084*; 7 July 1944; Venezuela, Táchira, Páramo de la Negra; 2,745–3,045 m; F (holo).

Eupatorium symphyopappus Steyerm., Fieldiana Bot. 28(3): 636. 1953, nom. nov.

Eupatorium tepuianum Steyerm., Fieldiana Bot. 28(3): 638. 1953. *J. A. Steyermark 59504*; 29 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 1,810 m; F (holo).

Eupatorium vetularum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 190. 1944. *P. C. Standley 84404*; 23 Jan. 1941; Guatemala, Dept. Totonicapán, region of Chiu Jolom, mountains above Totonicapán; 2,800–3,100 m; F (holo) = *E. caeciliae* Rob., 1976.

Eupatorium zunilanum Standl. & Steyerm., Field Mus. Nat. Hist., Bot Ser. 23(4): 191. 1944. *J. A. Steyermark 34744*; 22 Jan. 1940; Guatemala, Dept. Quezaltenango, Volcán Zunil; 2,500–3,800 m; F (holo).

Gnaphalium caeruleocanum Steyerm., Fieldiana Bot. 28(3): 639. 1953. *J. A. Steyermark 62573*; 6 May 1945; Venezuela, Sucre, Cerro Turumiquire; 2,200–2,500 m; F (holo).

Gnaphalium standleyi Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 99. 1944. *P. C. Standley 81097*; 28 Dec. 1940; Guatemala, Dept. Huehuetenango, region of Chemal, Sierra de los Cuchumatanes; 3,300 m; F (holo).

Gongylolepis fruticosa Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 437. 1957. *J. A. Steyermark & J. J. Wurdack 1136*; 26 Feb. 1955; Venezuela, Bolívar, Chimantá Massif, Agparaman-tepui; 1,880–1,955 m; F, NY (holo).

Gongylolepis terramarae Steyerm., Ann. Missouri Bot. Gard. 74: 115. 1987. *J. A. Steyermark & B. K. Holst 130629*; 24 Feb. 1985; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca; 1,220–1,350 m; MO (holo), VEN.

Grindelia acutifolia Steyerm., Ann. Missouri Bot. Gard. 21: 498. 1934. *E. O. Wooton s.n.*; 16 Aug. 1910; U.S.A., New Mexico. Johnson's Mesa; US (holo).

Grindelia aggregata Steyerm., Ann Missouri Bot. Gard. 21: 566. 1934. *J. W. Congdon s.n.*; 27 Aug. 1902; Canada, British Columbia, Victoria; MO (holo).

Grindelia arenicola Steyerm., Ann. Missouri Bot. Gard. 21: 229. 1934. *J. T. Howell 5473*; 14 Sep. 1930; U.S.A., California, Mendocino Co., Mendocino county plain, 4.5 mi. N of Ft. Bragg; CAS (holo), GH, MO, UC.

Grindelia arenicola Steyerm. var. *pachyphylla* Steyerm., Ann. Missouri Bot. Gard. 21: 596. 1934. *J. T. Howell 8106*; 27 Sep. 1931; U.S.A., California, Mendocino Co., 6 mi. S of Point Arena; CAS (holo), GH, MO.

Grindelia arenicola Steyerm. f. *trichophora* Steyerm., Ann. Missouri Bot. Gard. 21: 596. 1934. *W. F. Schmitt*

s.n.; 1913; U.S.A., California, San Mateo Co., Half-moon Bay; US (holo).

Grindelia arizonica A. Gray var. *dentata* Steyerm., Ann. Missouri Bot. Gard. 21: 508. 1934. *O. B. Metcalfe 744*; 19 Sep. 1903; U.S.A., New Mexico, Bear Mt., near Silver City; GH, MO, MINN, ND-G, NY, RM, US (holo).

Grindelia arizonica A. Gray var. *microphylla* Steyerm., Ann. Missouri Bot. Gard. 21: 508. 1934. *A. Davidson 736 (96)* ; 7 Sep. 1902; U.S.A., Arizona, along San Franciso River, 10 mi. N of Clifton; GH (holo), PH, RM, UC.

Grindelia arizonica A. Gray var. *stenophylla* Steyerm., Ann. Missouri Bot. Gard. 21: 507. 1934. *E. O. Wooton 2568*; 12 Aug. 1904; U.S.A., Colorado, near Bayfield; US (holo).

Grindelia blakei Steyerm., Ann. Missouri Bot. Gard. 21: 567. 1934. *J. A. Moore & J. A. Steyermark 3686*; 9 Aug. 1931; U.S.A., California, Humboldt Co., Eureka; MO (holo).

Grindelia camporum E. Greene var. *abbreviata* Steyerm., Ann. Missouri Bot. Gard. 21: 228. 1934. *Hoffman s.n.*; 23 Sep. 1927; U.S.A., California, Los Angeles Co., Lancaster; SBBG (holo).

Grindelia camporum E. Greene var. *australis* Steyerm., Ann. Missouri Bot. Gard. 21: 228. 1934. *P. A. Munz & I. M. Johnston 11157*; 4 Sep. 1928; U.S.A., California, Los Angeles Co., 3 mi. E of Elizabeth Lake; RSA (holo).

Grindelia camporum E. Greene var. *interioris* (Jepson) Steyerm. f. *foliacea* Steyerm., Ann. Missouri Bot. Gard. 21: 538. 1934. *J. T. Howell 5201*; 30 May 1930; U.S.A., California, Solano Co., 1 mi. from Vacaville on road to Elmira; CAS (holo), GH, RSA.

Grindelia camporum E. Greene var. *parviflora* Steyerm., Ann. Missouri Bot. Gard. 21: 534. 1934. *J. T. Howell 5496*; 28 Sep. 1930; U.S.A., California, Contra Costa County, Liberty School on Marsh Creek Road; CAS (holo), MO (1015935).

Grindelia confusa Steyerm., Field Mus. Nat. Hist., Bot. Ser. 17(5): 442. 1938. *H. LeSueur 1016*; 17 Aug. 1936; Mexico, Chihuahua, Namiquipa plains; F (holo).

Grindelia greenei Steyerm., Ann. Missouri Bot. Gard. 21: 517. 1934. *C. R. Orcutt 1204*; 1924; Mexico, Nuevo León, Monterey; US (holo).

Grindelia greenmanii Steyerm., Ann. Missouri Bot. Gard. 21: 460. 1934. *E. Palmer 471*; 10–13 July 1880; Mexico, Coahuila, Lerios; GH (holo), PA, US.

Grindelia hallii Steyerm., Ann. Missouri Bot. Gard. 21: 229. 1934. *L. R. Abrams 3957*; 30 June 1903; U.S.A., California, San Diego Co., Cuyamaca Lake; F, GH, MO (130219), NY (holo), RSA.

Grindelia havardii Steyerm., Ann. Missouri Bot. Gard. 21: 474. 1934. *J. A. Moore & J. A. Steyermark 3607*; 23 July 1931; U.S.A., Texas, Culberson Co., near mouth of Mckittrick Canyon, Guadalupe Mts.; MO (holo).

Grindelia hirsutula Hook. & Arn. var. *brevisquama* Steyerm., Ann. Missouri Bot. Gard. 21: 572. 1934. *J. T. Howell 5338*; 13 July 1930; U.S.A., California, Sonoma Co., Black Point Road; CAS (holo), UC.

Grindelia hirsutula Hook. & Arn. var. *brevisquama* Steyerm. f. *glabrata* Steyerm., Ann. Missouri Bot. Gard. 21: 573. 1934. *J. T. Howell 5221*; 8 June 1930; U.S.A., California, Sonoma Co., 8 mi. W of Petaluma, on Bodega Road; CAS, GH, MO (holo—1016008), RSA = *G. hirsutula* Hook. & Arn. var. *hirsutula*.

Grindelia hirsutula Hook. & Arn. var. *brevisquama* Steyerm. f. *pedunculoides* Steyerm., Ann. Missouri Bot. Gard. 21: 574. 1934. *A. Eastwood s.n.*; 7 May 1900; U.S.A., California, Calistoga; GH, UC (holo).

Grindelia hirsutula Hook. & Arn. var. *brevisquama* Steyerm. f. *tomentulosa* Steyerm., Ann. Missouri Bot. Gard. 21: 574. 1934. *W. Suksdorf 279*; 23 June 1913; U.S.A., California, San Mateo Co., Crystal Springs Lake; MO (holo—850778) = *G. hirsutula* Hook. & Arn. var. *hirsutula*, 1981.

Grindelia hirsutula Hook. & Arn. f. *cacumena* Steyerm., Ann. Missouri Bot. Gard. 21: 571. 1934. *H. N. Bolander 389*; 1866; U.S.A., California, Oakland Hills; NY, US (holo).

Grindelia hirsutula Hook. & Arn. var. *calva* Steyerm., Ann. Missouri Bot. Gard. 21: 575. 1934. *F. E. Roadhouse 65*; Spring 1905; U.S.A., California, San Luis Obispo Co., San Luis Obispo; UC (holo).

Grindelia hirsutula Hook. & Arn. var. *subintegra* Steyerm., Ann. Missouri Bot. Gard. 21: 229. 1934. *J. T. Howell 11414*; 1 July 1933; U.S.A., California, Ventura Co., 2 mi. E of Ojai; CAS, MO (holo—1044105).

Grindelia howellii Steyerm., Ann. Missouri Bot. Gard. 21: 549. 1934. *L. F. Henderson 2791*; 10 Aug. 1894; U.S.A., Idaho, Kootenai Co., St. Maries River; GH (holo), RM, US.

Grindelia humilis Hook. & Arn. f. *pubescens* Steyerm., Ann. Missouri Bot. Gard. 21: 527. 1934. *J. T. Howell 10805*; 8 Oct. 1932; U.S.A., California, Napa Co., Cuttings Wharf, on Napa River; CAS (holo), MO (1028961).

Grindelia humilis Hook. & Arn. f. *reflexa* Steyerm., Ann. Missouri Bot. Gard. 21: 526. 1934. *E. L. Greene s.n.*; 15 Nov. 1883; U.S.A., California, Oakland; depository not indicated.

Grindelia inornata E. Greene var. *angusta* Steyerm., Ann. Missouri Bot. Gard. 21: 496. 1934. *H. L. Shantz 597*; 1903; U.S.A., Colorado, Colorado Springs; US (holo).

Grindelia integrifolia DC. f. *dentata* Steyerm., Ann. Missouri Bot. Gard. 21: 551. 1934. *J. C. Nelson 1670*; 14 July 1917; U.S.A., Oregon, Salem; GH (holo).

Grindelia integrifolia DC. var. *virgata* (Nutt.) T. & G. f. *villosa* Steyerm., Ann. Missouri Bot. Gard. 21: 553. 1934. *E. Hall 266*; 1871; U.S.A., Oregon; F, GH, MO (holo—130132 & 130036), NY, US.

Grindelia lanceolata Nutt. f. *latifolia* Steyerm., Ann. Missouri Bot. Gard. 21: 515. 1934. *W. Trelease s.n.*; 11 Sep. 1898; U.S.A., Missouri, Stone Co., Marble Cave; MO (holo).

Grindelia littoralis Steyerm., Ann. Missouri Bot. Gard. 21: 516. 1934. *Joor s.n.*; 20 Sep. 1884; U.S.A., Texas, Evergreen, Galveston Bay; MO (holo).

Grindelia maritima (E. Greene) Steyerm. f. *anomala* Steyerm., Ann. Missouri Bot. Gard. 21: 578. 1934. *J. T. Howell 11658*; 15 Sep. 1933; U.S.A., California, San Franciso, Laguna Honda; CAS, MO (holo).

Grindelia microcephala DC. var. *adenodonta* Steyerm., Ann. Missouri Bot. Gard. 21: 467. 1934. *F. Lindheimer 255*; July–Aug. 1844; U.S.A., Texas, 39 mi. W of San Felipe; CAL, G, MO (holo), PA.

Grindelia microcephala DC. var. *adenodonta* Steyerm. f. *angustior* Steyerm., Ann. Missouri Bot. Gard. 21: 469. 1934. *E. J. Palmer 33590*; 28 Apr. 1928; U.S.A., Texas, Uvalde Co., near Uvalde; MO (holo), NY.

Grindelia microcephala DC. var. *montana* Steyerm., Ann. Missouri Bot. Gard. 21: 470. 1934. *L. C. Smith*

135; 13 Aug. 1894; Mexico, Oaxaca, San Juan del Estado; GH (holo).

Grindelia microcephala DC. var. *pusilla* Steyerm., Ann. Missouri Bot. Gard. 21: 467. 1934. *E. Palmer 469*; 27–28 Jan. 1880; U.S.A., Texas, between the Frio and the Nueces Rivers, on the road to Laredo; GH (holo), MO, NY, US.

Grindelia nana Nutt. var. *altissima* Steyerm., Ann. Missouri Bot. Gard. 21: 244. 1934. *J. P. Tracy 4669*; 12 Sep. 1915; U.S.A., California, Humboldt Co., Eel River, at mouth of Laribee Creek; UC (holo), US.

Grindelia nana Nutt. var. *altissima* Steyerm. f. *puberula* Steyerm., Ann. Missouri Bot. Gard. 21: 545. 1934. *J. W. Blankinship s.n.*; 12 June 1924; U.S.A., California, Lake Co., Kelseyville; CAS (holo).

Grindelia nana Nutt. f. *longisquama* Steyerm., Ann. Missouri Bot. Gard. 21: 543. 1934. *Rev. Spalding s.n.*; n.d.; U.S.A., Idaho, near Clearwater (formerly in Oregon); GH (holo), NY.

Grindelia nana Nutt. var. *turbinella* Steyerm., Ann. Missouri Bot. Gard. 21: 545. 1934. *A. A. Heller 12579*; 7 Sep. 1917; U.S.A., California, Siskiyou County, Shasta Valley, 10 mi. S of Gazelle; CAS, GH (holo), MO (824996), NY, UC, US = *G. nana* Nutt. var. *nana*.

Grindelia nelsonii Steyerm., Ann. Missouri Bot. Gard. 21: 463. 1934. *E. W. Nelson 6864*; 8–12 Feb. 1903; Mexico, Michoacán, Los Reyes; GH, NY, US (holo).

Grindelia oxylepis E. Greene var. *capitellata* Steyerm., Ann. Missouri Bot. Gard. 21: 490. 1934. *E. Palmer 520*; 21–23 Oct. 1898; Mexico, Durango, Mapimí; GH (holo), MO, NY, UC, US.

Grindelia oxylepis E. Greene var. *eliqulata* Steyerm., Ann. Missouri Bot. Gard. 21: 490. 1934. *E. Palmer 316*; Sep. 1898; Mexico, Coahuila, Saltillo; GH (holo), MO, NY, UC, US.

Grindelia palmeri Steyerm., Ann. Missouri Bot. Gard. 21: 471. 1934. *E. Palmer 163*; 28 Sep.–3 Oct. 1902; Mexico, San Luis Potosí, Alvarez; GH, MO, NY, US (holo).

Grindelia revoluta Steyerm., Ann. Missouri Bot. Gard. 21: 496. 1934. *J. A. Moore & J. A. Steyermark 3784*; 30 Aug. 1931; U.S.A., Colorado, El Paso Co., 14 mi. S from Colorado Springs; MO (holo).

Grindelia robinsonii Steyerm., Ann. Missouri Bot. Gard. 21: 459. 1934. *C. A. Purpus 5722*; July 1911; Mexico, San Luis Potosí, Agua del Medio; GH, MO, NY, US (holo).

Grindelia rubricaulis DC. var. *elata* Steyerm., Ann. Missouri Bot. Gard. 21: 227. 1934. *J. T. Howell 6574*; 29 May 1931; U.S.A., California, Ventura Co., 7 mi. SW of Simi; CAS (holo), MO.

Grindelia rubricaulis DC. var. *latifolia* (Kell.) Steyerm. f. *minor* Steyerm., Ann. Missouri Bot. Gard. 21: 589. 1934. *A. Eastwood 794*; 13 June–3 July 1906; U.S.A., California, Casmailia; CAS, GH (holo), US.

Grindelia rubricaulis DC. var. *latifolia* (Kell.) Steyerm. f. *pubescens* Steyerm., Ann. Missouri Bot. Gard. 21: 589. 1934. *K. Brandegee s.n.*; 14 June 1909; U.S.A., California, Monterey Co., between Lucia and Little's Hot Springs; UC (holo).

Grindelia rubricaulis DC. var. *latifolia* (Kell.) Steyerm. f. *villosa* Steyerm., Ann. Missouri Bot. Gard. 21: 590. 1934. *C. P. Smith 1016*; 10 July 1905; U.S.A., California, Monterey Co., Pacific Grove, coast above Chinatown Point; GH (holo).

Grindelia rubricaulis DC. var. *permixta* Steyerm., Ann. Missouri Bot. Gard. 21: 582. 1934. *J. T. Howell 4352*; 22 July 1929; U.S.A., California, Alameda Co., San Leandro; CAS (holo).

Grindelia squarrosa (Pursh) Dunal f. *depressa* Steyerm., Ann. Missouri Bot. Gard. 21: 480. 1934. *J. A. Moore & J. A. Steyermark 3768*; 23 Aug. 1931; U.S.A., Utah, Salt Lake Co., 5 mi. W of Salt Lake City; depository not designated.

Grindelia squarrosa (Pursh) Dunal var. *nuda* (Wood) A. Gray f. *angustior* Steyerm., Ann. Missouri Bot. Gard. 21: 481. 1934. *R. Ferris & T. Duncan 3391*; 23 Aug. 1921; U.S.A., Texas, Floyd Co., 16 mi. E of Sockney on Quitaque Road; CAS, MO (holo), NY.

Grindelia stricta DC. var. *aestuarina* Steyerm., Ann. Missouri Bot. Gard. 21: 560. 1934. *J. M. Grant s.n.*; June 1928; U.S.A., Washington, Marysville; RM (holo).

Grindelia stricta DC. var. *aestuarina* Steyerm. f. *elongata* Steyerm., Ann. Missouri Bot. Gard. 21: 560. 1934. *J. T. Howell 7545*; 27 July 1931; Canada, British Columbia, Vancouver Island, Arm of Victoria Harbor 3 mi. from Victoria on Island Hwy.; CAS (holo), MO (1016655).

Grindelia stricta DC. var. *procumbens* Steyerm., Ann. Missouri Bot. Gard. 21: 559. 1934. *J. A. Moore & J. A. Steyermark 3687*; 9 Aug. 1931; U.S.A., California, Humboldt Co., 10 mi. N of Trinidad; MO (holo).

Grindelia sublanuginosa Steyerm., Ann. Missouri Bot. Gard. 21: 458. 1934. *E. W. Nelson 6523*; 5 Jan. 1903; Mexico, Jalisco, near Lake Chapala; NY, US (holo).

Grindelia tenella Steyerm., Ann. Missouri Bot. Gard. 21: 464. 1934. *Berlandier 766 (2186)*; Nov. 1830; Mexico, Tamaulipas, from Victoria to Tula; GH (holo), NY.

Helianthus mollis Lam. f. *flavida* Steyerm.; Rhodora 55: 108. 1953. *J. A. Steyermark 70126*; 21 Aug. 1950; U.S.A., Missouri, Shelby Co., route 36, 4.4 mi. NW of western limit of Lentner; F (holo).

Hieracium clivorum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 259. 1947. *J. A. Steyermark 50065*; 4 Aug. 1942; Guatemala, Dept. Huehuetenango, above San Juan Ixcoy, Sierra de los Cuchumatanes; 2,400 m; F (holo).

Hieracium culmenicola Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 100. 1944. *J. A. Steyermark 34815*; 22 Jan. 1940; Guatemala, Dept. Quezaltenango, Volcán Santo Tomás; 3,000–3,200 m; F (holo) = *H. guatemalense* Standl. & Steyerm., 1976.

Hieracium frigidum Wedd. f. *tamaense* Steyerm., Fieldiana Bot. 28(3): 641. 1953. *J. A. Steyermark 57215*; 14 July 1944; Venezuela, Táchira, Paramito between Quebrada de Palmar and Quebrada de Paramito, base of Páramo de Tamá; 2,500 m; F (holo).

Hieracium guatemalense Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 101. 1944. *J. A. Steyermark 34860*; 22 Jan. 1940; Guatemala, Dept. Quezaltenango, Volcán Zunil; 3,000–3,800 m; F (holo).

Hieracium jalapense Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 102. 1944. *J. A. Steyermark 32767*; 5 Dec. 1939; Guatemala, Dept. Jalapa, between Miramundo and summit of Montaña Miramundo; 2,000–2,500 m; F (holo) = *H. irazuense* Benth., 1976.

Hieracium minarum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 103. 1944. *J. A. Steyermark 29722*; 11 Oct. 1939; Guatemala, Dept. Zacapa, Sierra de las Minas; 1,000–1,500 m; F (holo) = *H. gronovii* L., 1976.

Hieracium ostreophyllum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 104. 1944. *J. A. Steyer-*

mark 36690; Feb. 1940; Guatemala, Dept. San Marcos, 6 mi. SW of Tajumulco, NW Volcán Tajumulco; 2,300–2,800 m; F (holo) = *H. fendleri* subsp. *ostreophyllum* (Standl. & Steyerm.) Beaman, 1975.

Hieracium tacanense Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 104. 1944. *J. A. Steyermark 36128*; 19 Feb. 1940; Guatemala, Dept. San Marcos, Between Sibinal and summit of Volcán Tacaná; 2,500–4,400 m; F (holo) = *H. irazuense* Benth., 1976.

Hymenostephium viride Steyerm., Fieldiana Bot. 28(3): 641. 1953. *J. A. Steyermark 57063*; 7 July 1944; Venezuela, Mérida, Dove Tovar; 2,975 m; F (holo).

Jungia guatemalensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 142. 1944. *H. von Tuerckheim 8410*; Mar. 1903; Guatemala, Dept. Alta Verapaz, Tactic; 1,800 m; F (holo).

Jungia reticulata Steyerm., Fieldiana Bot. 28(3): 642. 1953. *J. A. Steyermark 57310*; 15 July 1944; Venezuela, Táchira, base of Páramo de Tamá; 2,500–2,895 m; F (holo).

Laphamia quinqueflora Steyerm., Ann. Missouri Bot. Gard. 19: 392. 1932. *J. A. Moore & J. A. Steyermark 3547*; 20 July 1931; U.S.A., Texas, Culberson Co., Guadalupe Mountains, Lower McKittrick Canyon; GH (holo) = *Perityle quinqueflora* (Steyerm.) Shinners, 1981.

Liabum tajumulcense Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 27. 1943. *J. A. Steyermark 36543*; Feb. 1940; Guatemala, Dept. San Marcos, SW of Tajumulco, NW Volcán Tajumulco; 2,300–2,500 m; F (holo).

Liatris cylindracea Michx. f. *bartelli* Steyerm., Rhodora 59: 23. 1957. *K. E. Bartel s.n.*; 13 Aug. 1955; U.S.A., Indiana, Lake Co., lake sand along side road, Clark Road, NW of Gary; F (holo).

Lucilia venezuelensis Steyerm., Fieldiana Bot. 28(3): 644. 1953. *J. A. Steyermark 55657*; 13 Mar. 1944; Venezuela, Mérida, upper headwaters of Río Tormero, below El Aguila and above Chachopo; 3,650–3,965 m; F (holo).

Mikania auyantepuensis S. F. Blake var. *brevipedicellata* Steyerm., Fieldiana Bot. 28(3): 648. 1953. *J. A. Steyermark 58125*; 31 Aug. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,675 m; F (holo).

Mikania concinna Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 260. 1947. *J. A. Steyermark 43292*; 26 Jan. 1942; Guatemala, Dept. Zacapa, Sierra de las Minas, Volcán Gemelos; 3,000 m; F (holo).

Mikania guatemalensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 105. 1944. *C. C. Deam 40*; 25 Feb. 1905; Guatemala, Dept. Izabal, Puerto Barrios, sea level; F (holo) = *M. houstonia* var. *guatemalensis* (Standl. & Steyerm.) L. Williams, 1975.

Mikania hookeriana DC. var. *crassicaulis* Steyerm., Fieldiana Bot. 28(3): 658. 1953. *J. A. Steyermark 60015*; 10–11 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,585–1,600 m; F (holo).

Mikania huitzensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5); 260. 1947. *J. A. Steyermark 48662*; 14 July 1942; Guatemala, Dept. Huehuetenango, Sierra de los Cuchumatanes, Cerro Huitz; 1,500 2,600 m; F (holo) = *M. cordifolia* (L.f.) Willd., 1976.

Mikania lucida S. F. Blake f. *hirticaulis* Steyerm., Fieldiana Bot. 28(3): 659. 1953. *J. A. Steyermark 60735*; 28 Nov. 1944; Venezuela, Bolívar, Sororopan-tepui; 1,200 m; F (holo).

Mikania marahuacensis Steyerm. & Maguire, Acta Bot. Venez. 14(3): 28. 1984. *B. Maguire et al. 65616*; 15 Jan. 1981; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca; 2,685 m; VEN (holo), NY.

Mikania michelangeliana Steyerm., Ann. Missouri Bot. Gard. 71: 339. 1984. *J. A. Steyermark 129456*; 10 Oct. 1983; Venezuela, T.F. Amazonas, Cerro Marahuaca; 2,560 m; VEN (holo).

Mikania petrina Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5); 261. 1947. *J. A. Steyermark 47257*; 7 June 1942; Guatemala, Dept. Sololá, Volcán San Pedro, Lago de Atilan, above San Pedro; 2,500–2,800 m; F (holo).

Mikania phelpsii Maguire & Steyerm., Brittonia 7: 89. 1950. *J. A. Steyermark 59527*; 30 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 1,810–2,100 m; F (holo) = *M. lucida* S. F. Blake, 1939, 1964.

Mikania robinsoniana Steyerm., Fieldiana Bot. 28(3): 660. 1953, nom. nov. = *M. nigropunctata* var. *cryptodonta* Robinson, 1964.

Mikania stictophora Steyerm., Fieldiana Bot. 28(3): 660. 1953. *J. A. Steyermark 59860*; 4 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 2,130 m; F (holo) = *M. sprucei* Baker, 1964.

Oliganthes roraimensis Steyerm., Fieldiana Bot. 28(3): 662. 1953. *J. A. Steyermark 58678*; 25 Sep. 1944; Venezuela, Bolívar, Mt. Roraima; 2,040 m; F (holo) = *Pollalesta roraimensis* (Steyerm.) Aristeg., 1964.

Oritropium marahuacense Steyerm. & Maguire, Acta Bot. Venez. 14(3): 28. 1984. *J. A. Steyermark et al. 125925*; 31 Jan. 1982; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca; 2,580 m; NY, VEN (holo).

Oyedaea blakeana Steyerm., Fieldiana Bot. 28(3): 663. 1953. *J. A. Steyermark 58047*; 16 Aug. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,095–1,520 m; F (holo).

Oyedaea verbesinoides DC. var. *glabrior* Steyerm., Fieldiana Bot. 28(3): 664. 1953. *J. A. Steyermark 61612*; 20 Mar. 1945; Venezuela, Anzoátegui, Cerro Peonia; 1,800–2,000 m; F (holo).

Oyedaea verbesinoides DC. var. *hypomalaca* Steyerm., Fieldiana Bot. 28(3): 664. 1953. *J. A. Steyermark 62095*; 15 Apr. 1945; Venezuela, Monagas, Cerro Negro; 1,500–2,180 m; F (holo).

Pectis flava Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 106. 1944. *J. A. Steyermark 30415*; 24 Oct. 1939; Guatemala, Dept. Jutiapa, along railroad between Agua Blanca and Amatillo; 950–990 m; F (holo) = *P. uniaristata* DC. var. *holostemma* A. Gray, 1976.

Pectis venezuelensis Steyerm., Fieldiana Bot. 28(3): 666. 1953. *J. A. Steyermark 57528*; 31 July 1944; Venezuela, Bolívar, 5 km W of Upata; 500 m; F (holo).

Perymenium inamoenum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 143. 1944. *J. A. Steyermark 29737*; Oct. 1939; Guatemala, Dept. Zacapa, Sierra de las Minas, Finca Alejandria; 1,000–1,500 m; F (holo).

Perymenium jalapanum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 144. 1944. *J. A. Steyermark 32658*; Guatemala, Dept. Jalapa, between Muramundo and summit of Montaña Miramundo; 2,000–2,300 m; F (holo).

Piptocarpha jauaensis Aristeg. & Steyerm., Bol. Soc. Venez. Ci. Nat. 32: 402. 1976. *J. A. Steyermark et al. 109485*; 22–28 Feb. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Jaua; 1,800 m; F (holo).

Polymnia meridensis Steyerm., Fieldiana Bot. 28(3): 667. 1953. *J. A. Steyermark 57519*; 22 July 1944; Venezuela, Mérida, below Chachopo; 3,045 m; F (holo).

Polymnia standleyi Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 106. 1944. *J. A. Steyermark 36181*; 20 Feb. 1940; Guatemala, Dept. San Marcos, between La Vega Ridge along Río Vega, Volcán Tacaná; 2,500–3,000 m; F (holo) = *Rumfordia standleyi* (Steyerm.) Standl. & Steyerm., 1947.

Polymnia verapazensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 144. 1944. *H. von Tuerckheim II.1732*; Apr. 1907; Guatemala, Dept. Baja Verapaz, Pansal; 1,000 m; F (holo) = *Rumfordia guatemalensis* (Coult.) S. F. Blake, 1976.

Quelchia bracteata Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 435. 1957. *J. A. Steyermark & J. J. Wurdack 683*; 9 Feb. 1955; Venezuela, Bolívar, Chimantá Massif; 1,970 m; NY (holo), F.

Quelchia cardonae Steyerm., Fieldiana Bot. 28(3): 670. 1953. *F. Cardona 2288*; Oct. 1947; Venezuela, Bolívar, Cerro Acopan, Río Caroni; 2,200 m; F (holo).

Quelchia eriocaulis Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 435. 1957. *J. A. Steyermark & J. J. Wurdack 675*; 9 Feb. 1955; Venezuela, Bolívar, Chimantá Massif, Torono-tepui; 2,165–2,180 m; F (holo), NY.

Quelchia ×*grandifolia* Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 436. 1957. *J. A. Steyermark & J. J. Wurdack 756*; 12 Feb. 1955; Venezuela, Bolívar, Chimantá Massif; 2,185 m; F (holo).

Rojasianthe Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 411. 1940, gen. nov.

Rojasianthe superba Standl. & Steyerm., Field Mus. Nat. Hist., Bot Ser. 22(4): 315. 1940. *J. A. Steyermark 35835*; 16 Feb. 1940; Guatemala, Dept. San Marcos, Volcán Tajumulco; 3,300–3,900 m; F (holo).

Rudbeckia hirta L. f. *homochroma* Steyerm., Rhodora 40: 179. 1938. *J. A. Steyermark 11345*; 3 July 1936; U.S.A., Missouri, Oregon Co., 10 mi. W of New Liberty, Fristoe Purchase Unit, Clark National Forest; MO (holo).

Sabazia urticifolia (H.B.K.) DC. var. *venezuelensis* Steyerm., Fieldiana Bot. 28(3): 672. 1953. *J. A. Steyermark 55379*; 8 Feb. 1944; Venezuela, Lara, between Santo Domingo and Los Quebraditos, above Humocaro Bajo; 2,430–2,475 m; F (holo).

Salmea orthocephala Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 145. 1944. *P. C. Standley 59321*; 8 Dec. 1938; Guatemala, Dept. Guatemala, Concuá Bridge over Río Motagua; 300 m; F (holo).

Schaetzellia standleyi Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 107. 1944. *J. A. Steyermark 32041*; 26 Nov. 1939; Guatemala, Dept. Jutiapa, Laguna Retzana; 600 m; F (holo) = *Macvaughiella standleyi* (Steyerm.) King & Robs., 1976.

Schkuhria viscosissima Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 318. 1940. *P. C. Standley 62513*; 12–14 Jan. 1939; Guatemala, Dept. Quiché, near Sacapulas; 1,040–1,240 m; F (holo) = *Florestina pedata* (Cav.) Cassini, 1976.

Siegesbeckia nudicaulis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 262. 1947. *J. A. Steyermark 50114*; 5 Aug. 1942; Guatemala, Dept. Huehuetenango, Sierra de los Cuchumatanes, above San Juan Ixcoy; 2,800–3,400 m; F (holo).

Silphium perfoliatum L. f. *petiolatum* Palmer & Steyerm., Brittonia 10: 119. 1958. *J. A. Steyermark 80474*; 19 Oct. 1955; U.S.A., Missouri, Stone Co., above White River, along S and E side at base of N and NW facing wooded slopes, NE and SW of Mill Creek, 4 air mi. SW of Radical, 4.5–5 mi. NE of Baxter; F (holo).

Silphium terebinthinaceum Jacq. var. *lucy-brauniae* Steyerm., Rhodora 53: 134. 1951. *E. L. Braun s.n.*; 17 Aug. 1950; U.S.A., Ohio, Adams Co., 2.5 mi. N of Ohio route 348, N part of Jefferson Top, SE of Scrub Ridge; Herb. Braun (holo).

Soliva anthemidifolia R. Br. var. *lanuginosa* Steyerm., Fieldiana Bot. 28(3): 672. 1953. *J. A. Steyermark 55506*; 12 Feb. 1944; Venezuela, Lara, between Buenos Aires to Canyon of El Callado; 2,285–2,740 m; F (holo).

Stenopadus affinis Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 427. 1957. *J. A. Steyermark 75110*; 18 Apr. 1953; Venezuela, Bolívar, Chimantá Massif, Abacapa-tepui; 850–1,100 m; F (holo), NY.

Stenopadus chimantensis Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 1957. *J. A. Steyermark & J. J. Wurdack 652*; 9 Feb. 1955; Venezuela, Bolívar, Chimantá Massif, Torono-tepui; 2,165–2,180 m; NY (holo), F.

Stenopadus colombianus Cuatr. & Steyerm., Bot. Mus. Leafl. 17(3): 99. 1955. *R. E. Schultes & I. Cabrera 15031*; 23–25 Jan. 1952; Colombia, Comisaria del Vaupés, Río Kananari, Cerro Isibukuri, near summit; F (holo).

Stenopadus talaumifolius S. F. Blake var. *magnifolius* Steyerm., Fieldiana Bot. 28(3): 673. 1953. *F. Cardona 2190*; Sep. 1947; Venezuela, Bolívar, Cerro Arepuchi; 600 m; US (holo).

Stevia chortiana Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 108. 1944. *J. A. Steyermark 30866*; Oct. 1939; Guatemala, Dept. Chiquimula, between Finca San Jose and Montaña Nube; 1,200–1,700 m; F (holo) = *S. hirsuta* var. *chortiana* (Standl. & Steyerm.) Grashoff, 1974.

Stevia vulcanicola Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 27. 1943. *J. A. Steyermark 34757*; Jan. 1940; Guatemala, Dept. Quezaltenango, Volcán Santo Tomás; 2,500–3,700 m; F (holo) = *S. microchaeta* Schultz-Bip., 1976.

Stomatochaeta colveei Steyerm., Brittonia 32: 21. 1980. *J. A. Steyermark et al. 117407*; 26 May 1978; Venezuela, Bolívar, Cerro Guaiquinima; VEN (holo).

Tagetes sororia Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 146. 1944. *P. C. Standley 85228*; 29 Jan. 1941; Guatemala, Dept. Quezaltenango, N of Olintepeque; 2,500–2,800 m; F (holo) = *T. nelsonii* Greenm., 1976.

Trixis amphimalaca Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 147. 1944. *P. C. Standley 82538*; 6 Jan. 1941; Guatemala, Dept. Huehuetenango, N of Chiantla; 2,000–2,250 m; F (holo) = *T. nelsonii* Greenm., 1976.

Verbesina agricolarum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 319. 1940. *J. R. Johnston 1026*; 21 Sep. 1937; Guatemala, Dept. Chimaltenango, Finca La Alameda; F (holo).

Verbesina angusta Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 9(3): 426. 1957. *J. A. Steyermark & J. J. Wurdack 851*; 13 Feb. 1955; Venezuela, Bolívar, Chimantá Massif; 2,120 m; F, NY (holo).

Verbesina apleura S. F. Blake var. *foliolata* Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 109.

1944. *P. C. Standley 67540*; Mar. 1939; Guatemala, Dept. Quezaltenango, Volcán Santa María; 2,700 m; F (holo) = *V. apleura* S. F. Blake var. *apleura*, 1976.

Verbesina blakeana Steyerm., Fieldiana Bot. 28(3): 674. 1953. *J. A. Steyermark 56300*; 4 May 1944; Venezuela, Mérida, between Mucutuy and Mucuchachi; 1,065–2,430 m; F (holo).

Verbesina calciphila Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 262. 1947. *J. A. Steyermark 50132*; 6 Aug. 1942; Guatemala, Dept. Huehuetenango, Sierra de los Cuchumatanes; 3,700 m; F (holo).

Verbesina exalata Steyerm., Fieldiana Bot. 28(3): 675. 1953. *J. A. Steyermark 55176*; 5 Jan. 1944; Venezuela, Distr. Federal, above Caracas, Cordillera del Avila; 1,065–1,520 m; F (holo) = *V. turbacensis* H.B.K., 1964.

Verbesina guatemalensis Robinson & Greenmann var. *glabrata* Standl. & Steyerm., Field Mus. Bot. Ser. 23(2): 109. 1944. *J. A. Steyermark 29505*; Oct. 1939; Guatemala, Dept. Zacapa, Sierra de las Minas; 250–900 m; F (holo) = *V. guatemalensis* H. Robinson & Greenmann var. *guatemalensis*, 1976.

Verbesina minarum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 263. 1947. *J. A. Steyermark 42489*; 12–13 Jan. 1942; Guatemala, Dept. Zacapa, Sierra de las Minas, Río Repollal; 2,100–2,400 m; F (holo).

Verbesina negrensis Steyerm., Fieldiana Bot. 28(3): 675. 1953. *J. A. Steyermark 57066*; 7 July 1944; Venezuela, Mérida, between Barladores and Páramo de la Negra; 2,285–2,430 m; F (holo).

Verbesina petzalensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 147. 1944. *P. C. Standley 82921*; 9 Jan. 1941; Guatemala, Dept. Huehuetenango, near crossing of Río San Juan Ixtán, E of San Rafael Petzal;. 1,730 m; F (holo).

Verbesina tachirensis Steyerm., Fieldiana Bot. 28(3): 677. 1953. *J. A. Steyermark 57149*; 12 July 1944; Venezuela, Táchira, between Las Delicias and Paraguita, bordering Río Táchira; 1,675–1,890 m; F (holo).

Vernonia baldwinii Torr. f. *albiflora* Steyerm., Brittonia 10: 118. 1958. *E. J. Palmer 61259*; 7 Sep. 1955; U.S.A., Missouri, Lawrence Co., along Turnback Creek and U.S. Hwy. 166, 3.5 mi. E of Chesapeake; F (holo).

Vernonia corae Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 395. 1940. *J. A. Steyermark 36787*; 27 Feb. 1940; Guatemala, Dept. San Marcos, Volcán Tajumulco; 1,800–2,500 m; F (holo).

Veronia medialis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 148. 1944. *P. C. Standley 87473*; 17 Feb. 1941; Guatemala, Dept. Retalhuleu, Río Coyote, along road 4 km W of Tetalhuleu; 300 m; F (holo) = *V. arborescens* (L.) Sw., 1982.

Vernonia mima Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser 23(5): 264. 1947. *P. C. Standley 82871*; 9 Jan. 1941; Guatemala, Dept. Huehuetenango, near crossing of Río San Juan Ixtán, E of San Rafael Petzal; 1,730 m; F (holo).

Vernonia missurica Raf. f. *swinkii* Steyerm., Rhodora 59: 24. 1957. *F. A. Swink 2775*; 11 Aug. 1955; U.S.A., Illinois, Cook Co., prairie S of 95th St. and W of Hwy. 45, Argonne Forest Preserve S of Willow Springs; F (holo).

Viguiera shrevei Steyerm., Field Mus. Nat. Hist., Bot. Ser. 17(5): 421. 1938. *F. Shreve 8035*; 26 July 1937; Mexico, Chihuahua, near San Juanito, Distr. Bocoyna; 2,400 m; F (holo).

Zexmenia pinetorum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 149. 1944. *P. C. Standley 75590*; 28 Oct. 1940; Guatemala, Dept. Jutiapa, below Jutiapa and Plan de Urrutia; 900–1,200 m; F (holo) = *Wedelia pinetorum* (Standl. & Steyerm.) Becker, 1975.

BALSAMINACEAE

Impatiens pallida Nutt. f. *dichroma* Steyerm., Rhodora 40: 179. 1938. *J. A. Steyermark 25927*; 6 Sep. 1937; U.S.A., Missouri, Pike Co., Mississippi River, 1.5 mi. NW of Louisiana; MO (holo).

BERBERIDACEAE

Berberis johnstonii Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(3): 140. 1940. *J. R. Johnston 1525*; 14 Dec. 1938; Guatemala, Dept. Sacatepéquez, Parramos; F (holo) = *Mahonia johnstonii* (Standl. & Steyerm.) Standl. & Steyerm., 1943.

Mahonia volcania Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 6. 1943. *P. C. Standley 65221*; Feb. 1939; Guatemala, Volcán de Agua, above Santa María de Jesús; 3,000 m; F (holo).

Podophyllum peltatum L. f. *biltmoreanum* Steyerm., Rhodora 54: 134. 1952. *V. Bordener & C. Steyermark s.n.*; 16 Aug. 1950; U.S.A., Illinois, Lake Co., Biltmore Estates, S of Eaton Rd. and W of Kimberly Rd., 5 mi. N of Barrington; F (holo).

BETULACEAE

Corylus americana Walt. f. *indehiscens* Palmer & Steyerm., Ann. Missouri Bot. Gard. 22: 516. 1935. *B. F. Bush 10332*; 5 Sep. 1924; U.S.A., Missouri, Jackson Co., Greenwood; GH (holo).

BIGNONIACEAE

Pseudocalymma standleyi Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 236. 1947. *J. A. Steyermark 33533*; 5 Jan. 1940; Guatemala, Dept. Quezaltenango, Finca Pirineos and Finca Soledad, Volcán Santa María; 1,300–1,400 m; F (holo) = *Mansoa standleyi* (Steyerm.) A. Gentry, 1982.

BOMBACACEAE

Catostemma clarkii Steyerm., Ann. Missouri Bot. Gard. 74: 638. 1987. *H. A. Clark 8126*; 19 Aug. 1981; Venezuela, T.F. Amazonas, 10.8 km NE of San Carlos on road to Solano; 119 m; MO (holo).

Catostemma ebracteolatum Steyerm., Ann. Missouri Bot. Gard. 74: 641. 1987. *B. Maguire & L. Politi 2874*; 2 Feb. 1949; Venezuela, T.F. Amazonas, Cerro Sipapo (Paráque), water course above Intermediate Camp; MO (holo), NY.

Catostemma hirsutulum Steyerm., Ann. Missouri Bot. Gard. 74: 642. 1987. *J. A. Steyermark 74781*; 30–31 Mar. 1953; Venezuela, Bolívar, Chimantá Massif, NW slopes Abácapa, vicinity of camp 1 along Río Abácapa-tepui; F, MO (holo), VEN.

Catostemma marahuacensis Steyerm., Ann. Missouri Bot. Gard. 74: 643. 1987. *J. A. Steyermark & B. Holst 130878*; 28 Feb.–1 Mar. 1985; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca, 'Sima Camp' south central portion Caño Negro; 1,140 m; MO (holo—3327355).

Catostemma pubistylum Steyerm., Ann. Missouri Bot. Gard. 74: 643. 1987. *H. L. Clark & P. Maquirino 6742*; 3 Aug. 1978; Venezuela, T.F. Amazonas, IVIC

main study site, 4.3 km NE of San Carlos de Río Negro; 119 m; NY (holo).

Catostemma sancarlosiana Steyerm., Ann. Missouri Bot. Gard. 74: 644. 1987. *H. L. Clark & K. Clark 8117*; 16 Aug. 1981; Venezuela, T.F. Amazonas, 10.8 km NE of San Carlos on Solano Road; 119 m; MO (holo—3142831).

Pochota aracamuniana Steyerm., Ann. Missouri Bot. Gard.: in press. 1989. *R. L. Liesner & G. Carnevali 22559*; 28 Oct. 1987; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro Aracamuni, summit, Proa Camp; 1,400 m; MO (holo), VEN.

Pochota ewelii Steyerm., Ann. Missouri Bot. Gard. 75: 1077. 1988. *J. Ewel 135*; 23 Apr. 1964; Brazil, Dept. Amazonas, near Venezuela frontier, camino al Cerro Neblina desade Río Tucano; 1,250 m; MY (holo).

Pochota fuscolepidota Steyerm., Ann. Missouri Bot. Gard. 75: 1077. 1988. *R. L. Liesner 18452*; 8–9 Mar. 1985; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca; 1,100 m; MO (holo—3483071), VEN.

Pochota gracilis (Robyns) Steyerm., subsp. *bolivarensis* Steyerm., Ann. Missouri Bot. Gard. 75: 1078. 1988. *J. A. Steyermark 98206*; 17–29 Mar. 1967; Venezuela, Bolívar, Río Kanarakuni, southern base of Cerro Sarisariñama, Meseta de Jaua; 400 m; NY, VEN (holo).

Pochota liesneri Steyerm., Ann. Missouri Bot. Gard. 75: 1079. 1988. *R. L. Liesner 18637*; 14 Mar. 1985; Venezuela, T.F. Amazonas, Dept. Atabapo, Salto Yureba, Cerro Yureba, lower Ventuari; 350 m; MO (holo—3483072), VEN.

Pochota mawarinumae Steyerm., Ann. Missouri Bot. Gard. 75: 1079. 1988. *R. L. Liesner 16355*; 2 Mar. 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, near Cerro de la Neblina Base Camp, Río Mawarinuma; 140 m; MO (holo—3483069, 3483068), VEN.

Pochota redmondii Steyerm., Ann. Missouri Bot. Gard. 75: 1081. 1988. *R. L. Liesner & B. Holst 21248*; 19 Feb. 1987; Venezuela, T.F. Amazonas, Dept. Atures, stream 0.5–2 km E of Río Coro-Coro, W of Serranía de Yutaje; 200 m; MO (holo—3483070), NY, VEN.

Pochota robynsii Steyerm. & Stevens, Ann. Missouri Bot. Gard. 75: 1586, nom. nov.

Pochota tepuiensis Steyerm., Ann. Missouri Bot. Gard. 75: 1081. 1988. *J. A. Steyermark et al. 108938*; 11–12 Feb. 1974; Venezuela, Bolívar, Meseta de Jaua, Cerro Sarisariñama, summit; VEN (holo).

Scleronema neblinense Steyerm., Ann. Missouri Bot. Gard. 74: 645. 1987. *B. Maguire et al. 60181*; 15 Nov. 1986; Brazil, Amazonas, Serra de Neblina, vicinity Base Camp, Caño Tucano, Rio Cauaburi; 100 m; MO (holo), NY.

BONNETIACEAE = Theaceae

BORAGINACEAE

Lithospermum canescens (Michx.) Lehm. f. *pallidum* Palmer & Steyerm., Rhodora 57: 316. 1955. *J. A. Steyermark 73223*; 30 Apr. 1952; U.S.A., Missouri, Pike Co., Hwy. 54, 0.5 mi. SW of jct. with Hwy. 154, 4 mi. WSW of Curryville; F (holo), MO.

Mertensia virginica (L.) Pers. f. *rosea* Steyerm., Rhodora 62: 131. 1960. *J. A. Steyermark 67235*; 17 Apr. 1949; U.S.A., Missouri, Cass Co., N side of Big Creek, 4 mi. SE of Pleasant Hill; F (holo).

BRASSICACEAE

Cardamine balnearia Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 157. 1944. *P. C. Standley 83332*; 14 Jan. 1941; Guatemala, Dept. Quezaltenango, Aguas Amargas, Volcán Zunil; 2,450 m; F (holo).

Cardamine bulbosa (Schreb.) Britt., Sterns & Pogg. f. *fontinalis* Palmer & Steyerm., Ann. Missouri Bot. Gard. 25: 771. 1938. *J. A. Steyermark 12414*; 2 Aug. 1936; U.S.A., Missouri, Shannon Co., Pulltight Spring, near Current River; MO (holo—1175572) = *C. bulbosa* (Schreb.) Britt., Sterns & Pogg var. *bulbosa*, 1981.

Cardamine eremita Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 53. 1944. *J. A. Steyermark 50143*; 6 Aug. 1942; Guatemala, Dept. Huehuetenango, between Tojquiá and Caxix bluff, summit of Sierra de los Cuchumatanes; 3,700 m; F (holo).

Cardamine jejuna Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 54. 1944. *J. A. Steyermark 50569*; 15 Aug. 1942; Guatemala, Dept. Huehuetenango, Cerro Pixpix, Sierra de los Cuchumatanes; 2,800 m; F (holo).

Romanschulzia alpina Standl. & Steyerm., Fieldiana Bot. 24(4): 377. 1946. *J. A. Steyermark 50144*; n.d.; Guatemala, Huehuetenango, Sierra de los Cuchumatanes, between Tojquiá and Caxin bluff; F (holo) = *Sisymbrium standleyi* Rollins, 1956.

Selenia oinosepala Steyerm., Field Mus. Nat. Hist., Bot. Ser. 17(5): 422. 1938. *E. Whitehouse s.n.*; 28 Feb. 1930; U.S.A., Texas, San Benito; F, TEX (holo).

BROMELIACEAE

Aechmea siapensis L. B. Smith & Steyerm., Ann. Missouri Bot. Gard.: in press. 1989. *R. L. Liesner & F. Delascio 21904*; 13 Oct. 1987; Venezuela, T.F. Amazonas, Río Siapa, 130 km E of San Carlos de Río Negro; 180 m; MO, US (holo), VEN.

Billbergia manarae Steyerm., Brittonia 30: 39. 1978. *J. A. Steyermark 112181*; 22 May 1976; Venezuela, Distr. Federal, Cerro Naiguata; US (holo), VEN.

Brewcaria L. B. Smith, Steyerm. & Robinson, Acta Bot. Venez. 14(3): 10. 1984, gen. nov.

Brewcaria duidensis L. B. Smith, Steyerm. & H. Robinson, Acta Bot. Venez. 14(3): 10. 1984. *J. A. Steyermark et al. 124582*; 16 Feb. 1981; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Duida; 1,500 m; MO (2911061 & 2911060), NY, US (holo), VEN.

Brewcaria marahuacae L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 714. 1986. *J. A. Steyermark et al. 126328*; 9–10 Feb. 1982; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca—Atuha—Shiho; 2,480 m; NY, US (holo), VEN.

Brocchinia oliva-estevae Steyerm. & L. B. Smith, Ann. Missouri Bot. Gard. 74: 85. 1987. *F. Oliva Esteva s.n.*; Dec. 1984; Venezuela, Bolívar, summit of Auyan-tepui, extreme N end above Angel Falls; VEN (holo).

Connellia smithiana Steyerm. & Luteyn, J. Bromel. Soc. 35(4): 153. 1985. *J. L. Luteyn & J. A. Steyermark 9610*; 18 Feb. 1984; Venezuela, Bolívar, Auyan-tepui; 2,100 m; NY, VEN (holo) = *Lindmania smithiana* (Steyerm. & Luteyn) L. B. Smith, 1986.

Connellia varadarajanii L. B. Smith & Steyerm., J. Bromel. Soc. 35(2): 52. 1985. *G. S. Varadarajan 1205*; 12 Jan. 1984; Venezuela, Bolívar, Auyan-tepui; 1,950–2,000 m; US (holo), VEN.

Cottendorfia arachnoidea L. B. Smith, Steyerm. & H. Robinson, Acta Bot. Venez. 14(3): 9. 1984. *J. A. Steyermark et al. 125996*; 1–2 Feb. 1982; Venezuela,

T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca Fhuif; 2,480–2,500 m; US (holo), NY, VEN = *Lindmania arachnoidea* (L. B. Smith, Steyerm. & H. Robinson) L. B. Smith, 1986.

Cottendorfia atrorosea L. B. Smith, Steyerm. & H. Robinson, Brittonia 33: 28. 1981. *J. A. Steyermark et al. 117982*; 9 Apr. 1979; Venezuela, Bolívar, cumbre del Cerro Guaiquinima; 1,650 m; US (holo), VEN = *Lindmania atrorosea* (L. B. Smith, Steyerm. & H. Robinson) L. B. Smith, 1986.

Cottendorfia aurea L. B. Smith, Steyerm. & H. Robinson, ined., mss. = *Lindmania aurea* L. B. Smith, Steyerm. & H. Robinson.

Cottendorfia brachyphylla var. *angustior* L. B. Smith, Steyerm. & H. Robinson, Brittonia 33: 28. 1981. *J. A. Steyermark et al. 116180*; 28 Feb. 1978; Venezuela, Bolívar, Auyan-tepui; 1,950 m; US (holo), VEN = *Lindmania brachyphylla* var. *angustior* (L. B. Smith, Steyerm. & H. Robinson) L. B. Smith, 1986.

Cottendorfia delascioana L. B. Smith, Steyerm. & H. Robinson, ined., mss. *J. A. Steyermark & F. Delascio 129203*; 30 Mar.–1 Apr. 1983; Venezuela; MO (iso—3230815).

Cottendorfia discolor L. B. Smith, Steyerm. & H. Robinson, ined., mss. = *Steyerbromelia discolor* L. B. Smith, Steyerm. & H. Robinson.

Cottendorfia geniculata (L. B. Smith) L. B. Smith var. *minor* L. B. Smith, Steyerm. & H. Robinson, Acta Bot. Venez. 14(3): 15. 1984. *J. A. Steyermark et al. 124526*; 17 Feb. 1981; Venezuela, T.F. Amazonas, Dept. Atures, Serranía Sipapo; 1,500 m; NY (holo), VEN = *Lindmania geniculata* var. *minor* (L. B. Smith, Steyerm. & H. Robinson) L. B. Smith, 1986.

Cottendorfia huberi L. B. Smith, Steyerm. & H. Robinson, ined., mss. = *Lindmania huberi* L. B. Smith & Steyerm.

Cottendorfia marahuacae L. B. Smith, Steyerm. & H. Robinson, Acta Bot. Venez. 14(3): 9. 1984. *B. Maguire et al. 65641*; 15 Jan. 1981; Venezuela, T.F. Amazonas, Cerro Marahuaca; MO (2911057), NY, US (holo) = *Lindmania marahuacae* (L. B. Smith, Steyerm. & H. Robinson) L. B. Smith, 1986.

Cottendorfia terramarae L. B. Smith, Steyerm. & H. Robinson, ined., mss. = *Lindmania terramarae* L. B. Smith, Steyerm. & H. Robinson, 1986.

Greigia ocellata L. B. Smith & Steyerm., Phytologia 16(2): 72. 1968. *J. A. Steyermark & M. Rabe 96951*; 29–30 Aug. 1966; Venezuela, Táchira, below Páramo de la Negra on road to Pregonero; 2,600 m; US (holo), VEN.

Guzmania membranacea L. B. Smith & Steyerm., Acta Bot. Venez. 2(5–8): 380. 1967. *J. A. Steyermark 95022*; 4 Mar. 1966; Venezuela, Paria Peninsula, narrow northern crest between Cerro de Humo and Cerro La Pavita; 1,250–1,273 m; US, VEN (holo).

Guzmania terrestris L. B. Smith & Steyerm., Ann. Missouri Bot. Gard. 73: 715. 1986. *J. A. Steyermark 129596*; 10–12 Oct. 1983; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca; 2,560 m; NY, US (holo), VEN.

Lindmania aurea L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 697. 1986. *J. A. Steyermark et al. 128611*; 5 Feb. 1982; Venezuela, Bolívar, Distr. Piar, Macizo del Chimantá; 1,850 m; MO (3228804), NY, US (holo), VEN.

Lindmania holstii Steyerm. & L. B. Smith, J. Bromel. Soc. 38(2): 51. 1988. *B. K. Holst & F. Oliva Esteva 3539*; 22 Mar. 1987; Venezuela, Bolívar, Distr. Piar, Murispán-tepui, summit; 2,300 m; F (holo), MO (3512232), NY, US, VEN.

Lindmania huberi L. B. Smith & Steyerm., Ann. Missouri Bot. Gard. 73: 699. 1986. *J. A. Steyermark et al. 128465*; 2–5 Feb. 1983; Venezuela, Bolívar, Distr. Piar, Macizo del Chimantá; 1,850 m; MO (3228812), NY, US (holo), VEN.

Lindmania imitans L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 697. 1986. *J. A. Steyermark et al. 128474*; 2–5 Feb. 1983; Venezuela, Bolívar, Distr. Piar, Macizo del Chimantá; 1,850 m; MO (3340851), US (holo), VEN.

Lindmania piresii L. B. Smith, Steyerm. & Luteyn, Ann. Missouri Bot. Gard. 73: 698. 1986. *J. Murca Pires 15010 (33)*; 10 Feb. 1975; Brazil, Amazonas, Serra Araca; IPEAN, US (holo).

Lindmania riparia L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 695. 1986. *J. A. Steyermark 93895*; 15 May 1964; Venezuela, Bolívar, Auyan-tepui; 2,050–2,300 m; MAC, NY, US (holo).

Lindmania saxicola L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 693. 1986. *J. A. Steyermark et al. 128945*; 7–8 Feb. 1983; Venezuela, Bolívar, Distr. Piar, Macizo del Chimantá; 2,450 m; US (holo), VEN.

Lindmania sessilis L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 693. 1986. *J. A. Steyermark et al. 128104*; 26–29 Jan. 1983; Venezuela, Bolívar, Distr. Piar, Macizo del Chimantá; 2,000 m; US (holo), MO (128104), VEN.

Lindmania terramarae L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 698. 1986. *J. A. Steyermark & F. Delascio 129067*; 26 Mar. 1983; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca; 2,800 m; MO (3230813), NY, US (holo), VEN.

Navia albiflora L. B. Smith, Steyerm. & H. Robinson, Acta Bot. Venez. 14(3): 11. 1984. *J. A. Steyermark et al. 126421*; 10 Feb. 1982; Venezuela, T.F. Amazonas; Dept. Atabapo, Cerro Duida; NY, US (holo), VEN.

Navia aliciae L. B. Smith, Steyerm. & H. Robinson, Acta Bot. Venez. 14(3): 13. 1984. *J. A. Steyermark et al. 125654*; 28–30 Jan., 6–8 Feb. 1982; Venezuela, T.F. Amazonas, Dept. Atabapo, Río Cunucunuma; 180–210 m; NY, US (holo), VEN.

Navia arida L. B. Smith & J. A. Steyerm., Bol. Soc. Venez. Ci. Nat. 23: 62. 1962. *J. A. Steyermark 89698*; 1 Sep. 1961; Venezuela, Bolívar, Sierra de Lema, Sabana de Triana; 300 m; VEN (holo).

Navia berryana L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 712. 1986. *J. A. Steyermark et al. 130318-A*; 1–2 Mar. 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, near and N of Cerro Vinilla; 440–600 m; US (holo), VEN.

Navia breweri L. B. Smith & Steyerm., Acta Bot. Venez. 2(5–8): 380. 1967. *C. Brewer Jr. 248*; 4 Jan. 1965; Venezuela, lower part of Cerro Jaua, near Río Canaracuni; 600–700 m; US (holo), VEN.

Navia carnevalii L. B. Smith & Steyerm., Ann. Missouri Bot. Gard.: in press. 1989. *R. L. Liesner & G. Carnevali 22322*; 22 Oct. 1987; Venezuela, T.F. Amazonas, Cerro Aracamuni, Quebrada Camp; 600 m; MO, US (holo), VEN.

Navia connata L. B. Smith & Steyerm., Bol. Soc. Venez. Ci. Nat. 25: 50. 1963. *J. A. Steyermark 90223*; 29 Dec. 1961; Venezuela, Sierra Ichun; 625–725 m; VEN (holo).

Navia crassicaulis L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 708. 1986. *R. L. Liesner 16026*; 16–18 Feb. 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, Camp III, Neblina and Massif, NW Plateau (arm); 1,750–1,850 m; MO (3340862), US (holo).

Navia culcitaria L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 712. 1986. *O. Huber 6184*; 13 June 1981; Venezuela, T.F. Amazonas, Dept. Río Negro, ca. 20 km al SW de Mauaca; 760 m; US (holo), VEN.

Navia delascionis L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 709. 1986. *J. A. Steyermark et al. 130410*; 1–2 Mar. 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, vicinity and northward from Cerro Vinilla; US (holo), MO (3340845), VEN.

Navia emergens L. B. Smith, Steyerm. & H. Robinson, Brittonia 33: 31. 1981. *J. A. Steyermark et al. 117298*; 24 May 1978; Venezuela, Bolívar, del Cerro Guaiquinima, 1 km río arriba del Salto Szczerbanari; 730–900 m; US (holo), VEN.

Navia filifera L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 713. 1986. *R. L. Liesner 16025*; 16–18 Feb. 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, Neblina, Camp III; 1,750–1,850 m; MO (3340858), US (holo).

Navia geaster L. B. Smith, Steyerm. & H. Robinson, Acta Bot. Venez. 14(3): 14. 1984. *J. A. Steyermark et al. 123846*; 11–12, 14 Jan. 1981; Venezuela, Bolívar, Distr. Heres, Cerro Marutani; 1,200 m; NY, US (holo), VEN.

Navia grafii Steyerm. & Holst, Ernstia 38: 44. 1986. *J. A. Steyermark et al. 131850*; 10 Apr. 1986; Venezuela, T.F. Amazonas, base of Cerro Yutaje; MO, US, VEN (holo).

Navia huberiana L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 706. 1986. *O. Huber 5058*; 7 Mar. 1980; Venezuela, T.F. Amazonas, Dept. Atabapo, 12 km W of Esmeralda, entre el Cerro Duida y el Río Orinoco; 125 m; US (holo), VEN.

Navia igneosicola L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 713. 1986. *J. A. Steyermark et al. 122478*; 14 May 1980; Venezuela, T.F. Amazonas, Dept. Atures, 35 km SE of Puerto Ayacucho; 150 m; NY, US (holo), VEN.

Navia incrassata L. B. Smith & Steyerm., Phytologia 16(2): 74. 1968. *J. A. Steyermark 97881*; Venezuela, Bolívar, Meseta de Jaua, Cerro Jaua; 1,922–2,100 m; US (holo), VEN.

Navia intermedia L. B. Smith & Steyerm., Phytologia 16(2): 74. 1968. *J. A. Steyermark 97865*; 22–27 Mar. 1967; Venezuela, Bolívar, Meseta de Jaua, Cerro Jaua; 1,922–2,100 m; US (holo), VEN.

Navia iosothrix L. B. Smith & Steyerm., Ann. Missouri Bot. Gard.: in press. 1989. *R. L. Liesner & F. Delascio 22203*; 20 Oct. 1987; Venezuela, T.F. Amazonas, Cerro Aracamuni, Quebrada Camp; 600 m; MO, US (holo), VEN.

Navia jauana L. B. Smith, Steyerm. & H. Robinson, Bol. Soc. Venez. Ci. Nat. 32: 287. 1976. *J. A. Steyermark et al. 108895*; 10 Feb. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Sarisariñama; 1,400 m; US (holo), VEN.

Navia lactea L. B. Smith, Steyerm. & H. Robinson, Acta Bot. Venez. 14(3): 14. 1984. *B. Maguire et al. 65705*; 15 Jan. 1981; Venezuela, T.F. Amazonas, Cerro Sipapo; NY, US (holo), VEN.

Navia lasiantha L. B. Smith & Steyerm., Phytologia 16(2): 75. 1968. *J. A. Steyermark 97865a*; 22–27 Mar. 1967; Venezuela, Bolívar, Meseta de Jaua, Cerro Jaua; 1,922–2,100 m; US (holo), VEN.

Navia liesneri L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 709. 1986. *R. L. Liesner & C. Brewer 15866*; 11 Feb. 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro de Neblina, Puerto Chimo Camp; 150–1,800 m; MO (3340861), US (holo).

Navia linearis L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 709. 1986. *J. A. Steyermark 129646*; 13–14 Oct. 1983; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca; 1,560 m; US (holo), VEN.

Navia luzuloides L. B. Smith, Steyerm. & H. Robinson, Bol. Soc. Venez. Ci. Nat. 32: 289. 1976. *J. A. Steyermark et al. 109633*; 27 Feb. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Jaua; 2,000 m; US (holo), VEN.

Navia navicularis L. B. Smith & Steyerm., Bol. Soc. Venez. Ci. Nat. 25: 52. 1963. *J. A. Steyermark 90199*; 27 Dec. 1961; Venezuela, Bolívar, Sierra Ichun; VEN (holo).

Navia ovoidea L. B. Smith, Steyerm. & H. Robinson, Brittonia 33: 31. 1981. *J. A. Steyermark et al. 117361*; 25 May 1978; Venezuela, Bolívar, Cerro Guaiquinima; US (holo), VEN.

Navia patria L. B. Smith & Steyerm., Ann. Missouri Bot. Gard.: in press. 1989. *R. L. Liesner & F. Delascio 22041*; 17 Oct. 1987; Venezuela, T.F. Amazonas, Cerro Aracamuni, summit, Popa Camp; 1,550 m; MO, US (holo), VEN.

Navia pedemontana L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 708. 1986. *J. A. Steyermark & F. Delascio 129063*; 22–23, 28–29 Mar., 1–4 Apr. 1984; Venezuela, T.F. Amazonas, Dept. Atabapo, Culebra, Río Cunucunuma; 200–220 m; US (holo), VEN.

Navia piresii L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 712. 1986. *J. Murca Pires 15014 (37)*; 10 Feb. 1975; Brazil, Amazonas, Serra Araca; IPEAN, US (holo).

Navia platyphylla L. B. Smith & Steyerm., Ann. Missouri Bot. Gard.: in press. 1989. *R. L. Liesner & F. Delascio 22062*; 17 Oct. 1987; Venezuela, T.F. Amazonas, Cerro Aracamuni, summit, Popa Camp; 1,550 m; MO, US (holo), VEN.

Navia plowmanii L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 703. 1986. *W. W. Thomas & T. Plowman 3030*; 13–15 Apr. 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro Neblina, 3.5 km W of Pico Zuloaga; 2,000 m; NY, US (holo), VEN.

Navia polyglomerata L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 704. 1986. *W. W. Thomas 3261*; 26 Apr. 1984; Venezuela, T.F. Amazonas, banks of Río Marawinuma, 2–6 km E of Base Camp; 160 m; MO (3488107), NY, US (holo), VEN.

Navia scirpiflora L. B. Smith, Steyerm. & H. Robinson, Bol. Soc. Venez. Ci. Nat. 32: 307. 1976. *J. A. Steyermark et al. 108880*; 10 Feb. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Sarasariñama; 1,410 m; US (holo), VEN.

Navia terramarae L. B. Smith & Steyerm., Ann. Missouri Bot. Gard.: in press. 1989. *R. L. Liesner & F. Delascio 21998*; 16 Oct. 1987; Venezuela, T.F. Amazonas, Cerro Aracamuni, summit, Popa Camp; 1,550 m; MO, US (holo), VEN.

Navia thomasii L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 703. 1986. *W. W. Thomas 3245*; 26 Apr. 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro Neblina, ESE facing slope above Río Marawinuma, E of 'Puerto Chimo' Camp; 600 m; NY, US (holo), VEN.

Pitcairnia venezuelana L. B. Smith & Steyerm., Phytologia 16(2): 76. 1968. *J. A. Steyermark & M. Rabe 96472*; 24 Aug. 1966; Venezuela, Portuguesa, 5 km ENE of Agua Blanca, 22 km NE of Acarigua; 190 m; US (holo), VEN.

Steyerbromelia diffusa L. B. Smith, Steyerm. & H. Robinson, Ann. Missouri Bot. Gard. 73: 700. 1986. *J. A. Steyermark et al. 130072*; 24 28 Feb. 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro Aratitiyope; 990–1,670 m; MO (3237102, 3237103), NY, US (holo), VEN.

Tillandsia abysmophila L. B. Smith & Steyerm., Ann. Missouri Bot. Gard. 73: 714. 1986. *J. A. Steyermark et al. 130135*; 24–28 Feb. 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro Aratitiyope; 990–1,670 m; MO (3242834), NY, US (holo), VEN.

Vriesea capituligera Steyerm., J. Bromel. Soc. 32(3): 113. 1982. *J. A. Steyermark & V. Carreño Espinosa 123808*; 7 Dec. 1980; Venezuela, Edo. Yaracuy, Distr. San Felipe, Vuelta de Pavo, 5 mi. S Candelaria; 1,200 m; VEN (holo).

Vriesea splendens (Brongn.) Lemaire var. *oinochroma* Steyerm., Bull. Bromel. Soc. 17(3): 53. 1967. *J. A. Steyermark 95320*; Venezuela, Carabobo, tributarios del Río San Gian; US, VEN (holo).

BRUNELLIACEAE

Brunellia integrifolia Szyszyl. var. *ptariana* Steyerm., Fieldiana Bot. 28(1): 244. 1952. *J. A. Steyermark 59847*; 4 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 2,130 m; F (holo).

Brunellia neblinensis Steyerm. & Cuatr., Ann. Missouri Bot. Gard. 74: 635. 1987. *J. Ewel 209*; 29 Apr. 1964; Venezuela–Brazilian border, Cerro de la Neblina; 1,500 m; NY (holo).

Brunellia paucijuga Steyerm., Phytologia 9(6): 344. 1964. *J. A. Steyermark 53873*; 16 Aug. 1943; Ecuador, Prov. El Oro, between Curtincapa and Guagra Uma; 2,790–2,880 m; F (holo).

Brunellia zamorensis Steyerm., Phytologia 9(6): 344. 1964. *J. A. Steyermark 53576*; 13 July 1943; Ecuador, Prov. Santiago-Zamora, arenillas along Río Tintas, 10 leagues SE of El Pan; 2,195 m; F (holo).

BURMANNIACEAE

Burmannia carrenoi Steyerm., Acta Bot. Venez. 6: 89. 1971. *J. A. Steyermark et al. 104418*; 25 Dec. 1970; Venezuela, Bolívar, vicinity of K.134 S of El Dorado, Río Anawa-ray-paru; 1,350 m; NY, U, US, VEN (holo) = *B. kalbreyeri* Oliv., 1986.

Burmannia foliosa Gleason subsp. *marahuacensis* Maguire & Steyerm., Acta Bot. Venez. 14(3): 19. 1984. *J. A. Steyermark et al. 124383*; n.d.; Venezuela, T.F. Amazonas, Cerra Marahuaca; MO (2911054), NY (holo), VEN = *B. foliosa* Gleason subsp. *foliosa*, 1986.

Burmannia sanariapoana Steyerm., Fieldiana Bot. 28(1): 165. 1951. *J. A. Steyermark 58466*; 8 Sep. 1944; Venezuela, T.F. Amazonas, tributary of Orinoco, near Río Sanariapo, vicinity of Sanariapo; 100 m; F (holo), GH, NY, U, US.

BURSERACEAE

Bursera permollis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 166. 1944. *P. C. Standley 75245*; Oct.–Nov. 1940; Guatemala, Dept. Jutiapa, vicinity of Jutiapa; 850 m; F (holo).

Dacryodes chimantensis Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 445. 1967. *J. A. Steyermark 75358*; 14 May 1953; Venezuela, Bolívar, Chimantá-tepui (Torono-tepui), Chimantá Massif; 1,000 m; NY (holo).

Dacryodes costanensis Steyerm., Acta Bot. Venez. 10: 235. 1975. *L. Aristeguieta 3036*; Apr. 1958; Venezuela, Miranda, Bosque de Los Guayabitos, arriba de Baruta; 1,350 m; VEN (holo).

Protium ptarianum Steyerm., Fieldiana Bot. 28(2): 275. 1952. *J. A. Steyermark 59994*; 10–11 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,585-1,600 m; F (holo).

Protium ptarianum Steyerm. var. *angusitor* Steyerm., Fieldiana Bot. 28(2): 276. 1952. *J. A. Steyermark 59987*; 10–11 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,585–1,600 m; F (holo).

Protium puberulenta Steyerm., Fieldiana Bot. 28(2): 276. 1952. *J. A. Steyermark 60460*; 23 Nov. 1944; Venezuela, Bolívar, 8 mi. NW of Kavanayen; 1,220 m; F (holo).

Trattinickia glabra Steyerm., Fieldiana Bot. 28(2): 277. 1952. *J. A. Steyermark 60312*; 18 Nov. 1944; Venezuela, Bolívar, between Santa Teresita de Kavanayen and base of Ptari-tepui; 1,220 m; F (holo).

CACTACEAE

Bonifazia Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 66. 1944, gen. nov.

Bonifazia quezalteca Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 66. 1944. *P. C. Standley 85603*; 1 Feb. 1941; Guatemala, Dept. Quezaltenango, above Mujuliá, between San Martín Chile Verde and Colombia; 1,800 m; F (holo) = *Epiphyllum quezaltecum* (Steyerm.) L. Williams, 1961.

Heliocereus heterodoxus Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 67. 1944. *J. A. Steyermark 36291*; 21 Feb. 1940; Guatemala, Dept. San Marcos, along Río Vega between San Rafael and NE part of Volcán Tacaná; 2,500–3,000 m; F (holo) = *H. cinnabarinus* (Eichl.) Britt. & Rose, 1961.

CAMPANULACEAE

Lobelia laxiflora H.B.K. f. *lutea* Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 98. 1944. *P. C. Standley 67195*; 1 Mar. 1939; Guatemala, Dept. Quezaltenango, above Santa María de Jesús; 1,650 m; F (holo) = *L. laxiflora* H.B.K. var. *laxiflora*, 1976.

Lobelia siphilitica L. f. *purpurea* Palmer & Steyerm., Brittonia 10: 118. 1958. *J. A. Steyermark 79674*; 19 Sep. 1955; U.S.A., Missouri, Adair Co., along Chariton River, 2.5 mi. S of Youngstown; F (holo).

Siphocampylus tillettii Steyerm., Brittonia 30: 50. 1978. *S. S. Tillett et al. 752–329*; 2 Feb. 1975; Venezuela, T.F. Amazonas, Cerro Marahuaca; 2,750 m; NY (holo).

CANELLACEAE

Cinnamodendron venezuelense Steyerm., Fieldiana Bot. 28(2): 402. 1952. *J. A. Steyermark 61950*; 9 Apr. 1945; Venezuela, Monagas, SW of Caripe, along Quebrada Colorado Grande; 850–1,350 m; F (holo).

CAPPARACEAE

Capparis calciphila Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 158. 1944. *J. A. Steyermark 45616*; 1–2 Apr. 1942; Guatemala, Dept. Alta Verapaz, Cerro Chinajá; 150–700 m; F (holo).

Capparis grandipetala Maguire & Steyerm., in press, Mem. New York Bot. Gard. *N. T. Silva & U. Brazao 60719*; 22 Dec. 1965; Brazil; NY (holo), MO (3291196).

Capparis guaguaensis Steyerm., Fieldiana Bot. 28(1): 238. 1951. *J. A. Steyermark 62800*; 18 May 1945; Venezuela, Sucre, above Cuchivano, along Río Guagua, tributary to Río Manzanares; 230–300 m; F (holo).

CAPRIFOLIACEAE

Sambucus canadensis L. f. *rubra* Palmer & Steyerm., Ann. Missouri Bot. Gard. 25: 773, 1938. *E. J. Palmer 18928*; 3 Sep. 1920; U.S.A., Missouri, Atchison Co., Watson; GH (holo).

Viburnum brunnescens Standl. & Steyerm., Field Mus. Natl. Hist., Bot. Ser. 23(2): 89. 1944. *J. A. Steyermark 49855*; 31 July 1942; Guatemala, Dept. Huehuetenango, Cruz de Limón, Sierra de los Cuchumatanes; 2,600–3,000 m; F (holo) = *V. jucundum* Morton, 1976.

Viburnum detractum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 90. 1943. *J. A. Steyermark 34590*; 22 Jan. 1940; Guatemala, Dept. Quezaltenango, Volcán Zunil, above Fuentes Georginas; 3,000 m; F (holo) = *V. jucundum* Morton var. *detractum* (Standl. & Steyerm.) D. Gibson, 1973.

Viburnum euryphyllum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 90. 1944. *J. A. Steyermark 48425*; 8 July 1942; Guatemala, Dept. Huehuetenango, between Tunima and Quisil, Sierra de los Cuchumatanes; 2,500–3,100 m; F (holo).

Viburnum mortonianum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 294. 1940. *J. A. Steyermark 31606*; 10 Nov. 1939; Guatemala, Dept. Chiquimula, Cerro Tixixí; 1,500 m; F (holo).

Viburnum tinoides L.f. var. *roraimense* (Killip & Smith) Steyerm. f. *turumiquirense* Steyerm.; Field Mus. Nat. Hist., Bot. Ser. 28(3): 619. 1953. *J. A. Steyermark 62691*; 10 May 1945; Venezuela, Sucre, Cerro Turumiquire; 1,300–1,800 m; F (holo).

CARYOPHYLLACEAE

Arenaria altorum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 49. 1944. *J. A. Steyermark 33091*; 12 Dec. 1939; Guatemala, Dept. Jalapa, near Minas de Croma, Potrero Carrillo; 1,500–1,700 m; F (holo).

Arenaria chiapensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 50. 1944. *Ghiesbreght 871*; 1864–1870; Mexico, Chiapas; F (holo).

Arenaria guatemalensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 50. 1944. *J. A. Steyermark 36268*; Feb. 1940; Guatemala, Dept. San Marcos, Río Vega, near San Rafael and Guatemala–Mexico border, Volcán Tacaná; 2,500–3,000 m; F (holo).

Arenaria patula Michx. f. *media* Steyerm., Rhodora 43: 331. 1941. *Gattinger s.n.*; May; U.S.A., Tennessee, rocky glades near Nashville; F (holo), G, M.

Arenaria patula Michx. f. *robusta* Steyerm., Rhodora 43: 330. 1941. *J. A. Steyermark 26652*; 27 May 1939; U.S.A., Missouri, Butler Co., along Gillis Bluff, section 8 and 17, 5 mi. SW of Giulin; F (holo), MO (1198045) = *Minuartia patula* var. *robusta* (Steyerm.) Maguire, 1988.

Cerastium juniperorum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 51. 1944. *J. A. Steyermark 48413*; 7 July 1942; Guatemala, Dept. Huehuetenango, Tunima, Sierra de los Cuchumatanes; 3,400–3,500 m; F (holo).

Drymaria firmula Steyerm., Fieldiana Bot. 28(1): 227. 1951. *J. A. Steyermark 56536*; 14 May 1944; Venezuela, Mérida, between El Molino and San Isidro Alto, Páramo de Los Colorados; 2,745–2,955 m; F (holo).

Drymaria minuscula Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 52. 1944. *J. A. Steyermark 50243*; 8 Aug. 1942; Guatemala, Dept. Huehuetenango, Chemal, summit of Sierra de los Cuchumatanes; 3,700 m; F (holo).

Stellaria ovata Willd. f. *paradoxa* Steyerm., Fieldiana Bot. 28(1): 228. 1951. *J. A. Steyermark 55217*; 3 Feb. 1944; Venezuela, Lara, above Humocaro Bajo, above Las Sabanetas, Los Aposentos; 2,500–2,530 m; F (holo).

Stellaria venezuelana Steyerm., Fieldiana Bot. 28(1): 229. 1951. *J. A. Steyermark 62739*; 11 May 1945; Venezuela, Sucre, Cerro de Diablo base; 2,000–2,100 m; F (holo).

CECROPIACEAE

Cecropia sylvicola Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 153. 1944. *P. C. Standley 90762*; Apr. 1941; Guatemala, Dept. Alta Verapaz, between Tactic & divide on road to Tamahu; 1,500–1,600 m; F (holo).

CELASTRACEAE

Maytenus agostinii Steyerm., Ernstia 23: 34. 1984. *G. Agostini & M. Farinas 84*; 28 Oct. 1963; Venezuela, Aragua, Parque Nacional Henri Pittier; VEN (holo).

Maytenus apiculata Steyerm., Fieldiana Bot. 28(2): 334. 1952. *J. A. Steyermark 60385*; 20–21 Nov. 1944; Venezuela, Bolívar, Quebrada O-paru-ma; 1,065–1,220 m; F (holo).

Maytenus coriacea Steyerm., Fieldiana Bot. 28(2): 337. 1952. *J. A. Steyermark 56509*; 14 May 1944; Venezuela, Mérida, above El Molino; 2,010–2135 m; F (holo).

Maytenus guianensis Klotzsch f. *crenulata* Steyerm.; Fieldiana Bot. 28(2): 338. 1952. *J. A. Steyermark 61731*; 23 Mar. 1945; Venezuela, Anzoátegui, Fila Grande; 900–1,400 m; F (holo).

Maytenus huberi Steyerm., Ann. Missouri Bot. Gard. 75: 1062. 1988. *O. Huber 441*; 29 Jan. 1977; Venezuela, T.F. Amazonas, Dept. Atures, cuenca del Río Manapiare, en los cerros ubicados entre el Cerro Morrocoy al sur y Serranía Colmena al Norte; 200–300 m; VEN (holo).

Maytenus insculpta Steyerm., Ann. Missouri Bot. Gard. 75: 1063. 1988. *O. Huber 1229*; 16 Oct. 1977; Venezuela, T.F. Amazonas, Dept. Atures, cuenca del Río Manapiare, los cerros al N del Cerro Morrocoy, 12 km W of San Juan de Manapiare; 225 m; MO, VEN (holo).

Maytenus jauaensis Steyerm., Bol. Soc. Venez. Ci. Nat. 32: 346. 1976. *J. A. Steyermark et al. 109252*; 19–

20 Feb. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Sarasariñama; 1,350 m; VEN (holo).

Maytenus longistipitata Steyerm., Ann. Missouri Bot. Gard. 75: 1064. 1988. *B. Maguire et al. 53731*; 12 Sep. 1962; Venezuela, Bolívar, Cerro Uroi, summit, N portion, Río Uroi, Río Chicanán; 700 m; MO, VEN (holo).

Maytenus neblinae Steyerm., Ann. Missouri Bot. Gard. 75: 1064. 1988. *T. Plowman & W. Thomas 13610*; 15 Apr. 1984; Venezuela, T.F. Amazonas, Cerro de la Neblina, 26 km ENE of Base Camp; 2,000 m; F, MO (holo), VEN.

Maytenus parvifolia Steyerm., Fieldiana Bot. 28(2): 338. 1952. *J. A. Steyermark 55832*; 30 Mar. 1944; Venezuela, Mérida, between Pinango and Las Corales; 3,333 m; F (holo).

Maytenus pittieriana Steyerm., Fieldiana Bot. 28(2): 338. 1952. *Ll. Williams 13650*; Dec. 1939; Venezuela, Distr. Federal, above La Guaira; 750 m; F (holo).

Maytenus pustulata Steyerm., Ann. Missouri Bot. Gard. 75: 1064. 1988. *R. L. Liesner 16720*; 5 Mar. 1984; Venezuela, T.F. Amazonas, Cerro de la Neblina, Camp IV, 15 km NNE of Pico Phelps; 780 m; MO (holo), VEN.

Microtropis ilicina Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 170. 1944. *J. A. Steyermark 43284*; 26 Jan. 1942; Guatemala, Dept. Zacapa, S Volcán Gemelos, Sierra de las Minas; 2,100–3,200 m; F (holo).

Zinowiewia aymardii Steyerm., Ann. Missouri Bot. Gard. 75: 1064. 1988. *G. Aymard 4631*; 21 Oct. 1986; Venezuela, Bolívar, Distr. Sifontes, 7 km NW of Caserio El Pilón, 58 km W of Sta. Elena de Uairén; 850 m; MO (holo), PORT.

CHRYSOBALANACEAE

Licania costaricensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 335. 1940. *A. Smith F1779*; 14 Mar. 1939; Costa Rica, Prov. Alajuela, Villa Quesada, Cantón de San Carlos; 825 m; F (holo).

CLETHRACEAE

Clethra bimatris Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 17. 1943. *H. Kuylen 151*; July 1927; Guatemala, Dept. Izabal, Entre Ríos; F (holo) = *C. macrophylla* Mart. & Gal., 1961.

Clethra johnstonii Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 258. 1940. *J. R. Johnston 1255*; 20 May 1938; Guatemala, Dept. Guatemala, Volcán de Pacaya, above Las Calderas; F (holo).

Clethra licanioides Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 17. 1943. *J. A. Steyermark 33124*; 12 Dec. 1939; Guatemala, Dept. Jalapa, Potrero Carrillo, 13 mi. NE of Jalapa; 1,500–1,700 m; F (holo).

Clethra pachecoana Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 259. 1940. *P. C. Standley 65123*; 11 Feb. 1939. Guatemala, Dept. Sacatepéquez, Volcán de Agua, above Santa María de Jesús; 2,250–3,000 m; F (holo).

Clethra rugosa Steyerm., Phytologia 9(6): 347. 1964. *M. Acosta Solis 5054*; 20 July 1943; Ecuador, Prov. Santiago-Zamora, Campansa, Cordillera Oriental; 2,850 m; F (holo).

Clethra skutchii Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 260. 1940. *A. F. Skutch 1453*; 14 Oct. 1934; Guatemala, Dept. Quezaltenango, Palmar; 1,350 m; F (holo).

CLUSIACEAE

Caraipa ferruginea Steyerm., Fieldiana Bot. 28(2): 384. 1952. *Ll. Williams 14140*; 2 Feb. 1942; Venezuela, T.F. Amazonas, Yavita; 128 m; F (holo) = *C. punctulata* Ducke, 1978.

Caraipa longipedicellata Steyerm., Fieldiana Bot. 28(2): 385. 1952. *J. A. Steyermark 60708*; 28 Nov. 1944; Venezuela, Bolívar, between Ptari-tepui and Sororopan-tepui; 1,220 m; F (holo).

Chrysochlamys pauciflora Steyerm., Fieldiana Bot. 28(2): 386. 1952. *J. A. Steyermark 60566*; 25 Nov. 1944; Venezuela, Bolívar, Quebrada O-paru-ma; 915–1,065 m; F (holo).

Clusia cerroana Steyerm., Fieldiana Bot. 28(2): 386. 1952. *J. A. Steyermark 59702*; 1 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,700–1,800 m; F (holo).

Clusia hexacarpa Gleason var. *ptaritepuiana* Steyerm., Fieldiana Bot. 28(2): 387. 1952. *J. A. Steyermark 59866*; 4 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,800 m; F (holo).

Clusia imbricata Steyerm., Fieldiana Bot. 28(2): 387. 1952. *J. A. Steyermark 59699*; 1 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,700–1,800 m; F (holo).

Clusia lusoria Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 63. 1944. *J. A. Steyermark 30987*; 2 Nov. 1939; Guatemala, Dept. Chiquimula, Montaña Norte to El Jutal, Cerro Brujo SE of Concepción de las Minas; 1,700–2,000 m; F (holo).

Clusia pusilla Steyerm., Fieldiana Bot. 28(2): 390. 1952. *J. A. Steyermark 59396*; 26 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,220 m; F (holo).

Clusia reducta Steyerm., Fieldiana Bot. 28(2): 391. 1952. *Ll. Williams 14898*; 26 Mar. 1942; Venezuela, T.F. Amazonas, Río Guianía; 125 m; F (holo).

Clusia roraimana Steyerm., Fieldiana Bot. 28(2): 391. 1952. *J. A. Steyermark 58606*; 25 Sep. 1944; Venezuela, Bolívar, Mt. Roraima; 1,030–1,115 m; F (holo).

Clusia williamsii Steyerm., Fieldiana Bot. 28(2): 392. 1952. *Ll. Williams 14143*; 2 Feb. 1942; Venezuela, T.F. Amazonas, Yavita; 128 m; F (holo).

Havetia laurifolia H.B.K. var. *venezuelana* Steyerm., Fieldiana Bot. 28(2): 392. 1952. *J. A. Steyermark 56592*; 18 May 1944; Venezuela, Mérida, above Tabay; 2,285–2,745 m; F (holo).

Hypericum arbuscula Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 63. 1944. *J. R. Johnston 1812*; 11 Apr. 1941; Guatemala, Dept. Baja Verapaz, Patal; F (holo).

Hypericum calcicola Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 64. 1944. *J. A. Steyermark 50160*; 6 Aug. 1942; Guatemala, Dept. Huehuetenango, Sierra de los Cuchumatanes; 3,700 m; F (holo).

Hypericum caracasanum Willd. var. *turumiquirense* Steyerm., Fieldiana Bot. 28(2): 393. 1952. *J. A. Steyermark 62579*; 6 May 1945; Venezuela, Sucre, Cerro Turumiquire; 2,360–2,500 m; F (holo).

Hypericum ericifolium Steyerm., Fieldiana Bot. 28(2): 393. 1952. *J. A. Steyermark 57212*; 14 July 1944; Venezuela, Táchira, Paramito; 2,500 m; F (holo).

Hypericum meridense Steyerm., Fieldiana Bot. 28(2): 394. 1952. *J. A. Steyermark 56272*; 3 May 1944; Venezuela, Mérida, Páramo de Pozo Negro; 2,590–3,220 m; F (holo).

Hypericum pseudocaracasanum Steyerm., Fieldiana Bot. 28(2): 394. 1952. *J. A. Steyermark 55346*; 6 Feb. 1944; Venezuela, Trujillo, La Quebrada Cortijo; 2,600–2,800 m; F (holo).

Hypericum pseudomaculatum Mack. & Bush f. *flavidum* Steyerm., Rhodora 41: 585. 1939. *J. A. Steyermark 56061*; 31 May 1938; U.S.A., Missouri, McDonald Co., along Mill Creek, 5 mi. SE of Pineville; F (holo), MO.

Mahurea sororopantepuiana Steyerm., Fieldiana Bot. 28(2): 395. 1952. *J. A. Steyermark 60129*; 14 Nov. 1944; Venezuela, Bolívar, Sororopan-tepui; 2,255 m; F (holo).

Moronobea ptaritepuiana Steyerm., Fieldiana Bot. 28(2): 395. 1952. *J. A. Steyermark 59985*; 10–11 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,585–1,600 m; F (holo).

Moronobea ptaritepuiana Steyerm. f. *rosea* Steyerm., Fieldiana Bot. 28(2): 397. 1952. *J. A. Steyermark 60892*; 7 Dec. 1944; Venezuela, Bolívar, Carrao-tepui; 2,470–2,500 m; F (holo).

Oedematopus ptaritepuiensis Steyerm., Fieldiana Bot. 28(2): 398. 1952. *J. A. Steyermark 59719*; 1 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,700–1,800 m; F (holo).

Rheedia macrantha Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 65. 1944. *P. C. Standley 90524*; 1 Apr. 1941; Guatemala, Dept. Alta Verapaz, Río Frio, ca. 8 km below Tactic; 1,400 m; F (holo).

Tovomita angustata Steyerm., Fieldiana Bot. 28(2): 399. 1952. *J. A. Steyermark 60475*; 23 Nov. 1944; Venezuela, ca. 8 km NW of Kavanayen; 1,220 m; F (holo).

Tovomita atropurpurea Steyerm., Fieldiana Bot. 28(2): 399. 1952. *J. A. Steyermark 59973*; 10–11 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,585–1,600 m; F (holo).

Tovomita duidae Steyerm., Fieldiana Bot. 28(2): 400. 1952. *J. A. Steyermark 57975*; 25–26 Aug. 1944; Venezuela, T.F. Amazonas, Caño Negro, Cerro Duida; 305–1,095 m; F (holo).

COMBRETACEAE

Buchenavia ptariensis Steyerm., Fieldiana Bot. 28(2): 423. 1952. *J. A. Steyermark 60271*; 15–17 Nov. 1944; Venezuela, Bolívar, between Ptari-tepui and Sororopan-tepui; 1,615 m; F (holo).

COMMELINACEAE

Aneilema ecuadoriensis Steyerm., Phytologia 9(6): 339. 1964. *J. A. Steyermark 52813*; 3 June 1943; Ecuador, Prov. Azuay, between Chacanceo and Río Blanco, on road to Molleturo; 1,220 m; F (holo).

Campelia standleyi Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 32. 1944. *J. A. Steyermark 37187*; Mar. 1940; Guatemala, Dept. San Marcos, above Finca El Porvenir, on Todos Santos Chiquitos, Volcán Tajumulco; 1,300–1,500 m; F (holo).

Commelina alpestris Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 213. 1947. *J. A. Steyermark 50265*; 8 Aug. 1942; Guatemala, Dept. Huehuetenango, Sierra de los Cuchumatanes, vicinity of Chemal; 3,700 m; F (holo).

Commelina erecta L. var. *angustifolia* (Michx.) Fern. f. *cana* Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 32. 1944. *J. A. Steyermark 29136*; 5 Oct. 1939; Guatemala, Dept. Zacapa, along RR between La Fragua and Estanzuela; 200 m; F (holo).

Commelina erecta L. f. *candida* Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 33. 1944. *J. A. Steyermark 29267*; 7 Oct. 1939; Guatemala, Dept. Zacapa, between Zacapa and Santa Marta; 200 m; F (holo).

Commelina standleyi Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 33. 1944. *J. A. Steyermark 29644*; Oct. 1939; Guatemala, Dept. Zacapa, Sierra de las Minas, Finca Alejandría; 1,000–1,500 m; F (holo).

Dichorisandra diederichsanae Steyerm., Acta Bot. Venez. 8: 111. 1973. *J. A. Steyermark 106178*; 17–19 June 1972; Venezuela, Yaracuy, El Amparo hacia Candelaria; 1,220–1,250 m; VEN (holo).

Tinantia erecta (Jacq.) Schecht. f. *puberula* Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 34. 1944. *H. S. Gentry 2525*; Aug. 1936; Mexico, Chihuahua, Sierra Canelo, Río Mayo; F (holo).

Tinanatia leiocalyx C. B. Clarke f. *glabra* Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 34. 1944. *C. A. Purpus 16201*; Sep. 1934; Mexico, Veracruz, El Fortín; F (holo).

Tinantia longipedunculata Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 35. 1944. *Heyde & Lux 6392*; Jan. 1894; Guatemala, Dept. Escuintla, Santa Lucia; 300 m; F (holo).

Tinantia standleyi Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 35. 1944. *J. A. Steyermark 33605*; Jan. 1940; Guatemala, Dept. Quezaltenango, Volcán Santa María, between Santa María de Jesús and Calahuache; 1,300–1,500 m; F (holo).

Tradescantia aguensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 36. 1944. *P. C. Standley 59358*; Dec. 1938; Guatemala, Dept. Sacatepéquez, Volcán de Agua, N of Santa María de Jesús; 1,800–2,100 m; F (holo) = *Aneilema aguensis* (Standl. & Steyerm.) Standl. & Steyerm., 1944.

Tradescantia disgrega Kunth f. *glandulosa* Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 36. 1944. *J. A. Steyermark 29751*; Oct. 1939; Guatemala, Dept. Zacapa, Sierra de las Minas, between Río Hondo and summit of mountain at Finca Alejandría; 1,000–1,500 m; F (holo) = *Tripogandra disgrega* Kunth f. *glandulosa* (Standl. & Steyerm.) Standl. & Steyerm., 1952.

Tradescantia disgrega Kunth f. *pubescens* Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 37. 1944. *J. Morales R. 1106*; Oct. 1929; Guatemala, Dept. Guatemala; F (holo) = *Tripogandra disgrega* Kunth f. *pubescens* (Standl. & Steyerm.) Standl. & Steyerm., 1952.

Tradescantia guatemalensis C. B. Clarke f. *alba* Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 37. 1944. *P. C. Standley 58025*; Nov. 1938–Feb. 1939; Guatemala, Dept. Sacatepéquez, near Antigua; 1,500–1,600 m; F (holo).

Tradescantia standleyi Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 36. 1944. *J. A. Steyermark 31696*; Nov. 1939; Guatemala, Dept. Chiquimula, summit of Montaña Nonojá, E of Camotán; 1,800 m; F (holo).

Tradescantia venezuelensis Steyerm., Fieldiana Bot. 28(1): 152. 1951. *J. A. Steyermark 62688*; 10 May 1945; Venezuela, Sucre, Cerro Turumiquire; 1,300–1,800 m; F (holo).

Zebrina huehueteca Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 213. 1947. *J. A. Steyermark*

51016; 22 Aug. 1942; Guatemala, Dept. Huehuetenango, along Río Trapichillo; 1,000–2,100 m; F (holo).

CONNARACEAE

Pseudoconnarus krukovii Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(3): 141. 1940. *B. A. Krukoff 6455*; 14 Sep.–11 Oct. 1934; Brazil, Amazonas, Mun. Humayta, near Tres Casas; A, BM, BR, F (holo), G, K, MO, NY, U, US = *P. macrophyllus* (Poepp. & Endl.) Radl., 1983.

Rourea krukovii Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(3): 142. 1940. *B. A. Krukoff 8556*; 11 Sep.–26 Oct. 1936; Brazil, Amazonas, Mun. São Paulo de Olivenca, near Palmares; A, BM, BR, F, G, K, MO, NY (holo), S, U.

CONVOLVULACEAE

Dicranostyles costanensis Steyerm. & Austin, Ann. Missouri Bot. Gard. 57: 155–157. 1970. *J. A. Steyermark et al. 100263*; n.d.; Venezuela, Yaracuy, Cerro La Chapa; 1,200–1,400 m; VEN (holo).

Dicranostyles imatacensis Steyerm., Acta Bot. Venez, 3: 190. 1968. *J. A. Steyermark 87129*; 31 Oct. 1960; Venezuela, Terr. Delta Amacuro, San Victor, Río Amacuro, Sierra Imataca; 65–80 m; NY (holo) = *D. guianensis* A. Mennega, 1982.

Ipomoea heterodoxa Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 82. 1944. *P. Gentle 871*; Dec. 1933; Belize, Maskall; F (holo).

Ipomoea ophioides Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 82. 1944. *P. C. Standley 7884*; Dec. 1940; Guatemala, Dept. Santa Rosa, region of La Morenita, NE of Chiquimulilla; 400 m; F (holo).

Ipomoea santae-rosae Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 81. 1944. *P. C. Standley 79287*; Nov.–Dec. 1940; Guatemala, Dept. Santa Rosa, near Chiquimulilla; 325 m; F (holo).

Ipomoea saxorum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 81. 1944. *J. A. Steyermark 30254*; 22 Oct. 1939; Guatemala, Dept. Chiquimula, gorge of Río Chiquimula, between Santa Barbara and Petapilla; 350–420 m; F (holo).

Itzaea Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 83. 1944, gen. nov.

Jacquemontia guatemalensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 84. 1944. *J. A. Steyermark 30066*; Oct. 1939; Guatemala, Dept. Chiquimula, Chiquimula; 400 m; F (holo) = *J. agrestis* (Choisy) Meisn., 1982.

Jacquemontia pinetorum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 372. 1940. *J. A. Steyermark 38533*; 1 Apr. 1940; Guatemala, Dept. Izabal, Montaña del Mico; 65–6,000 m; F (holo).

Maripa stellulata Steyerm., Acta Bot. Venez. 3: 209. 1968. *J. A. & C. Steyermark 95456*; 2 Apr. 1966; Venezuela, Carabobo, Río San Gian, Planta Electrica; 350–550 m; MO, NY, U, US, VEN (holo).

CRASSULACEAE

Echeveria bicolor (H.B.K.) E. Walther var. *turumiquirensis* Steyerm., Fieldiana Bot. 28(2): 244. 1952. *J. A. Steyermark 62491*; 5 May 1945; Venezuela, Sucre, Cerro Turumiquire; 1,700–2,000 m; F (holo).

Echeveria huehueteca Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 159. 1944. *J. A. Steyermark 50934*; 19 Aug. 1942; Guatemala, Dept. Huehuetenango; Cumbre Papal; 1,400–3,000 m; F (holo).

Echeveria macrantha Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 159. 1944. *J. A. Steyermark 32808*; 6 Dec. 1939; Guatemala, Dept. Jalapa, Montaña Miramundo at Buena Vista; 2,000–2,200 m; F (holo).

Tillaea venezuelensis Steyerm., Fieldiana Bot. 28(4): 914. 1957. *J. A. Steyermark 55906*; 15 Apr. 1944; Venezuela, Mérida, between Chachopo and Los Apartaderos, near El Aquila; 3,030 m; F (holo).

CRUCIFERAE see Brassicaceae

CUCURBITACEAE

Ahzolia Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 92. 1944, gen. nov.

Anguria simplicifolia Steyerm., Fieldiana Bot. 28(3): 620. 1953. *J. A. Steyermark 60161*; 15 Nov. 1944; Venezuela, Bolívar, Sororopan-tepui; 2,130–2,250 m; F (holo).

Corallocarpus guatemalensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 93. 1944. *P. C. Standley 74623*; Oct. 1940; Guatemala, Dept. Zacapa, Zacapa; 200 m; F (holo) = *Doyerea emetocathartica* Grosourdy, 1976.

Elaterium macrophyllum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 94. 1944. *H. von Tuerckheim II.1728*; Apr. 1907; Guatemala, Dept. Baja Verapaz, above Pansal; 1,400 m; F (holo) = *Rytidostylis macrophyllus* (Standl. & Steyerm.) Dieterle, 1976.

Rytidostylis brevisetosa Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 148. 1965. *J. A. Steyermark 91499*; 7 June 1963; Venezuela, Distr. Federal, between Hacienda El Limón and Junquito-Colonia Tovar road; 1,750 m; VEN (holo).

Sicydium araguense Steyerm. & Trujillo, Bol. Soc. Venez. Ci. Nat. 25: 245. 1964. *J. A. Steyermark 89813*; 20 Oct. 1961; Venezuela, Aragua, Parque Nacional Henri Pittier; 1,500–1,700 m; US, VEN (holo).

Sicydium glabrum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 95. 1944. *J. A. Steyermark 34273*; 17 Jan. 1940; Guatemala, Dept. Quezaltenango, Montaña Chícharro, Volcán Santa María; 1,400–1,500 m; F (holo).

Sicyos guatemalensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 96. 1944. *J. A. Steyermark 32140*; 28 Nov. 1939; Guatemala, Dept. Jalapa, vicinity of Jalapa; 1,300 m; F (holo).

Tecunumania Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 96. 1944, gen. nov.

Tecunumania quetzalteca Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 97. 1944. *P. C. Standley 68931*; 15 Mar. 1939; Guatemala, Dept. San Marcos, Finca Vergel, near Rodeo; 900 m; F (holo).

CUNONIACEAE

Weinmannia neblinensis Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *B. Maguire et al. 42226*; 25 Nov. 1957; Venezuela, T.F. Amazonas, Cerro de la Neblina, Caño Grande; 1,200–2,200 m; MO (3291190), NY (holo).

CUPRESSACEAE

Juniperus standleyi Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 3. 1944. *J. A. Steyermark 36137*; Feb.

1940; Guatemala, Dept. San Marcos, Volcán Tacaná; 4,100–4,400 m; F (holo).

CYPERACEAE

Bulbostylis svensoniana Steyerm., Fieldiana Bot. 28(1): 37. 1951. *J. A. Steyermark 57629*; 2 Aug. 1944; Venezuela, Bolívar, between Upata and Río Caroni; 400 m; F (holo).

Carex azuayae Steyerm., Phytologia 9(6): 337. 1964. *J. A. Steyermark 53105*; 15 June 1943; Ecuador, Prov. Azuay, near Toreador; 3,785–3,900 m; F (holo).

Carex culmenicola Steyerm., Fieldiana Bot. 28(1): 65. 1951. *J. A. Steyermark 62605*; 6 May 1944; Venezuela, Sucre, Cerro Turumiquire; 2,500 m; F (holo).

Carex huehueteca Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 195. 1947. *J. A. Steyermark 49055*; 18 July 1942; Guatemala, Dept. Huehuetenango, Cananá, Sierra de los Cuchumatanes; 2,500 m; F (holo).

Carex larensis Steyerm., Fieldiana Bot. 28(1): 66. 1951. *J. A. Steyermark 55470*; 11 Feb. 1944; Venezuela, Lara, between Buenos Aires and Páramo de las Rosas; 2,285–3,290 m; F (holo).

Carex roraimensis Steyerm., Fieldiana Bot. 28(1): 67. 1951. *J. A. Steyermark 58870*; 28 Sep. 1944; Venezuela, Bolívar, Mt. Roraima, Summit Camp, Great Central Rift, Central Swamp; 2,700–2,740 m; F (holo).

Carex standleyana Steyerm., Ceiba 3: 23. 1952. *L. O. Williams 13178*; 6 July 1947; Guatemala, Dept. Jalapa, mountains above Aguacate; 2,150 m; F (holo).

Carex tachirensis Steyerm., Fieldiana Bot. 28(1): 68. 1951. *J. A. Steyermark 57367*; 15 July 1944; Venezuela, near Colombia–Venezuela border, Tachira, Páramo de Tamá; 3,045–3,475 m; F (holo).

Carex tamana Steyerm., Fieldiana Bot. 28(1): 70. 1951. *J. A. Steyermark 57401*; 15 July 1944; Venezuela, near Colombia–Venezuela border, Táchira, Páramo de Tamá; 3,045–3,475 m; F (holo).

Carex tojquianensis Standl. & Steyerm, Ceiba 4: 64. 1953. *J. A. Steyermark 50150*; 6 Aug. 1942; Guatemala, Dept. Huehuetenango, summit Sierra de los Cuchumatanes, between Tojquia and Caxix bluff; 3,700 m; F (holo).

Carex toreadora Steyerm., Phytologia 9(6): 338. 1964. *J. A. Steyermark 53095*; 15 July 1943; Ecuador, Prov. Azuay, near Toreador; 3,785–3,900 m; F (holo).

Carex tunimanenisis Standl. & Steyerm., Ceiba 4: 65. 1953. *J. A. Steyermark 48334*; 7 July 1942; Guatemala, Dept. Huehuetenango, near Tunima, Sierra de los Cuchumatanes; 3,400–3,500 m; F (holo).

Carex turumiquirensis Steyerm., Fieldiana Bot. 28(1): 70. 1951. *J. A. Steyermark 62705*; 10 May 1945; Venezuela, Sucre, Cerro Turumiquire, headwaters of Río Manzanares and Río de Amana; 1,900–2,000 m; F (holo).

Carex venosivaginata Standl. & Steyerm., Ceiba 4: 67–68. 1953. *J. A. Steyermark 48554*; 14 July 1942; Guatemala, Dept. Huehuetenango, Cerro Huitz, Sierra de los Cuchumatanes; 2,600 m; F (holo).

Cladium costatum Steyerm., Fieldiana Bot. 28(1): 50. 1951. *J. A. Steyermark 60829*; 3 Dec. 1944; Venezuela, Bolívar, Quebrada Sororopan between Santa Teresita de Kavanayen and Río Tek-Yunsen; 1,375 m; F (holo).

Fimbristylis tamaensis Steyerm., Fieldiana Bot. 28(1): 39. 1951. *J. A. Steyermark 57422*; 17 July 1944; Colombia–Venezuela border, along Río Táchira, between Delicias and Paraquita; 1,675–1,980 m; F (holo).

Hypolytrum tepuianum Steyerm., Fieldiana Bot. 28(1): 51. 1951. *J. A. Steyermark 60238*; 15–17 Nov. 1944; Venezuela, Bolívar, vicinity 'Misia Kathy Camp' on mesa between Ptari-tepui and Sororopan-tepui; 1,615 m; F (holo) = *Mapania tepuiana* (Steyerm.) T. Koyama, 1967.

Mapania maguireana T. Koyama & Steyerm., Mem. New York Bot. Gard. 17(1): 63. 1967. *B. Maguire & D. B. Fanshawe 32351*; Guyana, Membaru–Kurupung trail, Kakaralli forest; 1,000 m; NY (holo).

Oreobolus venezuelensis Steyerm., Bol. Soc. Venez. Ci. Nat. 11: 308. 1950. *J. A. Steyermark 57198*; 14 July 1944; Venezuela, Táchira, paramito at base of Páramo de Tamá; 2,500 m; F (holo).

Rhynchospora bolivarana Steyerm., Fieldiana Bot. 28(1): 40. 1951. *J. A. Steyermark 60206*; 15 Nov. 1944; Venezuela, Bolívar, Salto de Iwaracuru-meru, W end Sororopan-tepui; 1,500 m; F (holo).

Rhynchospora culmenicola Steyerm., Fieldiana Bot. 28(1): 41. 1951. *J. A. Steyermark 62110*; 15 Apr. 1945; Venezuela, Monagas, Cerro Negro; 2,180 m; F (holo) = *R. dissitiflora* Steudel, 1972.

Rhynchospora duidae Steyerm., Fieldiana Bot. 28(1): 43. 1951. *J. A. Steyermark 68254*; 2 Sep. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,065–1,220 m; F (holo).

Rhynchospora karuaiana Steyerm., Fieldiana Bot. 28(1): 43. 1951. *J. A. Steyermark 60334*; 18 Nov. 1944; Venezuela, Bolívar, Río Karuai, between Teresita de Kavanayen and base of Ptari-tepui; 1,200 m; F (holo) = *R. triflora* (Poir.) Vah., 1972.

Rhynchospora paramora Steyerm., Fieldiana Bot. 28(1): 44. 1951. *J. A. Steyermark 56550*; 14 May 1944; Venezuela, Mérida, Páramo de los Colorados, between El Molino and San Isidro Alto; 2,745–2,955 m; F (holo).

Rhynchospora ptaritepuiana Steyerm., Fieldiana Bot. 28(1): 45. 1951. *J. A. Steyermark 59830*; 4 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 2,130 m; F (holo) = *R. lechleri* Steudel, 1972.

Rhynchospora sanariapensis Steyerm., Fieldiana Bot. 28(1): 46. 1951. *J. A. Steyermark 58469*; 8 Sep. 1944; Venezuela, T.F. Amazonas, tributary of Orinoco River, near Río Sanariapo, vicinity of Sanariapo; F (holo).

Rhynchospora sororopana Steyerm., Fieldiana Bot. 28(1): 46. 1951. *J. A. Steyermark 60831*; 3 Dec. 1944; Venezuela, Bolívar, between Santa Terresita de Kavanayen and Río Tek-Yunsen, along Quebrada Sororopan; F (holo) = *R. biflora* Bockeler, 1972.

Rhynchospora tamana Steyerm., Fieldiana Bot. 28(1): 47. 1951. *J. A. Steyermark 57404*; 15 July 1944; Venezuela, Táchira, Páramo de Tamá, along border; 3,045–3,475 m; F (holo).

Rhynchospora tepuiana Steyerm., Fieldiana Bot. 28(1): 48. 1951. *J. A. Steyermark 58652*; 25 Sep. 1944; Venezuela, Bolívar, Mt. Roraima, near Rondon Camp; 2,040 m; F (holo) = *R. flexuosa* C. B. Clarke subsp. *tepuiana* Steyerm., 1972.

Rhynchospora tomentosa Steyerm., Fieldiana Bot. 28(1): 49. 1951. *J. A. Steyermark 57391*; 15 July 1944; Venezuela, Táchira, Páramo de Tamá, on border; 3,045–3,475 m; F (holo).

Rhynchospora trichochaeta C. B. Clarke var. *venezuelensis* Steyerm., Fieldiana Bot. 28(1): 49. 1951. *J. A.*

Steyermark 57587; 1 Aug. 1944; Venezuela, Bolívar, between Ciudad Bolívar and Río Caroni; 100 m; F (holo) = *R. subplumosa* C. B. Clarke, 1972.

Uncinia meridensis Steyerm., Fieldiana Bot. 28(1): 61. 1951. *J. A. Steyermark 57039*; 6 July 1944; Venezuela, Mérida, El Aquila above Páramo de Mucuchies; 4,025 m; F (holo).

Vesicarex Steyerm., Fieldiana Bot. 28(1): 63. 1951 gen. nov.

Vesicarex collumanthus Steyerm., Fieldiana Bot. 28(1): 63. 1951. *J. A. Steyermark 57040*; 6 July 1944; Venezuela, Mérida, El Aquila, above Páramo de Mucuchies; 4,025 m; F (holo).

DICHAPETALACEAE

Dichapetalum bullatum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 169. 1944. *J. A. Steyermark 39874*; 7 Dec. 1941; Guatemala, Dept. Izabal, along road between Puerto Barrios and Santo Tomás; sea level; F (holo).

DILLENIACEAE

Doliocarpus esmeraldae Steyerm., Fieldiana Bot. 28(2): 366. 1952. *J. A. Steyermark 57879*; 23 Aug. 1944; Venezuela, T.F. Amazonas, between Sabana Grande and SE base of Cerro Duida; 200 m; F (holo).

Doliocarpus ptariensis Steyerm., Fieldiana Bot. 28(2): 367. 1952. *J. A. Steyermark 59972*; 10–11 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,585–1,600 m; F (holo).

DIOSCOREACEAE

Dioscorea abysmophila Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *B. Maguire et al. 42319*; 8–9 Dec. 1957; Venezuela; MO (3291186), NY (holo).

Dioscorea bolivarensis Steyerm., Fieldiana Bot. 28(1): 158. 1951. *J. A. Steyermark 57551*; 31 July 1944; Venezuela, Bolívar, W of Upata, Río Upata; 500 m; F (holo).

Dioscorea lasseriana Steyerm., Fieldiana Bot. 28(1): 158. 1951. *J. A. Steyermark 61836*; 5 Apr. 1949; Venezuela, Monagas, between La Sabana de las Piedras and Cerro Negro, NW of Caripe; 1,200-1,500 m; F (holo).

Dioscorea neblinensis Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *B. Maguire et al. 37328*; 16 Jan. 1954; Venezuela; MO (3291183), NY (holo).

Dioscorea sororopana Steyerm., Fieldiana Bot. 28(1): 159. 1951. *J. A. Steyermark 60124*; 14 Nov. 1944; Venezuela, Bolívar, Sororopan-tepui; 2,255 m; F (holo).

DIPSACACEAE

Dipsacus sylvestris Huds. f. *albidus* Steyerm., Rhodora 60: 174–175. 1959. *K. E. Bartel 1*; 25 Aug. 1957; U.S.A., Illinois, Cook Co., Chicago, Mt. Hope Cemetery on 115th St.; F (holo).

DIPTEROCARPACEAE

Pakaraimaea dipterocarpacea Maguire & Ashton subsp. *nitida* Maguire & Steyerm., Mem. New York Bot. Gard. 32: 308. 1981. *J. A. Steyermark et al. 113438*; 20–25 Jan. 1977; Venezuela, Bolívar, Cerro Guaiquinima; 750 m; NY (holo). VEN.

DROSERACEAE

Drosera arenicola Steyerm., Fieldiana Bot. 28(2): 243. 1952. *J. A. Steyermark 60920*; 16–17 Sep. 1944; Venezuela, Bolívar, vicinity of Santa Teresita de Kavanayen; 1,220 m; F (holo).

Drosera felix Steyerm. & L. B. Smith, Rhodora 76: 491. 1974. *J. A. Steyermark et al. 105468*; 19 Feb. 1972; Venezuela, Bolívar, carretera El Dorado to Santa Elena de Uairen, S of El Dorado; 1,200–1,400 m; MO (2670118), NY, US, VEN (holo).

Drosera sanariapoana Steyerm., Fieldiana Bot. 28(2): 243. 1952. *J. A. Steyermark 58472*; 8 Sep. 1944; Venezuela, T.F. Amazonas, vicinity of Sanariapo; 100 m; F (holo).

Drosera tenella Willd. var. *esmeraldae* Steyerm., Fieldiana Bot. 28(2): 244. 1952. *J. A. Steyermark 57850*; 22 Aug. 1944; Venezuela, T.F. Amazonas, between Esmeralda savanna and SE base of Cerro Duida; 200 m; F (holo) = *D. esmeraldae* (Steyerm.) Maguire & Wurd., 1957.

EBENACEAE

Diospyros anzoateguiensis Steyerm., Fieldiana Bot. 28(3): 489. 1953. *J. A. Steyermark 61513*; 16 Mar. 1945; Venezuela, Anzoátegui, between Bergantín and San José; 300–400 m; F (holo).

Diospyros johnstoniana Standl. & Steyerm., Fieldiana Bot. 22(3): 165. 1940. *P. C. Standley 59934*; Guatemala, Dept. Sacatepéquez, along Río Guacalate, near Pastores; 1,600 m; F (holo).

Diospyros virginiana L. f. *pumila* Palmer & Steyerm., Ann. Missouri Bot. Gard 22: 616. 1935. *B. F. Bush 7041*; 6 June 1913; U.S.A., Missouri, Dodson; GH (holo) = *D. virginiana* L. var. *pubescens* (Pursh) Dippel f. *pumila* (Palmer & Steyerm.) Steyerm., 1960.

Diosypros zacapana Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 263. 1940. *J. A. Steyermark 29490*; 10 Oct. 1939; Guatemala, Dept. Zacapa, Sierra de las Minas; 250–400 m; F (holo) = *D. yatesiana* Standl., 1967.

ELAEOCARPACEAE

Sloanea autanae Steyerm., Pittieria 7: 13. 1978. *J. A. Steyermark 105222*; 21–22 Sep. 1971; Venezuela, T.F. Amazonas, Cerro Autana; 1,230–1,270 m; VEN (holo) = *S. steyermarkii* C. E. Smith subsp. *autanae* (Steyerm.) Steyerm., 1988.

Sloanea bolivarensis Steyerm.; Ann. Missouri Bot. Gard. 75: 1572. 1988. *R. L. Liesner & A. González 11479*; 10 Apr. 1981; Venezuela, Bolívar, 7 km NE of Ciudad Píar; 350–500 m; VEN (holo), MO.

Sloanea breviseta Steyerm., Fieldiana Bot. 28(2): 357. 1952. *J. A. Steyermark 62215*; 19 Apr. 1945; Venezuela, Monagas, Montaña de Aguacate; 600–900 m; F (holo).

Sloanea carrenoi Steyerm., Bol. Soc. Venez. Ci. Nat. 32: 349. 1976. *J. A. Steyermark et al. 109699*; 28 Feb.–1,2,5 Mar. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Jaua; VEN (holo).

Sloanea cataniapensis Steyerm., Ann. Missouri Bot. Gard. 75: 1572. 1988. *J. A. Steyermark et al. 122215*; Venezuela, T.F. Amazonas, Dept. Atures, N side of Río Cataniapo, 48 km SE of Puerto Ayacucho; 200–300 m; MO, VEN (holo).

Sloanea caudata Steyerm., Fieldiana Bot. 28(2): 357. 1952. *J. A. Steyermark 60544*; 25 Nov. 1944; Ven-

ezuela, Bolívar, Quebrada O-paru-ma; 915–1,065 m; F (holo).

Sloanea cavicola Steyerm., Bol. Soc. Venez. Ci. Nat. 32: 351. 1976. *J. A. Steyermark et al. 109039*; 13 Feb. 1974;. Venezuela, Bolívar, Meseta del Jaua, Cerro Sarasariñama; 1,320 m; MO (2582381), VEN (holo).

Sloanea davidsei Steyerm., Ann. Missouri Bot. Gard. 75: 1575. 1988. *G. Davidse 27733*; 23–25 July 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, Río Pacimoni, between its mouth and its jct. with the Río Baria and Río Yatua; 80 m; MO, VEN (holo).

Sloanea jauaensis Steyerm., Bol. Soc. Venez. Ci. Nat. 32: 353. 1976. *J. A. Steyermark et al. 109841*; 28 Feb.–1,2,5 Mar. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Jaua; 1,810–1,880 m; VEN (holo) = *S. steyermarkii* C. E. Smith subsp. *jauaensis* (Steyerm.) Steyerm., 1988.

Sloanea jauaensis Steyerm. var. *minor* Steyerm., Bol. Soc. Venez. Ci. Nat. 32: 354, 1976. *J. A. Steyermark et al. 109695*; 28 Feb. 1976; Venezuela, Bolívar, Meseta del Jaua, Cerro Jaua; 1,810–1,880 m; VEN (holo) = *S. steyermarkii* C. E. Smith subsp. *jauaensis* (Steyerm.) Steyerm., 1988.

Sloanea larensis Steyerm., Acta Bot. Venez. 10: 239. 1975. *J. A. Steyermark et al. 110148*; 6 July 1974; Venezuela, Lara, Distrito Jiménez, Cubiro; 1,850–1,950 m; VEN (holo).

Sloanea longiaristata Steyerm., Ann. Missouri Bot. Gard. 75: 1577. 1988. *R. Liesner 18455*; 8–9 Mar. 1985; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca, 1–2 km N of Sima Camp; 1,100 m; MO, VEN (holo).

Sloanea maroana Steyerm., Pittieria 7: 14. 1978. *J. A. Steyermark & G. S. Bunting 102799*; Venezuela, T.F. Amazonas, 1 km al este de Maroa; VEN (holo) = *S. floribunda* Spruce ex Benth., 1988.

Sloanea megacarpa Steyerm. & Marcano Berti, Bol. Soc. Venez. Ci. Nat. 26: 467. 1966. *L. Marcano Berti 418*; 29 Nov.–18 Dec. 1964; Venezuela, T.F. Delta Amacuro; E of Río Grande, NE of El Palmar; VEN (holo).

Sloanea merevariensis Pittier ex Steyerm., Ann. Missouri Bot. Gard. 75: 1579. 1988. *F. Cardona 1051* (also numbered *1053, 1055*); n.d.; Venezuela, Bolívar, Alto Río Guaña (Merevari) near Brazil frontier; F (holo), US, VEN.

Sloanea onotillo Steyerm., Fieldiana Bot. 28(2): 358. 1952. *J. A. Steyermark 61016*; 20 Feb. 1945; Venezuela, Anzoátegui, along Río León by Quebrada Danta; 500 m; F (holo).

Sloanea onotillo Steyerm. var *major* Steyerm., Fieldiana Bot. 28(2): 359. 1952. *J. A. Steyermark 61726*; 23 Mar. 1945; Venezuela, Anzoátegui, Río Marville, Fila Grande; 900–1,400 m; F (holo).

Sloanea parvifructa Steyerm., Ann. Missouri Bot. Gard. 75: 1579. 1988. *N. T. Silva & U. Brazão 60865*; 23 Jan. 1966; Brazil (near Venezuelan border), Serra de Neblina, Río Negro, Río Cauaburí, Río Maturacá, between Missão Salesiana and Serra Pirapucú; 800–1,000 m; MO (holo), NY.

Sloanea petenensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 172. 1944. *J. A. Steyermark 45309*; 25 Mar. 1942; Guatemala, Dept. Petén, forest between Finca Yalpemech, along Río San Diego, and San Diego on Río Cancuén; 50–150 m; F (holo).

Sloanea pittieriana Steyerm., Fieldiana Bot. 28(2): 359. 1952. *J. A. Steyermark 60261*; 15–17 Nov. 1944; Venezuela, Bolívar, between Ptari-tepui and Sororopan-tepui; 1,615 m; F (holo).

Sloanea ptariana Steyerm., Fieldiana Bot. 28(2): 360. 1952. *J. A. Steyermark 60668*; 28 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,220 m; F (holo).

Sloanea sipapoana Steyerm., Ann. Missouri Bot. Gard. 75: 1580–1581. 1988. *B. Maguire & L. Politi 27674*; 15 Dec. 1948; Venezuela, T.F. Amazonas, Cerro Sipapo (Paráque), Camp Savanna; 1,500 m; MO (holo), NY.

Sloanea subpsilocarpa Steyerm., Ann. Missouri Bot. Gard. 75: 1583. 1988. *L. Marcano Berti 447*; 29 Nov.–18 Dec. 1964; Venezuela, T.F. Delta Amacuro, E de Río Grande, ENE El Palmar, near limits of Bolívar; VEN (holo), MO, NY.

Sloanea venezuelana Steyerm., Fieldiana Bot. 28(2): 361. 1952. *J. A. Steyermark 62216*; 19 Apr. 1945: Venezuela, Monagas, Montaña de Aguacate; 600–900 m; F (holo).

Sloanea wurdackii Steyerm., Ann. Missouri Bot. Gard. 75: 1583. 1988. *J. Wurdack & J. Monachino 41017*; 30 Dec. 1955; Venezuela, Bolívar, Río Paraguaza, just below Raudal Maraca (ca. 110 km above river mouth); 115 m; MO (holo), NY.

Sloanea yapacanae Steyerm., Pittieria 7: 15. 1978. *J. A. Steyermark & G. S. Bunting 103186*; Venezuela, T.F. Amazonas, Cerro Yapacana; 1,000–1,200 m; VEN (holo) = *S. steyermarkii* C. E. Smith subsp. *jauaensis* (Steyerm.) Steyerm., 1988.

ELATINACEAE

Elatine fassettiana Steyerm., Fieldiana Bot. 28(2): 400. 1952. *J. A. Steyermark 55905*; 16 Apr. 1944; Venezuela, Mérida, near El Aguila; 3,960 m; F (holo), MO (1621390).

ERICACEAE

Befaria neblinensis Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 141. 1978. *B. Maguire & J. Murca Pires 60477*; 2 Dec. 1965; Venezuela, T.F. Amazonas, Cerro de la Neblina; 2,500–2,800 m; NY (holo), VEN. Note: *Bejaria* is the correct spelling.

Cavendishia neblinae Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 165. 1978. *B. Maguire et al. 37254*; Venezuela, T.F. Amazonas, Cerro de la Neblina; 1,500–1,700 m; NY (holo), US.

Cavendishia salicifolia Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 167. 1978. *B. Maguire & D. B. Fanshawe 32430*; 29 Oct.–4 Nov. 1951; Guyana, Membaru–Kurupung trail; NY (holo), US.

Ceratostema glandulifera Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 160. 1978. *S. S. Tillett et al. 45057*; 8 Aug. 1960; Guyana, upper Mazaruni River, Mt. Ayanganna; 1,370–1,525 m; NY (holo).

Ledothamnus atroadenus Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 249. 1978. *J. A. Steyermark 73886*; 13 Apr. 1953; Venezuela, Bolívar, Chimantá Massif, Abacapa-tepui; 2,125–2,300 m; F, NY (holo), VEN.

Ledothamnus decumbens Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 143. 1978. *J. A. Steyermark & J. J. Wurdack 737*; 11 Feb. 1955; Venezuela, Bolívar, Chimantá Massif; 2,200 m; F, NY (holo), VEN.

Ledothamnus jauaensis Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 146. 1978. *J. A. Steyermark 97918*; 22–27 Mar. 1967; Venezuela, Bolívar, Meseta de Jaua, Cerro Sarasariñama; 2,000 m; NY (holo), VEN.

Ledothamnus luteus Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard 29(1): 146. 1978 *J. A. Steyermark & J. J. Wurdack 953*; 20 Feb. 1955; Venezuela, Bolívar, Chimantá Massif; 1,895–1,910 m; F, NY (holo), VEN.

Ledothamnus stenopetalus Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 149. 1978. *J. A. Steyermark 97944*; 22–27 Mar. 1967; Venezuela, Bolívar, Meseta de Jaua, Cerro Sarasariñama; 1,922–2,100 m; NY (holo), VEN.

Ledothamnus steyermarkii A. C. Smith subsp. *longisetus* Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 152. 1978. *J. A. Steyermark 97878*; 22–27 Mar. 1967; Venezuela, Bolívar, Meseta de Jaua, Cerro Sarasariñama; 1,922–2,100 m; NY (holo), VEN.

Mycerinus chimantensis Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 177. 1978. *J. A. Steyermark & J. J. Wurdack 825*; 13 Feb. 1955; Venezuela, Bolívar, Chimantá Massif; 2,210 m; F, NY (holo), VEN.

Mycerinus viridiflorus Steyerm. & Maguire, Bol. Soc. Ci. Nat. 32: 373. 1976. *J. A. Steyermark et al. 109181*; 16–18 Feb. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Sarisariñama; 1,400 m; VEN (holo).

Orthaea merumensis Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 168. 1978. *S. S. Tillett et al. 44867*; 12 July 1960; Guyana, Merume Mts., upper Mazaruni River basin; 520 m; NY (holo).

Orthaea paruensis Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 171. 1978. *R. S. Cowan & J. J. Wurdack 31061*; 31 Jan. 1951; Venezuela, T.F. Amazonas, Serranía Parú, Río Parú, Caño Asisa, along W Rim; 2,000 m; NY (holo).

Orthaea pubifolia Maguire, Steyerm. & Luteyn, Mem. New York Gard. 29(1): 171. 1978. *B. Maguire & D. Fanshawe 32339*; 29 Oct.–4 Nov. 1951; Guyana, Pakaraima Mts., Membaru–Kurupung trail; 1,000 m; NY (holo).

Orthaea thibaudioides Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 173. 1978. *B. Maguire et al. 30945*; 15 Jan. 1951; Venezuela, T.F. Amazonas, Cerro Moriche, Río Ventuari; 1,250 m; NY (holo).

Orthaea venamensis Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 174. 1978. *J. A. Steyermark et al. 92423*; 29–30 Dec. 1963; Venezuela, Bolívar, Cerro Venamo; 950–1,150 m; NY, VEN (holo).

Orthaea wurdackii Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 174. 1978. *B. Maguire et al. 42350*; 11 Dec. 1957; Venezuela, T.F. Amazonas, Cerro de la Neblina, Río Yatua; 1,900 m; NY (holo).

Pernettia saxicola Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 139. 1944. *J. A. Steyermark 36110*; 19 Feb. 1940; Guatemala, Dept. San Marcos, Volcán Tacaná; 4,400 m; F (holo).

Psammisia breweri Steyerm. & Maguire, Bol. Soc. Venez. Ci. Nat. 32: 377. 1976. *J. A. Steyermark et al. 109076*; 12–15 Feb. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Sarasariñama; 1,000 m; VEN (holo) = *Psammisia urichiana* (Britt.) A. C. Smith, 1978.

Rhododendron roseum (Loisel.) Rehder f. *albidum* Steyerm., Rhodora 62: 131. 1960. *J. A. Steyermark 8522*; 24 May 1933; U.S.A., Missouri, Ste. Genevieve County, E of Chimney rocks, along River Aux Vases, 5 mi. E of Pickle; MO, UMO (holo).

Tepuia intermedia Steyerm., Acta Bot. Venez. 2: 303. 1967. *J. A. Steyermark 93980*; 15 May 1964; Venezuela, Bolívar, Auyan-tepui; 2,050–2,300 m; VEN (holo).

Tepuia multiglandulosa Steyerm. & Maguire, Acta Bot. Venez. 2: 301. 1967. *J. A. Steyermark 75733*; 19 June 1953; Venezuela, Bolívar, Auyan-tepui; 2,000 m; VEN (holo).

Tepuia tatei Camp var. *chimantana* Steyerm. & Maguire, Acta Bot. Venez. 2: 308. 1967. *J. A. Steyermark & J. J. Wurdack 387*; 4 Feb. 1955; Venezuela, Bolívar, Auyan-tepui; 1,925–1,940 m; VEN (holo).

Tepuia vareschii Steyerm., Acta Bot. Venez. 2: 306. 1967. *V. Vareschi & E. Foldats 4966*; Apr. 1956; Venezuela, Bolívar, Auyan-tepui; 2,300 m; VEN (holo).

Thibaudia breweri Steyerm. & Maguire, Bol. Soc. Venez. Ci. Nat. 32: 378. 1976. *J. A. Steyermark et al. 109315*; 22–28 Feb. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Jaua; 1,750–1,800 m; VEN (holo).

Thibaudia carrenoi Steyerm. & Maguire, Bol. Soc. Venez. Ci. Nat. 32: 380. 1976. *J. A. Steyermark et al. 109298*; 22–28 Feb. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Jaua; 1,750–1,800 m; VEN (holo).

Thibaudia dolichandra Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 180. 1978. *B. & C. K. Maguire 35149*; 11 Feb. 1953; Venezuela, T.F. Amazonas, Cerro Yutaje, Serranía Yutaje; 1,400 m; NY (holo).

Thibaudia jauaensis Steyerm. & Maguire, Bol. Soc. Venez. Ci. Nat. 32: 383. 1976. *J. A. Steyermark et al. 109584*; 27 Feb. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Jaua; 2,228–2,250 m; VEN (holo).

Thibaudia longipes Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 185. 1978. *B. Maguire et al. 29564*; 20 Nov. 1950; Venezuela, T.F. Amazonas, Cerro Duida; NY (holo).

Thibaudia smithiana Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 186. 1978. *B. Maguire & L. Politi 28349*; 14 Jan. 1949; Venezuela, T.F. Amazonas, Cerro Sipapo (Paraque); 1,815 m; NY (holo).

Vaccinium chimantense Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 189. 1978. *J. A. Steyermark & J. J. Wurdack 669*; 9 Feb. 1955; Venezuela, Bolívar, Chimantá Massif, Torono-tepui; 2,165–2,180 m; F, NY (holo), VEN.

Vaccinium haematinum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 139. 1944. *J. A. Steyermark 48572*; 14 July 1942; Guatemala, Dept. Huehuetenango, Cerro Huitz; 1,500–2,600 m; F (holo).

Vaccinium minarum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23: 219. 1947. *J. A. Steyermark 43295*; 26 Jan. 1942; Guatemala, Dept. Zacapa, Volcán Gemelos, Sierra de las Minas; 2,100–3,200 m; F (holo).

Vaccinium puberulum Klotzsch var. *jauaensis* Maguire, Steyerm. & Luteyn, Mem. New York Bot. Gard. 29(1): 192. 1978. *J. A. Steyermark 98054*; 22–27 Mar. 1967; Venezuela, Bolívar, Meseta de Jaua, Cerro Sarasariñama; 1,922–2,100 m; NY, VEN (holo).

ERIOCAULACEAE

Paepalanthus holstii Steyerm., Ann. Missouri Bot. Gard. 75: 311. 1988. *B. K. Holst 3523*; 22 May 1987;

Venezuela, Bolívar, Distr. Piar, Murisipán-tepui, summit; 2,300 m; MO (holo–3446413), VEN.

Paepalanthus meseticola Mold. & Steyerm., Bol. Soc. Venez. Ci. Nat. 32: 281. 1976. *J. A. Steyermark et al. 109389*; 22–28 Feb. 1974; Venezuela, Bolívar, Cerro Jaua; Mold. Herbarium (holo). VEN.

Paepalanthus venetifolius Mold. & Steyerm., Bol. Soc. Venez. Ci. Nat. 32: 284. 1976. *J. A. Steyermark et al. 109405*; 22–28 Feb. 1974; Venezuela, Bolívar, Meseta de Jaua, Cerro Jaua; 1,750–1,800 m; Mold. Herbarium (holo), VEN.

ERTHROXYLACEAE

Erthroxylon venezuelense Steyerm., Fieldiana Bot. 28(2): 271. 1952. *J. A. Steyermark 60371*; 20–21 Nov. 1944; Venezuela, Bolívar, Quebrada O-paru-ma, between Santa Teresita de Kavanayen and Río Pacairao; 1,065–1,220 m; F (holo) = *Erthroxylum mucronatum* Benth., 1966.

EUPHORBIACEAE

Amanoa pubescens Steyerm., Fieldiana Bot. 28(2): 304. 1952. *Ll. Williams 14439*; 20 Feb. 1942; Venezuela, T.F. Amazonas, Río Guainía; 128 m; F (holo).

Bernardia venezuelana Steyerm., Fieldiana Bot. 28(2): 306. 1952. *J. A. Steyermark 55603*; 27–28 Feb. 1944; Venezuela, Distr. Federal, Cordillera del Avila; F (holo).

Chaetocarpus williamsii Steyerm., Fieldiana Bot. 28(2): 306. 1952. *Ll. Williams 14312*; 12 Feb. 1942; Venezuela, T.F. Amazonas, Río Guainía, Maroa; 127 m; F (holo).

Conceveiba krukoffii Steyerm., Field Mus. Nat. Hist., Bot. Ser. 17(5): 414. 1938. *B. A. Krukoff 8396*; 26 Oct.–11 Dec. 1936; Brazil, Amazonas, Mun. São Paulo de Olivenca, basin of Creek Belem, basin of Rio Solimões; MO (1253872), NY (holo) = *C. guianensis* Aublet, 1967.

Conceveiba magnifica Steyerm., Field Mus. Nat. Hist., Bot. Ser. 17(5): 414. 1938. *B. A. Krukoff 8698*; 26 Oct.–11 Dec. 1936; Brazil, Amazonas, Mun. São Paulo de Olivenca, basin of Creek Belem, basin of Rio Solimões; MO (1250474), NU (holo).

Conceveiba simulata Steyerm., Field Mus. Nat. Hist., Bot. Ser. 17(5): 416. 1938. *B. A. Krukoff 8616*; 26 Oct.–11 Dec. 1936; Brazil, Amazonas, Mun. São Paulo de Olivenca, basin of Creek Belem, basin of Rio Solimões; MO (1254141), NY (holo) = *C. guianensis* Aublet, 1967.

Conceveibastrum ptarianum Steyerm., Fieldiana Bot. 28(2): 308. 1952. *J. A. Steyermark 60021*; 10–11 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,585–1,600 m; F (holo) = *Conceveiba ptariana* (Steyerm.) Jabl., 1967.

Croizatia Steyerm., Fieldiana Bot. 28(2): 1952, gen nov.

Croizatia naiguatensis Steyerm., Brittonia 30(1): 40. 1978. *S. S. Tillett et al. 82*; 7 Dec. 1973; Venezuela, Distr. Federal, Cerro Naiguata; 2,000 m; DAV, VEN (holo).

Croizatia neotropica Steyerm., Fieldiana Bot. 28(2): 309. 1952. *J. A. Steyermark 61523*; 18 Mar. 1945; Venezuela, Anzoátegui, Quebrada Seca, E of Bergantín; F (holo).

Croton chamanus Steyerm., Fieldiana Bot. 28(2): 312. 1952. *J. A. Steyermark 56232*; 2 May 1944; Venezuela, Mérida, Río Chama, above Los González; 1,220–1,820 m; F (holo).

Croton croizatii Steyerm., Fieldiana Bot. 28(2): 312. 1952. *J. A. Steyermark 56124*; 26 Apr. 1944; Venezuela, Mérida, near Hacienda Agua Blanca; 975 m; F (holo).

Croton deserticolus Steyerm., Fieldiana Bot. 28(2): 313. 1952. *J. A. Steyermark 56821*; 28 May 1944; Venezuela, Lara, between Carora and Barquisimeto; 500 m; F (holo).

Croton douradensis Steyerm., Los Angeles Co. Mus. Contr. Sci. 21: 4. 1958. *E. Y. Dawson 14973*; n.d.; Brazil, Goiás, S Serra Dourada; F, LAM, R (holo).

Croton guaiquinimae Steyerm., Brittonia 32: 21. 1980; *J. A. Steyermark et al. 117473*; 26 May 1978; Venezuela, Bolívar, Cerro Guaiquinima; VEN (holo).

Croton huberi Steyerm., Brittonia 30: 41. 1978. *O. Huber. & A. Cleef 543*; 4 Mar. 1977; Venezuela, Distr. Federal, Parque Nacional El Avila; 2,000 m; VEN (holo).

Croton inaequilobus Steyerm.; Los Angeles Co. Mus. Contr. Sci. 21: 7. 1958. *E. Y. Dawson 14685*; 25 Apr. 1956; Brazil, Goiás, Chapada dos Veadeiros 14 mi. S of Veadeiros; F, LAM, R (holo).

Croton kavanayensis Steyerm., Fieldiana Bot. 28(2): 313. 1952. *J. A. Steyermark 60386*; 20–21 Nov. 1944; Venezuela, Bolívar, Quebrada O-paru-ma; 1,065–1,220 m; F (holo).

Croton larensis Steyerm., Fieldiana Bot. 28(2): 314. 1952. *J. A. Steyermark 56806*; 28 May 1944; Venezuela, Lara, between Trujillo–Lara boundary; 305 m; F (holo).

Croton roraimensis Croizat var. *subintegrus* Steyerm., Fieldiana Bot. 28(2): 315. 1952. *J. A. Steyermark 59925*; 7 Nov. 1944; Venezuela, Bolivar, Ptari-tepui; 2,410–2,450 m; F (holo) = *C. roraimensis* Croizat var. *roraimensis*.

Croton standleyi Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(3): 151. 1940. *M. E. Davidson 892*; 12 July 1938; Panamá, Chiriquí, Distr. Boquete, Volcán Chiriquí; 2,100 m; F (holo), MO (1172438) = *C. pungens* Jacq., 1967.

Croton subincanus Muell. Arg. var. *guaiquinimensis* Steyerm., ined.?. *J. A. Steyermark et al. 113330*; 20–25 Jan. 1977; Venezuela, Bolívar, Cerro Guaiquinima, a lo largo del Río Szczerbanari (Río Carapo); MO (iso—2774296).

Croton sucrensis Steyerm., Fieldiana Bot. 28(2): 315. 1952. *J. A. Steyermark 62875*; 23 May 1945; Venezuela, Sucre, E of Cumana, near Quetepe, between km 18 and 20; 30 m; F (holo).

Croton turumiquirensis Steyerm., Fieldiana Bot. 28(2): 315. 1952. *J. A. Steyermark 62532*; 5 May 1945; Venezuela, Sucre, above La Trinidad SW of Cocollar; 2,100–2,200 m; F (holo).

Drypetes amazonica Steyerm., Field Mus. Nat. Hist., Bot. Ser. 17(5): 420. 1938. *B. A. Krukoff 6210*; 14 Sep.–11 Oct. 1934; Brazil, Amazonas, basin of Rio Madeira, Mun. Humayta, near Tres Casas; F, NY (holo).

Euphorbia cuchumatanensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 169. 1944. *J. A. Steyermark 51646*; 30 Aug. 1942; Guatemala, Dept. Huehuetenango, Sierra de los Cuchumatanes; 800–1,200 m; F (holo).

Euphorbia guatemalensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 119. 1944. *P. C. Standley 80907*; 22 Dec. 1940; Guatemala, Dept. Chimaltenango, between Chimaltenango and San Martín Jilotepeque; 1,500–1,700 m; F (holo).

Euphorbia latazi H.B.K. var. *glabra* Steyerm., Fieldiana Bot. 28(2): 316. 1952. *J. A. Steyermark 55924*; 15 Apr. 1944; Venezuela, Mérida, Moconoque; 2,510 m; F (holo).

Euphorbia machrisiae Steyerm., Los Angeles Co. Mus. Contr. Sci. 21: 11. 1958. *E. Y. Dawson 14594*; 24 Apr. 1956; Brazil, Goiás, Chapada dos Ceadeiros, 7 km S of Veadeiros; F, LAM, R (holo).

Euphorbia pantomalaca Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 120. 1944. *W. A. Kellerman 5175*; 10 Mar. 1905; Guatemala, Dept. Baja Verapaz, Sierra de las Minas, opposite El Rancho; F (holo).

Euphorbia senilis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 120. 1944. *J. A. Steyermark 50739*; 16 Aug. 1942; Guatemala, Dept. Huehuetenango, between San Ildefonso Ixtahuacán and Cuilco; 1,350–1,600 m; F (holo).

Euphorbia verapazensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 121. 1944. *C. L. Wilson 272*; 4 May 1939; Guatemala, Dept. Alta Verapaz, Río Chiacte; 480 m; F (holo).

Gymnanthes guatemalensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 122. 1944. *J. A. Steyermark 33501*; 5 Jan. 1940; Guatemala, Dept. Quezaltenango, S. Volcán Santa María; 1,300–1,400 m; F (holo).

"*Hieronyma*" *croizatii* Steyerm., Fieldiana Bot. 28(2): 317. 1952. *J. A. Steyermark 57005*; 25 June 1944; Venezuela, Distr. Federal, E of El Junquito; 1,980–2,130 m; F (holo). Note: *Hyeronima* is the correct spelling.

"*Hieronyma*" *oblonga* (Tul.) Muell. Arg. var. *genuina* Muell. Arg. f. *glabra* Steyerm., Fieldiana Bot. 28(4): 951. 1957. *J. A. Steyermark 60686*; 28 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,220 m; F (holo) = *Hyeronima oblonga* (Tul.) Muell. Arg. var. *oblonga*, 1967.

Jatropha standleyi Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(3): 152. 1940. *E. Matuda 2260*; July 1936; Mexico, Oaxaca, Tehuantepec; F (holo).

Mabea elata Steyerm., Field Mus. Nat. Hist., Bot. Ser. 17(5): 418. 1958. *G. Klug 3206*; Aug.–Sep. 1933; Perú, Loreto, between Balsapuerto and Moyobamba; 600–1,200 m; F (holo).

Mabea excelsa Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 123. 1944. *A. F. Skutch 2008*; 27 Dec. 1934; Guatemala, Dept. Quezaltenango, Colombia; 850 m; F (holo).

Mabea klugii Steyerm., Field Mus. Nat. Hist., Bot Ser. 17(5): 416. 1938. *G. Klug 1969*; Jan.–Feb. 1931; Colombia, Comisaria del Putumayo, Umbria; F (holo).

Mabea pirioides Steyerm., Field Mus. Nat. Hist., Bot. Ser. 17(5): 419. 1938. *B. A. Krukoff 1983*; 24 Oct. 1932; Brazil, Campo de Boa Esperanca, Maranhão, Maracassume River region; F (holo).

Mabea standleyi Steyerm., Field Mus. Nat. Hist., Bot. Ser. 17(5): 417. 1938. *G. Klug 2064*; Mar.–Apr. 1931; Perú, Dept. Loreto, Florida, Río Putumayo, at mouth of Río Zubineta; 200 m; F (holo).

Omphalea elaeophoroides Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(3): 152. 1940. *B. A. Krukoff 6297*; 14 Sep.–11 Oct. 1934; Brazil, Amazonas, Piraninhon, Mun. Humayta, near Tres Casas, basin of Río Madeira; F, NY (holo).

Pedilanthus camporum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 124. 1944. *P. C. Standley 87781*; 18 Feb. 1941; Guatemala, Dept. Retalhuleu, between Nueva Linda and Champerico; 120 m; F (holo) = *P. tithymaloides* (L.) Poiteau.

Phyllanthus bolivarensis Steyerm., Fieldiana Bot. 28(2): 317. 1952. *J. A. Steyermark 57688*; 31 July–1 Aug. 1944; Venezuela, Bolívar, 1–10 km NW of Upata; 700 m; F (holo).

Phyllanthus carrenoi Steyerm., Bol. Soc. Venez. Ci. Nat. 32: 343. 1976. *J. A. Steyermark et al. 109596*; 27 Feb. 1974; Venezuela, Bolívar, Cerro Jaua, Cumbre; 2,228–2,250 m; VEN (holo).

Phyllanthus croizatii Steyerm., Fieldiana Bot. 28(2): 317. 1952. *J. A. Steyermark 56854*; 29 May 1944; Venezuela, Yaracuy, near Taria; 75 m; F (holo).

Phyllanthus dawsonii Steyerm., Los Angeles Co. Mus. Contr. Sci. 21: 15. 1958, nom. nov.

Phyllanthus jablonskianus Steyerm. & Luteyn, Ann. Missouri Bot. Gard. 71: 317. 1984. *J. A. Steyermark 129816*; 8 Feb. 1984; Venezuela, T.F. Amazonas, Río Negro, Cerro de la Neblina; 1,880 m; MO (3223155), NY, VEN (holo).

Phyllanthus larensis Steyerm., Fieldiana Bot. 28(2): 318. 1952. *J. A. Steyermark 56813*; 28 May 1944; Venezuela, Lara between Trujillo–Lara boundary and Carora; 305 m; F (holo).

Phyllanthus longipes Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(3): 153. 1940. *P. H. Gentle 2619*; 13 May 1938; Belize, El Cayo Distr., Vaca; F (holo), MICH.

Phyllanthus major Steyerm., Fieldiana Bot. 28(2): 318. 1952. *J. A. Steyermark 59482*; 29 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 1,810 m; F (holo).

Phyllanthus minarum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 125. 1944. *J. A. Steyermark 43385*; 4 Feb. 1942; Guatemala, Dept. El Progreso, Sierra de las Minas; 2,400–2,500 m; F (holo).

Phyllanthus orinocensis Steyerm., Fieldiana Bot. 28(2): 321. 1952. *J. A. Steyermark 57891*; 23 Aug. 1944; Venezuela, T.F. Amazonas, SE base of Cerro Duida; 210 m; F (holo).

Phyllanthus tepuicola Steyerm., Acta Bot. Venez. 10: 236. 1975. *M. Fariñas et al. 433*; Jan.–Feb. 1969; Venezuela, T.F. Amazonas, Cerro Duida; 1,000 m; VEN (holo).

Phyllanthus vacciniifolius (Muell. Arg.) Muell. Arg. var. *vinillaensis* Steyerm., Ann. Missouri Bot. Gard. 71: 317. 1984. *J. A. Steyermark et al. 130328*; 1 Mar. 1984; Venezuela, T.F. Amazonas, Serranía Vinilla, N of Cerro Aratitiyope; 440 m; VEN (holo).

Phyllanthus websterianus Steyerm., Los Angeles Co. Mus. Contr. Sci. 21: 17. 1958. *E. Y. Dawson 14918*; 17 May 1956; Brazil, Goiás, Serra Dourado, 20 km E of Formoso; F, G, LAM, R (holo).

Phyllanthus zanthoxyloides Steyerm., Fieldiana Bot. 28(2): 321. 1952. *J. A. Steyermark 62189*; 19 Apr. 1945; Venezuela, Monagas, Montaña de Aguacate; 600–900 m; F (holo).

Richeria submembranacea Steyerm., Field Mus. Nat. Hist., Bot. Ser 17(5): 419. 1938. *B. A. Krukoff 8513*; 11 Sep.–26 Oct. 1936; Brazil, Amazonas, Mun. São. Paulo de Olivenca, near Palmares, basin of Rio Solimões; NY (holo) = *R. racemosa* (Poepp. & Endl.) Pax & K. Hoffm., 1967.

Senefelderopsis Steyerm., Bot. Mus. Leafl. 15(2): 45. 1951, gen. nov.

Senefelderopsis croizatii Steyerm., Bot. Mus. Leafl. 15(2): 46. 1951. *J. A. Steyermark 60849*; 4–5 Dec. 1944;

Venezuela, Bolívar, Carrao-tepui, SE base; 1,460–1,615 m; F (holo).

Stillingia cruenta Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 125. 1944. *P. C. Standley 91207*; 4 Apr. 1941; Guatemala, Dept. Baja Verapaz, above Santa Rosa; 1,500 m; F (holo).

Tetrorchidium brevifolium Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 126. 1944. *C. L. Wilson 188*; 11 Feb. 1939; Guatemala, Dept. Alta Verapaz, Rubelpec; F (holo).

FABACEAE

Aeschynomene eriocarpa Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 9. 1943. *J. A. Steyermark 29313*; 7 Oct. 1939; Guatemala, Zacapa, Santa Rosalía, 2 mi. S of Zacapa; 200 m; F (holo).

Aeschynomene tricholoma Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 10. 1943. *P. C. Standley 73714*; Oct. 1940; Guatemala, Dept. Chiquimula, near divide on road from Zacapa to Chiquimula; 660 m; F (holo).

Aldina berryi Cowan & Steyerm., Ann. Missouri Bot. Gard. 71: 312. 1984. *J. A. Steyermark et al. 117468*; 26 May 1978; Venezuela, Bolívar, Cerro Guaiquinima; 950 m; MO (3242295, 3234984), US, VEN (holo).

Apios americana Medic. f. *pilosa* Steyerm., Rhodora 40: 179. 1938. *J. A. Steyermark 11390*; 7 July 1936; U.S.A., Missouri, Butler Co., Clark National Forest, Wappapello Purchase Unit, Mud Creek, 2 mi. NW of Rombauer; MO (holo).

Calliandra carcerea Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 161. 1944. *J. A. Steyermark 42985*; 20 Jan. 1942; Guatemala, Dept. El Progreso, between Calera and Volcán Siglo; 2,000–2,200 m; F (holo).

Canavalia munda Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 10. 1943. *J. A. Steyermark 33179*; Dec. 1939; Guatemala, Dept. Quezaltenango, Finca Pirineos, Volcán Santa María; 1,300–1,500 m; F (holo).

Cassia fasciculata Michx. f. *jensenii* Palmer & Steyerm., Ann. Missouri Bot. Gard. 22: 574. 1925. *L. P. Jensen s.n.*; 20 Aug. 1928; U.S.A., Missouri, Franklin Co. Gray Summit; MO (holo).

Cladrastis lutea (Michx. f.) Koch. f. *tomentosa* Steyerm., Rhodora 40: 487. 1938. *E. J. Palmer 35387*; 15 May 1929; U.S.A., Alabama, Tuscaloosa Co., along rocky bluffs of Black Warrior River, near lock 14; F (holo).

Climacorachis guatemala Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 11. 1943. *P. C. Standley 82330*; Jan. 1941; Guatemala, Dept. Huehuetenango, Río Pucal, 14 km S Huehuetenango; 1,800 m; F (holo).

Crudia lacus Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 339. 1940. *J. A. Steyermark 39611*; 17 Apr. 1940; Guatemala, Dept. Izabal, shores of Lake Izabal, between Punta Dos Reales and Punta de Lechuga; sea level; F (holo).

Dalbergia pacifica Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 236. 1940. *P. C. Standley 62109*; 5 Jan. 1939. Guatemala, Dept. Suchitepéquez, Cocales; 215 m; F (holo).

Dipteryx phaeophylla Steyerm., Ann. Missouri Bot. Gard. 71: 313. 1984. *J. A. Steyermark et al. 113200*; 20–25 Jan. 1977; Venezuela, Bolívar, Cerro Guaiquinima; MO (2769905), VEN (holo) = *Spirotropis angustifolia* (DC.) Baill.

Erythrina poeppigiana (Walp.) O. F. Cook f. *redmondii* Steyerm. & Lasser, Phytologia 48(4): 286. 1981. *P. Redmond s.n.*; 9 Mar. 1981; Venezuela, Miranda, Los Chorros, Avenida principal, Caracas; MO (3234983), VEN (holo).

Galactia acuminata Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(3): 144. 1940. *E. Matuda 1741*; 12 Aug. 1937; Mexico, Chiapas, Finca Juárez; F (holo).

Galactia minarum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 342. 1940. *J. A. Steyermark 29640*; 11 Oct. 1939; Guatemala, Dept. Zacapa, Sierra de las Minas; 1,000–1,500 m; F (holo).

Galactia sparsiflora Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 162. 1944. *J. A. Steyermark 43837*; 11 Feb. 1942; Guatemala, Dept. El Progreso, E of Finca Piamonte, Sierra de las Minas; 2,500 m; F (holo).

Lonchocarpus modestus Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 56. 1944. *J. A. Steyermark 39238*; Apr. 1940; Guatemala, Dept. Izabal, Bay of Santo Tomás, between Escobas and Santo Tomás; sea level; F (holo).

Lonchocarpus phlebophyllus Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 56. 1944. *P. C. Standley 74569*; Oct. 1940; Guatemala, Dept. Chiquimula, between Ramírez & Cumbre de Chiquimula; 400–600 m; F (holo).

Machaerium fruticetorum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 240. 1940. *J. A. Steyermark 30689*; 27 Oct. 1939; Guatemala, Dept. Chiquimula, between Chiquimula and La Laguna; 500–1,000 m; F (holo).

Mimosa canahuensis Standl. & Steyerm., Field Mus. Nat Hist., Bot. Ser. 23(4): 163. 1944. *J. A. Steyermark 43758*; 10 Feb. 1942; Guatemala, Dept. El Progreso, Montan Canahuí; 1,600–2,300 m; F (holo).

Mimosa zacapana Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 57. 1944. *J. A. Steyermark 29018*; Oct. 1939; Guatemala, Dept. Zacapa, near Santa Rosalia; 250–350 m; F (holo).

Pachecoa Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 12. 1943, gen. nov.

Pachecoa guatemalensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 13. 1943. *P. C. Standley 75307*; Oct. 1940; Guatemala, Dept. Jutiapa, near Jutiapa; 850 m; F (holo).

Pithecolobium saxosum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 163. 1944. *P. C. Standley 74367*; 14 Oct. 1940; Guatemala, Dept. Chiquimula, Quebrada Shusho, above Chiquimula; 480 m; F (holo).

Pithecolobium zollerianum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 343. 1940. *J. A. Steyermark 37440*; 9 Mar. 1940; Guatemala, Dept. San Marcos, above Finca El Porvenir, up Loma Bandera Shac, Volcán Tajumulco; 1,300–1,500 m; F (holo).

Psoralea tenuiflora Pursh f. *alba* Steyerm., Rhodora 41: 585. 1939. *J. A. Steyermark 5779*; 3 June 1938; U.S.A., Missouri, Benton Co., along Osage River, 2.5 mi. W of Warsaw; MO (holo—1174669), F.

Rhynchosia jalapensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 57. 1944. *J. A. Steyermark 32945*; Dec. 1939; Guatemala, Dept. Jalapa, between Jalapa and San Pedro Pinula; 1,400 m; F (holo).

Swartzia cowanii Steyerm., Brittonia 33: 33. 1981. *J. A. Steyermark et al. 113463*; 22–24 Feb. (Jan. on label) 1977; Venezuela, Bolívar, Cerro Guaiquinima,

alrededores de Salto Szczerbanari, Río Szczerbanari (Río Caparo); MO (2775619); US, VEN (holo).

FAGACEAE

Quercus falcata Michx. f. *angustior* Palmer & Steyerm., Ann Missouri Bot. Gard. 25: 771. 1938. *J. A. Steyermark 12318*; 27 July 1936; U.S.A., Missouri, Oregon Co., along Eleven-Points River, 0.5 mi. N of McCormack Hollow, 3 mi. N of Greer; MO (holo).

Quercus × *inaequalis* Palmer & Steyerm., Ann. Missouri Bot. Gard. 22: 521. 1935. *E. J. Palmer 16342*; 11 Sep. 1919; U.S.A., Missouri, Butler Co., Poplar Bluff; GH (holo). (*Q. phellos* × *Q. velutina*)

Quercus ×*mutabilis* Palmer & Steyerm., Ann. Missouri Bot. Gard. 22: 521. 1935. *E. J. Palmer 26069*; 10 Sep. 1924; U.S.A., Missouri, Bates Co., Montieth Junction; GH (holo). (*Q. palustris* × *Q. shumardii* var. *schneckii*)

Quercus ×*vaga* Palmer & Steyerm., Ann Missouri Bot. Gard. 22: 521. 1935. *E. J. Palmer 25421*; 13 June 1924; U.S.A., Missouri, Nodaway Co., Maryville; GH (holo). (*Q. palustris* × *Q. velutina*)

FLACOURTIACEAE

Banara larensis Steyerm., Fieldiana Bot. 28(2): 404. 1952. *J. A. Steyermark 55424*; 10 Feb. 1944; Venezuela, Lara, between Las Sabanetas, Los Aposentos and Buenos Aires; 1,675–1,430 m; F (holo), K, NY, US.

Banara paucinervosa Steyerm., Fieldiana Bot. 28(2): 406. 1952. *J. A. Steyermark 55824*; 27 Mar. 1944; Venezuela, Mérida, above Las Cuadras along Quebrada Molino; 1,820–2,255 m; F (holo), NY, VEN = *Xylosma paucinervosa* (Steyerm.) Sleumer, 1980.

Bartholomaea Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 251. 1940, gen. nov.

Bartholomaea mollis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 252. 1940. *J. A. Steyermark 39452*; 27 Mar. 1939; Guatemala, Dept. Izabal, Río Dulce, near Livingston; F (holo).

Casearia tachirensis Steyerm., Fieldiana Bot. 28(2): 406. 1952. *J. A. Steyermark 57276*; 14 July 1944; Venezuela, Táchira, above Betania, at base of Páramo de Tamá; 2,285–2,430 m; F (holo), NY.

Euceraea sleumeriana Steyerm. & Maguire, Mem. New York Bot. Gard. 23: 870. 1972. *J. A. Steyermark 97851*; 22–27 Mar. 1967; Venezuela, Bolívar, Meseta de Jaua, Cerro Jaua; 1,922–2,100 m; L, NY, US, VEN (holo).

Hasseltia monagensis Steyerm., Fieldiana Bot. 28(2): 407. 1952. *J. A. Steyermark 61919*; 7 Apr. 1945; Venezuela, Monagas, Cerro de la Cueva de Dona Anita; 1,100–1,200 m; F (holo), NY, US, VEN = *H. floribunda* H.B.K., 1980.

Homalium anzoateguiensis Steyerm., Fieldiana Bot. 28(2): 410. 1952. *J. A. Steyermark 60993*; 20 Feb. 1945; Venezuela, Anzoátegui, along Río León by Quebrada Danta; 500 m; F (holo), L, NY, US, VEN = *H. racemosum* Jacq., 1980.

Ryania casiquiarensis Steyerm., Fieldiana Bot. 28(2): 411. 1952. *Ll. Williams 15564*; 25 May 1942; Venezuela, T.F. Amazonas, Capihuara, Alto Casiquiare; 118 m; A, F (holo), G, NY, US, VEN = *R. speciosa* Vahl. var. *tomentosa* (Miq.) Monachino, 1980.

Xylosma sessile Standl. & Steyerm., Field Mus Nat. Hist., Bot. Ser. 23(4): 177. 1944. *H. von Tuerckheim II.1617*; Jan. 1907; Guatemala, Dept. Alta Verapaz, Cobán; F (holo), US = *X. panamense* Turcz., 1980.

Xylosma trinervium Standl.& Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 178. 1944. *J. A. Steyermark 50876*; 18 Aug. 1942; Guatemala, Dept. Huehuetenango, along Río Cuilco, between Cuilco and San Juan; 1,200–1,300 m; F (holo) = *Neopringlei integrifolia* (Hemsley) S. Watson, 1980.

GARRYACEAE

Garrya corvorum Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(1): 16. 1943. *P. C. Standley 81651*; Dec. 1940; Guatemala, Dept. Huehuetenango, region of Chemal, Sierra de los Cuchumatanes at km 36; 3,300 m; F (holo).

GENTIANACEAE

Celiantha bella Maguire & Steyerm., Mem. New York Bot. Gard, 32: 383. 1981. *B. Maguire et al. 42096*; 19 Nov. 1957; Venezuela, T.F. Amazonas, Cerro de la Neblina; 1,800 m; NY (holo), US, VEN.

Centaurium rosans Standl. & Steyerm., Field Mus. Nat Hist., Bot. Ser. 23(2): 75. 1944. *J. A. Steyermark 34609*; Jan. 1940; Guatemala, Dept. Quezaltenango, Volcán Zunil; 2,500–3,000 m; F (holo) = *C. pauciflorum* (Mart. & Gal.) Rob., 1976.

Chorisepalum acuminatum Steyerm., Bol. Soc. Venez. Ci. Nat. 23: 75. 1962. *J. A. Steyermark & S. Nilsson 450*; 21 Apr. 1960; Venezuela, Bolívar, Cerro Venamo; 1,140 m; UP, VEN (holo) = *C. psychotroides* Ewan var. *acuminatum* (Steyerm.) Maguire, 1981.

Chorisepalum breweri Steyerm. & Maguire, Bol. Soc. Venez. Ci. Nat. 32: 392. 1976. *J. A. Steyermark et al. 109255*; 19–20 Feb. 1974; Venezuela Bolívar, Meseta del Jaua, Cerro Sarasariñama; 1,350 m; VEN (holo).

Gentiana guatemalensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 75. 1944. *P. C. Standley 81113*; Dec. 1940; Guatemala, Dept. Huehuetenango, region Chemal, Sierra de los Cuchumatanes; 3,300 m; F (holo).

Gentiana lewisiae Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 76. 1944. *P.C. Standley 84556*; Guatemala, Dept. Totonicapán, Pacajá, region of El Desconsuelo; 3,100–3,200 m; F (holo).

Gentiana pumilio Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 76. 1944. *J. A. Steyermark 35489*; Feb. 1940. Guatemala, Dept. San Marcos, between San Sebastián and summit of Volcán Tajumulco; 4,000 m; F (holo).

Lisianth[*i*]*us acutilobus* Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 439. 1966. *J. A. Steyermark & S. Nilsson 732*; 25 Apr. 1960; Venezuela, Bolívar, Río Aponguao at km 146; 1,220 m; VEN (holo) = *Irlbachia cardonae* (Gleason) Maguire, 1981. Note: *Lisianthius* is the correct spelling.

Lisianth[*i*]*us calciphilus* Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 267. 1940. *C. L. Wilson 356*; 22 Mar. 1939; Guatemala, Dept. Alta Verapaz, Finca Los Alpes; 1,200 m; F (holo) = *Lisianthius brevidentatus* (Hemsl.) O. Kuntze, 1969.

Lisianth[*i*]*us chimantensis* Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 461. 1967. *J. A. Steyermark & J. J. Wurdack 374-A*; 3 Feb. 1955; Venezuela, Bolívar, Chimantá Massif, Summit Camp; 1940

m; NY (holo) = *Celiantha chimantensis* (Steyerm. & Maguire) Maguire, 1981.

Lisianth[i]us elatus Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 267. 1940. *J. A. Steyermark 38526*; 1 Apr. 1940; Guatemala, Dept. Izabal, between Milla 49.5 and ridge 6 mi. from Izabal, Montaña del Mico; 65–600 m; F (holo).

Lisianth[i]us jauaensis Steyerm. & Maguire, Mem. New York Bot. Gard. 23: 879. 1972. *J. A. Steyermark 98068*; 22–27 Mar. 1967; Venezuela, Bolívar, Cerro Jaua; 1,922–2,100 m; VEN (holo).

Lisianth[i]us petenensis Standl. & Steyerm., Bull. Torrey Bot. Club 84(1): 46. 1957. *C. H. Lundell 3153*; 4 May 1933; Guatemala, Dept. Petén, Nicton, Lake Petén; US (holo).

Lisianth[i]us scabridulus Steyerm., Fieldiana Bot. 28(3): 496. 1953. *J. A. Steyermark 57979*; 25–26 Aug. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,200 m; F (holo) = *Irlbachia tatei* (Gleason) Maguire, 1981.

Macrocarpaea neblinae Maguire & Steyerm., Mem. New York Bot. Gard. 32: 332. 1981. *B. Maguire et al. 37103*; 6 Jan. 1954; Venezuela, T.F. Amazonas, Cerro de la Neblina; 2,000 m; NY (holo).

Macrocarpaea rugosa Steyerm., Bol. Soc. Venez. Ci. Nat. 25: 83. 1963. *J. A. Steyermark, & J. J. Wurdack 861*; 13 Feb. 1955; Venezuela, Bolívar, Chimantá Massif; 2,185–2,210 m; C, NY, VEN (holo).

Schultesia guianensis (Aublet) Malme f. *lutescens* Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 77. 1944. *P. C. Standley 76561*; Nov. 1940; Guatemala, Dept. Jalapa, near Jalapa; 1,360 m; F (holo).

Symbolanthus aracamuniensis Steyerm., Ann. Missouri Bot. Gard.: in press. 1989. *R. L. Liesner & F. Delascio 22079*; 17 Oct. 1987; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp; 1,550 m; MO (holo), VEN.

Symbolanthus huachamacariensis Steyerm., Ann. Missouri Bot. Gard. 75: 1083. 1988. *B. Maguire et al. 29859*; 4 Dec. 1950; Venezuela, T.F. Amazonas, Cerro Huachamacari; 1,700 m; NY, VEN (holo).

Symbolanthus sessilis Steyerm. & Maguire, Mem. New York Bot. Gard. 23: 879. 1972. *J. A. Steyermark 97958*; 22–27 Mar. 1967; Venezuela, Bolívar, Cerro Jaua; 1,922–2,100 m; NY, VEN (holo).

Symbolanthus yaviensis Steyerm., Ann. Missouri Bot. Gard. 75: 1084. 1988. *O. Huber 11849*; 24 Oct. 1986; Venezuela, T.F. Amazonas, Dept. Atures, summit of Cerro Yaví; 100 m; MO (holo), VEN.

Tapeinostemon breweri Steyermark & Maguire, Acta Bot. Venez. 14(3): 42. 1984. *B. Maguire et al. 65593*; 15 Jan. 1981; Venezuela, T.F. Amazonas, Cerro Marahuaca; 2,685; m; K, MG, MO, NY, US, VEN (holo).

Tapeinostemon jauaensis Steyerm. & Maguire, Bol. Soc. Venez. Ci. Nat. 32: 394. 1976. *J. A. Steyermark et al. 109535*; 26 Feb. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Jaua; 1,800 m; VEN (holo).

Tapeinostemon longiflorum Maguire & Steyerm., Mem. New York Bot. Gard. 32: 359. 1981. *B. Maguire et al. 42134*; 17 Nov. 1957; Venezuela, T.F. Amazonas, Cerro de la Neblina; 1,800 m; K, NY (holo), US, VEN.

Tapeinostemon longiflorum Maguire & Steyerm. var. *australe* Maguire & Steyerm., Mem. New York Bot. Gard. 32: 362. 1981. *J. A. Steyermark 103937*; 16–17 Oct. 1970; Venezuela, Cerro de la Neblina; NY (holo), VEN.

Tapeinostemon ptariense Steyerm., Lloydia 14(1): 61. 1951. *J. A. Steyermark 59861*; 4 Nov. 1944; Venezuela, Bolívar, Ptari-tepui, E. of 'Cave Rock'; 213 m; F (holo) = *T. spenneroides* Benth., 1981.

Tapeinostemon rugosum Maguire & Steyerm., Mem. New York Bot. Gard. 32: 366. 1981. *J. A. Steyermark & J. J. Wurdack 1227*; 1 Mar. 1955; Venezuela, Bolívar, Chimantá Massif, Torono-tepui; NY (holo), VEN.

Tapeinostemon zamoranum Steyerm., Lloydia 14(1): 63. 1951. *J. A. Steyermark 54560*; 10 Oct. 1943; Ecuador, Prov. Santiago-Zamora, vicinity of Rancho Achupallas, along Quebrada Honda; 2,500–2,700 m; F (holo).

Voyria allenii Steyerm., Ann. Missouri Bot. Gard. 28: 460. 1941. *P. H. Allen 2240*; Panama, Coclé, N of El Valle de Antón; F (holo) = *V. truncata* (Standl.) Standl. & Steyerm., 1969.

GESNERIACEAE

Besleria mortoniana Steyerm., Brittonia 22: 303. 1970. *J. A. Steyermark 94962*; 3 Mar. 1966; Venezuela, Sucre, Peninsula de Paria, Cerro de Humo; 1,060–1,273 m; US (holo), VEN.

Solenophora abietorum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 236. 1947. *J. A. Steyermark 48643*; 14 July 1942; Guatemala, Dept. Huehuetenango, Cerro Huitz, Sierra de los Cuchumatanes; 1,500–2,600 m; F (holo).

GRAMINEAE see Poaceae

GROSSULARIACEAE

Phyllonoma cacuminis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 335. 1940. *J. A. Steyermark 29870*; 13 Oct. 1939; Guatemala, Dept. Zacapa, Quebrada Alejandría, summit of Sierra de las Minas, vicinity of Finca Alejandría; 2,500 m; F (holo).

GUNNERACEAE

Gunnera pittieriana Badillo & Steyerm., Acta Bot. Venez. 8: 311. 1973. *V. M. Badillo 4866*; 18 June 1972; Venezuela, Aragua, Parque Nacional Henri Pittier, Alto de Choroni; MY (holo).

GUTTIFERAE = CLUSIACEAE

HELICONIACEAE

Heliconia schneeana Steyerm., Fieldiana Bot. 28(1): 161. 1951. *J. A. Steyermark 56083*; 25 Apr. 1944; Venezuela, Mérida, above La Azulita, Hacienda Agua Blanca; 1,310–1,340 m; F (holo).

HUMIRIACEAE

"*Houmiria*" *pilosa* Steyerm., Fieldiana Bot. 28(2): 270. 1952. *J. A. Steyermark 60289*; 15–17 Nov. 1944; Venezuela, Bolívar, between Ptari-tepui and Sororopan-tepui; 1,615 m; F (holo). Note: *Humiria* is the correct spelling.

HYDROPHYLLACEAE

Hydrophyllum appendiculatum Michx. f. *album* Steyerm., Rhodora 54: 257. 1952. *J. A. Steyermark 67519*; 19 May 1949; U.S.A., Missouri, Johnson Co., Knobnoster State Park, 3–5 mi. SW of Knobnoster; F (holo).

Phacelia hirsuta Nutt. f. *albiflora* Palmer & Steyerm.,

Brittonia 10: 116. 1958. *E. J. Palmer 65070*; 15 May 1957; U.S.A., Missouri, Newton Co., 1 mi. S of Granby; F (holo).

HYPERICACEAE = Clusiaceae

ICACINACEAE

Emmotum ptarianum Steyerm., Fieldiana Bot. 28(2): 341. 1952. *J. A. Steyermark 59974*; 10–11 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,585–1,600 m; F (holo) = *E. glabrum* Benth. ex Miers, 1978.

Oecopetalum greenmanii Standl. & Steyerm.; Field. Mus. Nat. Hist., Bot. Ser. 22(3): 154. 1940. *J. A. Steyermark 39516*; 16 Apr. 1940; Guatemala, Dept. Izabal, Río Dulce, 2–4 mi. W of Livingston; sea level; F (holo).

IRIDACEAE

Orthrosanthus chimboracensis (H.B.K.) Baker var. *acorifolius* (H.B.K.) Steyerm. f. *albus* Steyerm., Lloydia 11(1): 19. 1948. *J. A. Steyermark 55339a*; n.d.; Venezuela, Trujillo, La Quebrada Cortijo above Humocaro Bajo; F (holo) = *O. acorifolius* (Kunth) Ravenna, 1987.

Orthrosanthus chimboracensis (H.B.K.) Baker var. *centroamericanus* Steyerm., Lloydia 11(1): 17. 1948. *J. A. Steyermark 31913*; n.d.; Guatemala, Jutiapa, Volcán Suchitán, NW of Asunción Mita; F (holo).

Orthrosanthus chimboracensis (H.B.K.) Baker var. *exsertus* Foster f. *albus* Steyerm., Lloydia 11(1): 17. 1948. *Runyon 875*; 8 Apr. 1926; Mexico, Tamaulipas, Santa Rita, Ranch Tamaulipas; 1,500 m; US (holo) = *O. exsertus* (Foster) Ravenna, 1987.

Orthrosanthus chimboracensis (H.B.K.) Baker var. *intermedius* Steyerm., Lloydia 11(1): 19. 1948. Type not indicated.

Trimezia chimantensis Steyerm., Ann. Missouri Bot. Gard. 71: 301. 1984. *J. A. Steyermark et al. 128071*; 26–29 Jan. 1983; Venezuela, Bolívar, Distr. Piar, Macizo de Chimantá, sector centro-noreste del Chimantá-tepui; 2,000 m; VEN (holo).

Trimezia fosteriana Steyerm. Fieldiana Bot. 28(1): 160. 1951. *J. A. Steyermark 60834*; 4 Dec. 1944; Venezuela, Bolívar, Río Tek-Yunsen between Santa Teresita de Kavanayen and Carrao-tepui; 1,375 m; F (holo).

IXONANTHACEAE

Ochthocosmus attenuatus Steyerm. & Luteyn, Brittonia 32: 142. 1980. *J. A. Steyermark et al. 117570*; 15–16 Nov. 1978; Venezuela, Bolívar, near San Rafael de Camoiran, km 175 S of El Dorado; 1,090 m; NY (holo), VEN.

Ochthocosmus berryi Steyerm., Ann. Missouri Bot. Gard. 71: 313. 1984. *J. A. Steyermark et al. 130228*; 26 Feb. 1984; Venezuela, T.F. Amazonas, Cerro Aratitiyope; MO (3223161), VEN (holo).

Ochthocosmus grandifolius Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 421. 1966. *J. A. Steyermark et al. 92379*; 29–30 Dec. 1963; Venezuela, Bolívar, Cerro Venemo; 950–1,150 m; VEN (holo) = *O. roraimae* var. *grandifolius* (Steyerm.) Steyerm. & Luteyn, 1980.

Ochthocosmus longipedicellatus Steyerm. & Luteyn, Brittonia 32: 141. 1980. *J. A. Steyermark et al. 117569*; 15–18 Nov. 1978; Venezuela, Bolívar, km 175 S of El Dorado, near San Rafael de Camoiran; 1,090 m; NY, VEN (holo).

Ochthocosmus micranthus Steyerm., Ann. Missouri Bot. Gard 75: 318. 1988. *L. Hernández 348*; 13 Nov. 1986; Venezuela, Bolívar, Ayavaparú, 10 km SW of Wadacapiae; 1,100 m; MO, VEN (holo).

Ochthocosmus multiflorus Ducke var. *angustifolius* Steyerm. & Luteyn, Brittonia 32: 141. 1980. *B. Maguire et al. 30557*; 1 Jan. 1951; Venezuela, T.F. Amazonas, NW base Cerro Yapacana, Savanna No. 3; 125 m; NY, US, VEN (holo).

Ochthocosmus multiflorus Ducke var. *canaripoensis* Steyerm. & Luteyn, Brittonia 32: 141. 1980. *J. A. Steyermark et al. 113837*; 2 Mar. 1977; Venezuela, T.F. Amazonas, Canaripo, lado sur del Río Ventuari; 125 m; F, NY, VEN (holo).

JUGLANDACEAE

Carya buckleyi Sarg. var. *arkansana* Sarg. f. *glabra* Palmer & Steyerm., Ann. Missouri Bot. Gard. 25: 770. 1938. *J. A. Steyermark 11461*; 8 July 1936; U.S.A., Missouri, Butler Co., near Cane Creek, off N Fork Hollow, 10 mi. SE of Ellsinore; MO (holo—1130651) = *C. texana* Buckl. var. *texana*, 1981.

LAMIACEAE

Scutellaria nervosa Pursh f. *alba* Steyerm., Rhodora 54: 257. 1952. *J. A. Steyermark 68024*; 21 May 1949; U.S.A., Missouri, Chariton Co., along Yellow Creek, near Rothville; F (holo).

LAURACEAE

Benzoin aestivale (L.) Nees var. *pubescens* Palmer & Steyerm., Ann. Missouri Bot. Gard. 22: 545. 1935. *E. J. Palmer 21923*; 12 Sep. 1922; U.S.A., Missouri, Jasper Co., Alba; GH (holo) = *Lindera benzoin* (L.) Blume, 1981.

Ocotea laetevirens Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 114. 1944. *J. A. Steyermark 49189*; July 1942; Guatemala, Dept. Huehuetenango, Cerro Chiblac; 1,200–2,000 m; F (holo).

Ocotea verapazensis Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 114. 1944. *P. C. Standley 71421*; Apr. 1939; Guatemala, Dept. Alta Verapaz, Tactic; 1,480 m; F (holo).

Persea sessilis Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 115. 1944. *J. A. Steyermark 42487*; 12–13 Jan. 1942; Guatemala, Dept. Zacapa, Sierra de las Minas; 2,100–2,400 m; F (holo).

Persea vesticula Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 116. 1944. *J. A. Steyermark 36207*; 20 Feb. 1940; Guatemala, Dept. San Marcos, Volcán Tacaná; 2,500–3,000 m; F (holo).

Phoebe macrophylla Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 116. 1944. *P. C. Standley 70009*; Mar. 1939; Guatemala, Dept. Alta Verapaz, SE of Tactic; 1,500 m; F (holo) = *Ocotea standleyi* Allen, 1946.

Phoebe padiformis Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 117. 1944. *A. F. Skutch 1367*; Oct. 1934; Guatemala, Dept. Quezaltenango, Colomba; 575 m; F (holo).

Phoebe savannarum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(3): 118. 1944. *J. A. Steyermark 45712*; Apr. 1942; Guatemala, Dept. Alta Verapaz, Cerro Chinajá at Sachaj and Sacacao; 150–180 m; F (holo).

LECYTHIDACEAE

Lecythis karuaiensis Steyerm., Fieldiana Bot. 28(2): 422. 1952. *J. A. Steyermark 60767*; 29 Nov. 1944; Venezuela, Bolívar, base of Sororopan-tepui; 1,220 m; F (holo), MO (1621335) = *L. alutacea* (A. C. Smith) Mori, 1988.

LEGUMINOSAE = Fabaceae

LENNOACEAE

Lennoa madreporoides Llave & Lex subsp. *australis* Steyerm., Acta Bot. Venez. 3: 230. 1968. *J. A. Steyermark & A. Braun 94518*; 23 Jan. 1966; Venezuela, Falcón, Peninsula de Paraguaná, N of Coro; MO (1897510), NY, US, VEN (holo) = *L. madreporoides* Lexarza var. *madreporoides*, 1970.

LENTIBULARIACEAE

Genlisea esmeraldae Steyerm., Fieldiana Bot. 28(3): 534. 1953. *J. A. Steyermark 57835a*; 22 Aug. 1944; Venezuela, T.F. Amazonas; SE base of Cerro Duida; 200 m, F (holo) = *G. pygmaea* St. Hiliare, 1967.

Genlisea nigrocaulis Steyerm., Bull. Torrey Bot. Club 75(6): 657. 1948. *J. A. Steyermark 59644*; 1 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,600 m; F (holo) = *G. pygmaea* St. Hiliare, 1967.

Genlisea sanariapoana Steyerm., Fieldiana Bot. 28(3): 534. 1953. *J. A. Steyermark 58445*; 8 Sep. 1944; Venezuela, T.F. Amazonas, below mouth of Río Sanariapo, along Orinoco River; 100 m; F (holo).

Pinguicula clivorum Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(4): 179. 1944. *J. A. Steyermark 50061*; 4 Aug. 1942; Guatemala, Dept. Huehuetenango, above San Juan Ixcoy, Sierra de los Cuchumatanes; 2,400 m; F (holo) = *P. lilacina* Schlecht & Cham., 1974.

Utricularia amazonasana Steyerm., Fieldiana Bot. 28(3): 535. 1953. *J. A. Steyermark 58505*; 8 Sep. 1944; Venezuela, T.F. Amazonas, vicinity of Sanariapo; 100 m; F (holo) = *U. hydrocarpa* Vahl, 1967.

Utricularia arenicola Tutin var. *kavanayena* Steyerm., Fieldiana Bot. 28(3): 535. 1953. *J. A. Steyermark 59335*; 26 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,220 m; F (holo) = *U. nana* St. Hiliare & Girard, 1967.

Utricularia aureolimba Steyerm., Fieldiana Bot. 28(3): 535. 1953. *J. A. Steyermark 59351*; 26 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,220 m; F (holo) = *U. adpressa* Salzmann, 1967.

Utricularia aureomaculata Steyerm., Fieldiana Bot. 28(3): 536. 1953. *J. A. Steyermark 59852*; 4 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 2,130 m; F (holo).

Utricularia ayacuchae Steyerm., Fieldiana Bot. 28(3): 538. 1953. *J. A. Steyermark 58520*; 11 Sep. 1944; Venezuela, T.F. Amazonas, Puerto Ayacucho; 200 m; F (holo) = *U. cucullata* St. Hiliare & Girard, 1967.

Utricularia baldwinii Steyerm., Bull. Torrey Bot. Club 79(4): 310. 1952. *J. T. Baldwin, Jr. 4077*; 3 June 1944; Brazil, Terr. Amapá, Amapá; US (holo) = *U. amethystina* St. Hiliare & Girard, 1967.

Utricularia bolivarana Steyerm., Fieldiana Bot. 28(3): 538. 1953. *J. A. Steyermark 59191*; 3 Oct. 1944; Venezuela, Bolívar, S of Mt. Roraima, Gran Sabana; 1,065 m; F (holo) = *U. amethystina* St. Hiliare & Girard, 1967.

Utricularia campbelliana Oliver var. *minor* Steyerm., Fieldiana Bot. 28(3): 539. 1953. *J. A. Steyermark 59753*; 2 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 2,000–2,200 m; F (holo) = *U. campbelliana* Oliv. var. *campbelliana*, 1967.

Utricularia cearana Steyerm., Bull. Torrey Bot. Club 79(4): 310. 1952. *H. C. Cutler 8365*; 10 June 1952; Brazil, Ceara, 4 km N of Soure (Caucaia); F (holo).

Utricularia congesta Steyerm., Fieldiana Bot. 28(3): 539. 1953. *J. A. Steyermark 59404*; 26 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,220 m; F (holo) = *U. fimbriata* Kunth, 1967.

Utricularia congesta Steyerm. f. *diminutiva* Steyerm., Fieldiana Bot. 28(3): 540. 1953. *J. A. Steyermark 59195*; 3 Oct. 1944; Venezuela, Bolívar, S of Mt. Roraima, Gran Sabana; 1,065 m; F (holo).

Utricularia cuspidata Steyerm., Fieldiana Bot. 28(3): 542. 1953. *J. A. Steyermark 60119*; 14 Nov. 1944; Venezuela, Bolívar, Sororopan-tepui; 2,255 m; F (holo) = *U. calycifida* Benjamin, 1967.

Utricularia cutleri Steyerm., Bull. Torrey Bot. Club 79(4): 311. 1952. *H. C. Cutler 8363*; 10 June 1945; Brazil, Ceara, 4 km N of Soure (Caucaia); F (holo) = *U. viscosa* Spruce ex Oliver, 1967.

Utricularia dawsonii Steyerm., Los Angeles Co. Mus. Contr. Sci. 21: 20. 1958. *E. Y. Dawson 14770*; 1 May 1956; Brazil, Golás, Chapada dos Veadeiros, 10 km from Veadeiros on Cavalcante road; F (holo), LAM, R = *U. amethystina* St. Hiliare & Girard, 1967.

Utricularia heterochroma Steyerm., Fieldiana Bot. 28(3): 544. 1953. *J. A. Steyermark 59930*; 7 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 2,410–2,450 m; F (holo).

Utricularia humboldtii Schomb. f. *cuneata* Steyerm., Fieldiana Bot. 28(3): 544. 1953. *J. A. Steyermark 58229*; 2 Sep. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,025–1,200 m; F (holo) = *U. humboldtii* R. H. Schomb. var. *humboldtii*, 1967.

Utricularia kaieteurensis Steyerm., Bull. Torrey Bot. Club 75(6): 658. 1948. *B. Maguire & D. B. Fanshawe 23204*; 4 May 1944; Guyana, Kaieteur Plateau; F (holo), NY = *U. amethystina* St. Hiliare & Girard, 1967.

Utricularia maguirei Steyerm., Bull. Torrey Bot. Club 75(6): 659. 1948. *B. Maguire & D. B. Fanshawe 23249*; 5 May 1944; Guyana, Kaieteur Plateau; F (holo), NY = *U. calycifida* Benjamin, 1967.

Utricularia oliveriana Steyerm., Fieldiana Bot. 28(3): 546. 1953. *J. A. Steyermark 58446*; 8 Sep. 1944; Venezuela, T.F. Amazonas, below mouth of Río Sanariapo, along Orinoco River; 100 m; F (holo).

Utricularia oliveriana Steyerm. f. *parva* Steyerm., Fieldiana Bot. 28(3): 546. 1953. *J. A. Steyermark 59333*; 26 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,220 m; F (holo) = *U. oliveriana* Steyerm. var. *oliveriana*, 1967.

Utricularia orinocensis Steyerm., Fieldiana Bot. 28(3): 548. 1953. *J. A. Steyermark 58488*; 8 Sep. 1944; Venezuela, T.F. Amazonas, Sanariapo; 100 m, F (holo) = *U. fimbriata* Kunth, 1967.

Utricularia subpeltata Steyerm., Fieldiana Bot. 28(3): 548. 1953. *J. A. Steyermark 60477*; 23 Nov. 1944; Venezuela, Bolívar, between Santa Teresita de Kavanayen and ca. 8 km NW of Kavanayen; 1,220 m; F (holo) = *U. pubescens* Smith in Rees, 1967.

Utricularia tepuiana Steyerm., Fieldiana Bot. 28(3): 550. 1953. *J. A. Steyermark 59517*; 29 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 1,810 m; F (holo) = *U. amethystina* St. Hiliare & Girard, 1967.

Utricularia turumiquirensis Steyerm., Fieldiana Bot. 28(3): 552. 1953. *J. A. Steyermark 62752*; 11 May 1945; Venezuela, Sucre, between base of Cerro de Diablo and Cerro de Neveri, along headwaters of Río de Amana; 2,000 m; F (holo) = *U. amethystina* St. Hiliare & Girard, 1967.

Utricularia venezuelana Steyerm., Fieldiana Bot. 28(3): 552. 1953. *J. A. Steyermark 59625a*; 1 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,600 m; F (holo) = *U. pubescens* Smith in Rees, 1967.

Utricularia williamsii Steyerm., Ceiba 1: 126. 1950. *Ll. Williams 10639*; 17 Oct. 1946; Honduras, Dept. Morazán, near Hoya Grande, drainage of Río Yeguare; 1,500 m; F (holo) = *U. amethystina* St. Hiliare & Girard, 1967.

LILIACEAE

Camassia scilloides (Raf.) Cory f. *petersenii* Steyerm., Rhodora 40: 178. 1938. *J. A. Steyermark 22499*; 23 Apr. 1937; U.S.A., Missouri, St. Louis Co., Osage Hills, MO (holo—1174671).

Camassia scilloides (Raf.) Cory f. *variegata* Steyerm., Rhodora 51: 116. 1949. *J. A. Steyermark 28324*; 25 Apr. 1941; U.S.A., Missouri, Christian Co., Pedelo Creek, 4.5. mi. NE of Sparta; F (holo).

Excremis coarctata (Ruíz & Pavón) Baker f. *alba* Steyerm., Fieldiana Bot. 28(1): 153. 1951. *J. A. Steyermark 62963*; 16–17 June 1945; Venezuela, Miranda, above Los Chorros, Pico de Naiguata; 2,200–2,765 m; F (holo).

Nietneria paniculata Steyerm., Fieldiana Bot. 28(1): 153. 1951. *J. A. Steyermark 59362*; 26 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,220 m; F (holo).

Smilacina crassipes Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(5): 214. 1947. *J. A. Steyermark 51003*; 20 Aug. 1942; Guatemala, Dept. Huehuetenango, Cerro Pueblo Viejo; 1,900 m; F (holo) = *Maianthemum gigas* var. *crassipes* (Standl. & Steyerm.) LaFrankie, 1986.

Tofieldia duidae Steyerm., Fieldiana Bot. 28(1): 156. 1951. *J. A. Steyermark 58716*; 1 Sep. 1944; Venezuela, T.F. Amazonas, Cerro Duida, Brocchinia Hills; 1,700–1,980 m; F (holo).

Tofieldia sessiliflora Hook. var. *robustior* Steyerm., Fieldiana Bot. 28(1): 157. 1951. *J. A. Steyermark 55291*; 5 Feb. 1944; Venezuela, Lara, Las Sabanetas, above Los Aposentos, W of Humocaro Bajo; 2,530 m; F (holo).

Trillium ozarkanum Palmer & Steyerm., Ann. Missouri Bot. Gard. 22: 504. 1935. *J. A. Steyermark 18628*; 20 Apr. 1935; U.S.A., Missouri, Barry Co., 3 mi. S of Cassville; MO (holo) = *T. pusillum* Michx. var. *ozarkanum* (Palmer & Steyerm.) Steyerm., 1960.

Trillium recurvatum Beck f. *foliosum* Steyerm., Rhodora 61: 124. 1959. *W. Adams s.n.*; 6 Apr. 1949; U.S.A., Missouri, Cape Girardeau Co., Houck Woods, Bloomfield Road; SE Missouri State College (holo).

Trillium recurvatum Beck f. *petaloideum* Steyerm., Rhodora 61: 124. 1959. *W. Adams s.n.*; 6 Apr. 1949; U.S.A., Missouri, Cape Girardeau Co., Houck Woods, Bloomfield Road; SE Missouri State Univ. (holo).

Trillium recurvatum Beck f. *shayi* Palmer & Steyerm., Ann. Missouri Bot. Gard. 22: 504, 1935, nom. nov.

LIMNOCHARITACEAE

"*Hydrocleis*" *standleyi* Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 31. 1944. *J. A. Steyermark 30416*; Oct. 1939; Guatemala, Dept. Jutiapa, between Agua Blanca and Amatillo; 950 m; F (holo). Note: *Hydrocleys* is the correct spelling.

LINACEAE

Ochthocosmus see under Ixonanthaceae

LISSOCARPACEAE

Lissocarpa stenocarpa Steyerm., Ann. Missouri Bot. Gard. 74: 104. 1987. *J. A. Steyermark & B. K. Holst 130880*; 28 Feb.–1 Mar. 1985; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca; 1,140 m; MO (holo—3327360), VEN.

LOASACEAE

"*Cajaphora*" *larensis* Steyerm., Fieldiana Bot. 28(2): 412. 1952. *J. A. Steyermark 55528*; 12 Feb. 1944; Venezuela, Lara, between Buenos Aires to Canyon of El Callado, above Humocaro Alto; 2,285–2,740 m; F (holo). Note: *Caïophora* is the correct spelling.

"*Cajaphora*" *venezuelensis* Steyerm., Fieldiana Bot. 28(2): 414. 1952. *J. A. Steyermark 56594*; 18 May 1944; Venezuela, Mérida, La Isla, above Tabay; 2,285–2,745 m; F (holo).

Eucnide guatemalensis Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(4): 178. 1944. *J. A. Steyermark 50818*; 17 Aug. 1942; Guatemala, Dept. Huehuetenango, NW of Cuilco, Cerro Chiquihui, above Carrizal; 2,000 m; F (holo).

Schismocarpus matudai Steyerm., Bull. Torrey Bot. Club 80(2): 138. 1953. *E. Matuda 5330*; Mexico, Chiapas, along Río Cintalapa, between Jilquero and Piñuela, Mun. Escuintla; 500 m; Matuda Herbarium (holo).

LOGANIACEAE

"*Buddleia*" *amplexicaulis* Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 71. 1944. *P. C. Standley 65479*; 17 Feb. 1939; Guatemala, Dept. Quezaltenango, El Chorro, near Zunil; F (holo) = *Buddleja crotonoides* A. Gray, 1969. Note: *Buddleja* is the correct spelling.

"*Buddleia*" *australis* Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 72. 1944. *J. A. Steyermark 37276*; 8 Mar. 1940; Guatemala, Dept. San Marcos, Loma de la Paloma, above Finca El Porvenir, Volcán Tajamulco; 1,400–1,700 m; F (holo) = *Buddleja cordata* H.B.K., 1969.

"*Buddleia*" *euryphylla* Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(5): 223. 1947. *J. A. Steyermark 43628*; 7 Feb. 1942; Guatemala, Dept. El Progreso, Sierra de las Minas, Joya Pacayal; 2,500-3,000 m; F (holo).

"*Buddleia*" *stenoptera* Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 71. 1944. *J. A. Steyermark 35001*; 24 Jan. 1940; Guatemala, Dept. Quezaltenango, in Río Samalá, below Zunil; 2,500 m; F (holo) = *Buddleja crotonoides* A. Gray, 1969.

Spigelia carnosa Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 72. 1944. *J. A. Steyermark 48692*; 15 July 1942; Guatemala, Dept. Huehuetenango, between Yulhuitz and Maxbal, Sierra de los Cuchumatanes; 1,400–1,500 m; F (holo).

LORANTHACEAE

Phthirusa hippocrateoides Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 442. 1967. *J. A. Stey-*

ermark 75059; 17 Apr. 1953; Venezuela, Bolívar, Abacapa-tepui, Chimantá Massif; 1,312–1,500 m; NY (holo) = *Struthanthus syringifolius* Mart., 1982.

Phthirusa ptariana Steyerm., Fieldiana Bot. 28(1): 225. 1951. *J. A. Steyermark 59549*; 30 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 2,100–2,285 m; F (holo) = *Struthanthus syringifolius* Mart., 1982.

Phthirusa roraimensis Steyerm., Fieldiana Bot. 28(1): 224. 1951. *J. A. Steyermark 58943*; 30 Sep. 1944; Venezuela, Bolívar, Mt. Roraima; 2,040–2,255 m; F (holo).

Psittacanthus costanensis Steyerm., Acta Bot. Venez. 3: 189. 1968. *J. A. & C. Steyermark 95215*; 28 Mar. 1966; Venezuela, Carabobo, Río San Gian, S Borburata, La Toma; 750–1,000 m; NY, US, VEN (holo).

Psittacanthus mayanus Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 41. 1944. *P. Gentle 116*; 14 Sep. 1933; Belize, Santa Rita; F (holo).

Struthanthus brachybotrys Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 42. 1944. *P. C. Standley 82430*; Jan. 1941; Guatemala, Dept. Huehuetenango, Río Pucal ca. 14 km S of Huehuetenango; 1,790 m; F (holo).

Struthanthus chimantensis Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 443. 1967. *J. A. Steyermark 74816*; 5 Apr. 1953; Venezuela, Bolívar, Abacapa-tepui, Chimantá Massif; 750–1,100 m; MO (201171), VEN (holo) = *S. gracilis* (Gleason) Steyerm. & Maguire, 1967.

Struthanthus johnstonii Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 43. 1944. *J. R. Johnston 1887*; 2 Jan. 1941; Guatemala, Dept. Huehuetenango, W of Aguacatán; F (holo).

Struthanthus mucronatus Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 418. 1966. *J. A. Steyermark et al. 92336*; 29–30 Dec. 1963; Venezuela, Bolívar, Cerro Venamo; 950–1,150 m; VEN (holo) = *S. gracilis* (Gleason) Steyerm. & Maguire var. *mucronatus* (Steyerm.) Rizz., 1982.

Struthanthus oliganthus Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(4): 154. 1944. *J. A. Steyermark 50672*; 15 Aug. 1942; Guatemala, Dept. Huehuetenango, above San Ildefonso Ixtahuacán; 1,600–1,700 m; F (holo) = *Cladocolea oligantha* (Standl. & Steyerm.) Kuijt, 1974.

Struthanthus papillosus Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 43. 1944. *H. von Tuerckheim II.1240*; June 1906; Guatemala, Dept. Alta Verapaz, Cobán; 1,350 m; F (holo).

Struthanthus tenuifolius Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(4): 155. 1944. *J. A. Steyermark 51538*; 29 Aug. 1942; Guatemala, Dept. Huehuetenango, Ciénaga de Lagartero, below Miramar; 300 m; F (holo).

LYTHRACEAE

Cuphea serpyllifolia H.B.K. var. *tachirensis* Steyerm., Fieldiana Bot. 28(2): 420. 1952. *J. A. Steyermark 57162*; 12 July 1944; Venezuela, Táchira, between Villapaez and Betania along Río Táchira; 2,130–2,285 m; F (holo).

MAGNOLIACEAE

Magnolia chimantensis Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 443. 1967. *J. A. Steyermark 75840*; 20 June 1953; Venezuela, Bolívar, Apacara-tepui, Chimantá Massif; 2,200–2,300 m; VEN (holo).

Magnolia ptaritepuiana Steyerm., Fieldiana Bot. 28(1): 233. 1951. *J. A. Steyermark 59547*; 30 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 2,100–2,285 m; F (holo).

Magnolia roraimae Steyerm., Fieldiana Bot. 28(1): 234. 1951. *J. A. Steyermark 59000*; 30 Sep. 1944; Venezuela, Bolívar, Mt. Roraima; 2,155 m; F (holo).

MALPIGHIACEAE

Banisteria alternifolia Steyerm., Fieldiana Bot. 28(2): 280. 1952. *J. A. Steyermark 61914*; 7 Apr. 1945; Venezuela, Monagas, Cerro de la Cueva de Dona Anita; 1,100–1,200 m; F (holo).

Blepharandra cretacea (Gleason) Steyerm. var. *composita* Steyerm., Fieldiana Bot. 28(2): 281. 1952. *J. A. Steyermark 58191*; 1 Sep. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,700–1,980 m; F (holo) = *B. hypoleuca* (Benth.) Griseb., 1981.

Blepharandra ptariana Steyerm., Fieldiana Bot. 28(2): 282. 1952. *J. A. Steyermark 60310*; 18 Nov. 1944; Venezuela, Bolívar, Ptari-tepui 1,220 m; F (holo) = *B. hypoleuca* (Benth.) Griseb., 1978.

Burdachia duckei Steyerm., Fieldiana Bot. 28(2): 283. 1952. *A. Ducke 522*; 14 July 1937; Brazil, Manaus, Igarape de Cachoeira Grande; F (holo), MO (1157729).

Burdachia williamsii Steyerm., Fieldiana Bot. 28(2): 285. 1952. *Ll. Williams 14321*; 1942; Venezuela, T. F. Amazonas, Río Guainía, Maroa; 127 m; F (holo).

Byrsonima bolivarana Steyerm., Fieldiana Bot. 28(2): 287. 1952. *J. A. Steyermark 60272*; 15–17 Nov. 1944; Venezuela, Bolívar, between Sororopan-tepui and Ptari-tepui; 1,615 m; F (holo) = *B. chalcophylla* var. *carraoana* (Steyerm.) Anders., 1981.

Brysonima carraoana Steyerm., Fieldiana Bot. 28(2): 287. 1952. *J. A. Steyermark 60883*; 7 Dec. 1944; Venezuela, Bolívar, Carrao-tepui; 2,470–2,500 m; F (holo) = *B. chalcophylla* var. *carraoana* (Steyerm.) Anders., 1981.

Byrsonima leutzelburgii Steyerm., Fieldiana Bot. 28(2): 288. 1952, nom. nov.

Glandonia williamsii Steyerm., Fieldiana Bot. 28(2): 288. 1942. *Ll. Williams 14154*; 2 Feb. 1942; Venezuela, T.F. Amazonas, Yavita; 128 m; F (holo).

"*Heteropterys*" *quetepensis* Steyerm., Fieldiana Bot. 28(2): 292. 1952. *J. A. Steyermark 62880*; 23 May 1945; Venezuela, Sucre, E of Cumana, near Quetepe, between km 18–20; 30 m; F (holo). Note: *Heteropteris* is the correct (conserved) spelling.

Hiraea tepuiensis Steyerm., Fieldiana Bot. 28(2): 293. 1952. *A. S. Pinkus 90*; 28 Dec. 1939; Venezuela, Bolívar, vicinity Arabupu, Mt. Roraima; 1,500 m; F (holo).

Mascagnia excelsa Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(4): 168. 1944. *J. A. Steyermark 39456*; 14 Apr. 1940; Guatemala, Dept. Izabal, Río Dulce; sea level; F (holo).

"*Tetrapterys*" *phylladenophora* Maguire & Steyerm., Mem. New York Bot. Gard. 9: 481. 1957. *J. A. Steyermark & J. J. Wurdack 426*; 10–15 Feb. 1948; Venezuela, Bolívar, Uaipán-tepui; NY (holo) = *Tetrapteris rhodoptero* Oliver, 1981. Note: *Tetrapteris* is the correct spelling.

"*Tetrapterys*" *pusilla* Steyerm., Fieldiana Bot. 28(2): 294. 1952. *J. A. Steyermark 59391*; 26 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,220 m; F (holo).

MALVACEAE

Abutilon orientale Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(4): 173. 1944. *P. C. Standley 74420*; 15 Oct. 1940; Guatemala, Dept. Zacapa, along road between Agua Blanca & Cumbre de Chiquimula; 350–500 m; F (holo).

Abutilon pachecoanum Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 61. 1944. *P. C. Standley 83528*; Jan. 1941; Guatemala, Dept. Quezaltenango, near Las Nubes, S of San Martín Chile Verde; 2,250 m; F (holo).

Abutilon pseudogiganteum Steyerm., Fieldiana Bot. 28(2): 362. 1952. *J. A. Steyermark 61519*; 16 Mar. 1945; Venezuela, Anzoátegui, between San José & Cucuta; 600–700 m; F (holo).

Abutilon tridens Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(4): 173. 1944. *J. A. Steyermark 43439*; 4 Feb. 1942; Guatemala, Dept. El Progreso, hills between Finca Piamonte & slopes SE, Sierra de las Minas; 2,400 m; F (holo).

Abutilon turumiquirense Steyerm., Fieldiana Bot. 28(2): 63. 1952. *J. A. Steyermark 62689*; 10 May 1945; Venezuela, Sucre, Cerro Turumiquire; 1,300–1,800 m; F (holo).

Malvastrum guatemalense Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(4): 174. 1944. *P. C. Standley 78534*; 20–27 Nov. 1940; Guatemala, Dept. Santa Rosa, near Cuilapa; 900 m; F (holo).

Pavonia imatacensis Steyerm., Acta Bot. Venez. 3: 181. 1968. *J. A. Steyermark 88149*; 17 Dec. 1960; Venezuela, Bolívar, Sierra Imataca, Río Toro (Río Grande); 200–250 m; VEN (holo).

Pseudabutilon inornatum Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(1): 15. 1943. *P. C. Standley 61425*; Dec. 1938; Guatemala, Dept. Guatemala, near Amatitlán; 1,170 m; F (holo).

MARANTACEAE

Calathea acuminata Steyerm., Fieldiana Bot. 28(1): 161. 1951. *Ll. Williams 15532*; 24 May 1942; Venezuela, T.F. Amazonas, Alto Casiquiare, Capihuara; 120 m; F (holo).

Calathea coccinea Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 39. 1944. *J. A. Steyermark 79345*; Mar. 1940; Guatemala, Dept. San Marcos, above Finca El Porvenir, along Río Cabús, Volcán Tajumulco; 1,300–1,500 m; F (holo).

Calathea duidae Steyerm., Fieldiana Bot. 28(1): 162. 1951. *J. A. Steyermark 57888*; 23 Aug. 1944; Venezuela, T.F. Amazonas, SE base of Cerro Duida; 210 m; F (holo).

Calathea lasseriana Steyerm., Fieldiana Bot. 28(1): 163. 1951. *J. A. Steyermark 57920*; 23 Aug. 1944; Venezuela, T.F. Amazonas, SE base of Cerro Duida; 215 m; F (holo).

Ischnosiphon lasseriana Steyerm., Fieldiana Bot. 28(1): 164. 1951. *J. A. Steyermark 60557*; 15 Nov. 1944; Venezuela, Bolívar, below Santa Teresita de Kavanayen; F (holo).

Monotagma duidae Steyerm., Fieldiana Bot. 28(1): 164. 1951. *J. A. Steyermark 57807*; 22 Aug. 1944; Venezuela, T.F. Amazonas, SE base of Cerro Duida; 200 m; F (holo).

Monotagma yapacanensis Steyerm. & Bunting, Acta Bot. Venez. 8: 114. 1973. *J. A. Steyermark & G. Bunting 103062*; 3 May 1970; Venezuela, T.F. Amazonas, Cerro Yapacana; 125–400 m; VEN (holo).

Thymocarpus Nicolson, Steyerm. & Sivad., Brittonia 33: 22. 1981, Gen. nov.

Thymocarpus cannoides Nicolson, Steyerm. & Sivad., Brittonia 33: 24. 1981; *B. Maguire et al. 53608*; 5 Sep. 1962; Venezuela, Bolívar, SE end of Cerro Piton, Cordillera Epicara, alta Río Cuyuni; 40 m; MO (2892301), NY, US, VEN (holo).

MARCGRAVIACEAE

Marcgravia sororopaniana Steyerm., Fieldiana Bot. 28(2): 378. 1952. *J. A. Steyermark 60127*; 14 Nov. 1944; Venezuela, Bolívar, Sororopan-tepui; 2,255 m; F (holo).

Ruyschia longistylis Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(4): 175. 1944. *J. A. Steyermark 49545*; 26 July 1942; Guatemala, Dept. Huehuetenango, Cafetal of Finca Soledad, Sierra de los Cuchumatanes; 1,150 m; F (holo) = *R. enervia* Lundell, 1961.

Souroubea guianensis Aublet var. *tomentella* Steyerm., Fieldiana Bot. 28(2): 378. 1952. *J. A. Steyermark 60652*; 27 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,220 m; F (holo).

Souroubea micrantha Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 62. 1944. *P. C. Standley 72793*; Apr.–May 1939, Guatemala, Dept. Izabal, near Puerto Barrios; sea level; F (holo) = *S. triandra* Lundell, 1961.

Souroubea puberula Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(4): 175. 1944. *J. A. Steyermark 46862*; 2 June 1942; Guatemala, Dept. Suchitepéquez, Loma Grande, above Finca El Naranjo, Volcán de Santa Clara; 2,000 m; F (holo) = *S. exauriculata* Delpino, 1961.

MELASTOMATACEAE

Conostegia gleasoniana Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 22(5): 361. 1940. *P. C. Standley 70317*; 2 Apr. 1939; Guatemala, Dept. Alta Verapaz, Cocolá, NE of Carchá; 1,200 m; F (holo) = *C. hirtella* Cogn., 1963.

Conostegia volcanalis Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 136. 1944. *P. C. Standley 68152*; 8 Mar. 1939; Guatemala, Dept. Quezaltenango, Chiquihuite; 1,410 m; F (holo).

Diolena calciphila Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 133. 1944. *A. F. Skutch 1811*; 2 Dec. 1934; Guatemala, Dept. Quiché, Zona Reina; 750 m; F (holo) = *Triolena calciphila* (Standl. & Steyerm.) Standl. & L. Williams, 1963.

Diolena roseiflora Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 134. 1944. *J. A. Steyermark 41819*; 24 Dec. 1941; Guatemala, Dept. Izabal, along Río Tamejá, Cerro San Gil; 50 m; first cited specimen, type not designated. = *Triolena roseiflora* (Standl. & Steyerm.) Standl. & L. Williams, 1963.

Diolena stenophylla Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 135. 1944. *J. A. Steyermark 48728*; 15–16 July 1942; Guatemala, Dept. Huehuetenango, between Maxbal and lake to the SE; 1,500 m; F (holo) = *Triolena stenophylla* (Standl. & Steyerm). Standl. & L. Williams, 1963.

Miconia echinoidea Standl. & Steyerm., Field. Must. Nat. Hist., Bot. Ser. 23(4): 180. 1944. *J. A. Steyermark 48831*; 15–16 July 1942; Guatemala, Dept. Huehuetenango, vicinity of Maxbal, Sierra de los Cuchumatanes; 1,500 m; F (holo).

Miconia tixixensis Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(4): 181. 1944. *J. A. Steyermark 31585*; 10 Nov. 1939; Guatemala, Dept. Chiquimula, Cerro Tixixí; 1,500 m; F (holo).

Monochaetum guatemalense Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 136. 1944. *J. A. Steyermark 48512*; 10 July 1942; Guatemala, Dept. Huehuetenango, vicinity of Quetzal; 2,300 m; F (holo) = *Heterocentron elegans* (Schlecht.) Kuntze, 1963.

Rhynchanthera medialis Standl. & Steyerm. Field. Mus. Nat. Hist., Bot. Ser. 23: 137. 1944. *J. A. Steyermark 36386*; 22 Feb. 1940; Guatemala, Dept. San Marcos, along Quebrada Suchiate, near SE portion of Volcán Tacaná; 2,000–3,000 m; F (holo).

Triolena izabalensis Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 138. 1944. *C. L. Wilson 175*; 7 Feb. 1939; Guatemala, Dept. Izabal, near Río Lámpara; F (holo).

MELIACEAE

Guarea chirriactensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 167. 1944. *J. A. Steyermark 46355*; 10 May 1942; Guatemala, Dept. Alta Verapaz, along Route 5, between Chirreacté & Semococh; 500–900 m; F (holo) = *Trichilia chirriactensis* (Standl. & Steyerm.) Penn., 1981.

Trichilia privigna Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(4): 167. 1944. *J. A. Steyermark 45827*; 21 Apr. 1942; Guatemala, Dept. Petén, along Río Santa Isabel, between mouth of Río Sebol and El Porvenir; 100 m; F (holo) = *T. breviflora* S. F. Blake & Standl., 1981.

"*Trichilia ptariana*" Steyerm., Fieldiana Bot. 28(2): 278. 1952. *J. A. Steyermark 59979*; 10–11 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,585–1,600 m; F (holo) = *Matayba oligantha* Sandw., 1981. Note: The *Trichilia* name was a homonym, non A. C. Smith, 1933.

Trichilia subsimplex Steyerm., Fieldiana Bot. 28(2): 279. 1952. *J. A. Steyermark 58061*; 28–29 Aug. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 260 m; F (holo), NY, US, VEN = *T. pallida* Sw., 1981.

MENDONCIACEAE

Mendoncia guatemalensis Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(5): 245. 1947. *J. A. Steyermark 49270*; 23 July 1942; Guatemala, Dept. Huehuetenango, between Ixcán & Río Ixcán; 150–200 m; F (holo).

Mendoncia mellobarretoana Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 17(5): 421. 1938. *H. L. Mello Barreto 226*; 1 Dec. 1934; Brazil, Suyo, Jardim Botanicão Mun. Belo Horizonte, Minas Gerais; F (holo).

MENISPERMACEAE

Hyperbaena salvadorensis Steyerm., Ceiba 4: 301. 1955. *J. M. Tucker 979*; 23 Feb. 1942; El Salvador, Dept. San Miguel, Volcán San Miguel, 0.8 km SW of buildings of hacienda of Max Haltmeyer; F (holo).

Hyperbaena vulcania Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(1): 8. 1943. *P. C. Standley 63878*; Jan. 1939; Guatemala, Dept. Escuintla, near Barranco Hondo, above Las Lajas; 1,200 m; F (holo).

MONIMIACEAE

Mollinedia glabricaulis Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989.

Mollinedia neblinensis Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *N. T. Silva & U. Brazao 60678*; Brazil, Serra da Neblina, Rio Negro, Rio Cauaburi, Rio Maturacá, between Anta and Palmito camps; 600–1,300 m; MO (3291192), NY (holo).

Mollinedia ptariensis Steyerm., Fieldiana Bot. 28(1): 235. 1951; *J. A. Steyermark 60014*; 10–11 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,585–1,600 m; F (holo).

Mollinedia roraimensis Steyerm., Fieldiana Bot. 28(1): 236. 1951. *J. A. Steyermark 59004*; 30 Sep. 1944; Venezuela, Bolívar, Mt. Roraima; 2,040–2,255 m; F (holo).

Siparuna manarae Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 453. 1966. *B. J. Manara 51*; 27 June 1964; Venezuela, Distr. Federal, Cerro Naiguitá, Quebrada Río Chiquito; VEN (holo) = *S. stellulata* Perkins var. *marnarae* (Steyerm.) Steyerm., 1978.

Siparuna rugosa Steyerm., Phytologia 9(6): 342. 1964. *M. Acosta Solis 7008*; 18 Jan. 1944; Ecuador, Prov. Pichincha, bojada de Lache e Condor Machay, Cordillera Occidental; 2,700–3,100 m; F (holo).

Siparuna verrucosa Steyerm., Phytologia 9(6): 343. 1964. *M. Acosta Solis 8233*; 19 June 1944; Ecuador, Prov. Imbabura, Urcusique, faldas occidental del Cotacachi; 3,300 m; F (holo).

MORACEAE

Ficus cabusana Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 22(4): 226. 1940. *J. A. Steyermark 37583*; 12 Mar. 1940; Guatemala, Dept. San Marcos, Finca El Porvenir, on Potrero Matasán, along Río Cabús, Volcán Tajumulco; 1,000 1,300 m; F (holo).

Pseudolmedia simiarum Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(4): 154. 1944. *J. A. Steyermark 48741*; 15–16 July 1942; Guatemala, Dept. Huehuetenango, Maxbal; 1,500 m; F (holo).

MYRICACEAE

Myrica rotundata Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 441. 1967. *J. A. Steyermark 75804*; 20 June 1953; Venezuela, Bolívar, Apacara-tepui, Chimantá Massif; 2,000–2,150 m; VEN (holo).

MYRSINACEAE

Ardisia apoda Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(5): 219. 1947. *J. A. Steyermark 41923*; 25 Dec. 1941; Guatemala, Dept. Izabal, Cerro San Gil; 300–900 m; F (holo).

Ardisia carlsonae Steyerm., Ceiba 4: 301. 1955. *M. C. Carlson 1744*; n.d.; Mexico, Chiapas, around Los Arcos, Los Lagos, 3 mi. NW of Rancho San José and 34 mi. SE of Comitán; 1,600 m; F (holo) = *Oerstedianthus carlsonae* (Steyerm.) Lundell, 1983.

Ardisia meridensis Steyerm., Fieldiana Bot. 28(3): 454. 1953. *J. A. Steyermark 56325*; 6 May 1944; Venezuela, Mérida, between Mucuchachi & Canagua; 1,065–1,820 m; F (holo).

Ardisia vatteri Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(5): 220. 1947. *J. A. Steyermark 48558*; 14 July 1942; Guatemala, Dept. Huehuetenango, Cerro Huitz, Cerro de los Cuchumatanes; 1,500–2,600 m; F (holo) = *Gentlea vatteri* (Standl. & Steyerm.) Lundell, 1964.

Conomorpha apiculata Steyerm., Fieldiana Bot. 28(3): 456. 1953. *J. A. Steyermark 57986*; 25–26 Aug.

1944; Venezuela, T.F. Amazonas, Cerro Duida; 305–1,095 m; F (holo).

Conomorpha densipapillata Steyerm., Fieldiana Bot. 28(3): 457. 1953. *J. A. Steyermark 56539*; 14 May 1944; Venezuela, Mérida, Páramo de Los Colorados, between El Molino & San Isidro Alto; 2,745–2,955 m; F (holo).

Conomorpha depressa Steyerm., Fieldiana Bot. 28(3): 458. 1953. *J. A. Steyermark 60898*; 7 Dec. 1944; Venezuela, Bolívar, Carrao-tepui; 2,470–2,500 m; F (holo).

Conomorpha frigidicola Steyerm., Fieldiana Bot. 28(3): 458. 1953. *J. A. Steyermark 56516*; 14 May 1944; Venezuela, Mérida, between El Molino & ridge above San Isidro Alto; 2,430–2,895 m; F (holo) = *Cybianthus frigidicola* (Steyerm.) Agost., 1972.

Conomorpha hieronymoides Steyerm., Fieldiana Bot. 28(3): 460. 1953. *J. A. Steyermark 55295*; 5 Feb. 1944; Venezuela, Lara, Las Sabanetas; 2,530 m; F (holo) = *Cybianthus laurifolius* (Mez) Agost., 1972.

Conomorpha jajiensis Steyerm., Fieldiana Bot. 28(3): 462. 1953. *J. A. Steyermark 55980*; 21 Apr. 1944; Venezuela, Mérida, above Jaji, Los Quebraditos; 2,590 m; F (holo).

Conomorpha larensis Steyerm., Fieldiana Bot. 28(3): 463. 1953. *J. A. Steyermark 55392*; 8 Feb. 1944; Venezuela, Lara, above Humocaro Baja, S of Las Sabanetas; 2,430–2,745 m; F (holo).

Conomorpha lepidota Gleason f. *acutata* Steyerm., Fieldiana Bot. 28(3): 465. 1953. *J. A. Steyermark 58265*; 2 Sep. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,025–1,200 m; F (holo) = *Cybianthus lepidotus* (Gleason) Agost., 1972.

Conomorpha leprosa Steyerm., Fieldiana Bot. 28(3): 465. 1953. *J. A. Steyermark 59136*; 2 Oct. 1944; Venezuela, Bolívar, S of Mt. Roraima, Gran Sabana; 1,065 m; F (holo).

Conomorpha liriensis Steyerm., Fieldiana Bot. 28(3): 466. 1953. *J. A. Steyermark 57456*; 18 July 1944; Venezuela, Táchira, Alto de Lirio; 1,890–2,285 m; F (holo).

Conomorpha ptariensis Steyerm., Fieldiana Bot. 28(3): 466. 1953. *J. A. Steyermark 59632*; 1 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,600 m; F (holo), MO (1621331).

Conomorpha roraimae Steyerm., Fieldiana Bot. 28(3): 468. 1953. *J. A. Steyermark 58759*; 27 Sep. 1944; Venezuela, Bolívar, Mt. Roraima; 2,255–2,620 m; F (holo) = *Cybianthus roraimae* (Steyerm.) Agost., 1972.

Conomorpha sessilianthera Steyerm., Fieldiana Bot. 28(3): 471. 1953. *J. A. Steyermark 57253*; 14 July 1944; Venezuela, Táchira, Quebrada de Palmar at foot of Páramo de Tamá; 2,500 m; F (holo).

Conomorpha sulcata Steyerm., Fieldiana Bot. 28(3): 473. 1953. *J. A. Steyermark 57435*; 17 July 1944; Venezuela, Táchira, above Betania below Páramo de Tamá; 2,530 m; F (holo).

Conomorpha tamana Steyerm., Fieldiana Bot. 28(3): 475. 1953. *J. A. Steyermark 57359*; 15 July 1944; Venezuela, Táchira, base of Páramo de Tamá; 2,500–2,895 m; F (holo).

Grammadenia ptariensis Steyerm., Fieldiana Bot. 28(3): 476. 1953. *J. A. Steyermark 59497*; 29 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 1,810 m; F (holo).

Rapanea minima Steyerm., Fieldiana Bot. 28(3): 477. 1953. *J. A. Steyermark 58848*; 27 Sep. 1944; Venezuela, Bolívar, Mt. Roraima; 2,620–2,740 m; F (holo).

Rapanea reticulata Steyerm., Fieldiana Bot. 28(3): 477. 1953. *J. A. Steyermark 58983*; 30 Sep. 1944; Venezuela, Bolívar, Mt. Roraima; 2,040–2,255 m; F (holo).

Stylogyne turumiquirensis Steyerm., Fieldiana Bot. 28(3): 479. 1953. *J. A. Steyermark 62539*; 5 May 1945; Venezuela, Sucre, Cerro Turumiquire; 2,100–2,200 m; F (holo).

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Aulomyrcia amshoffiana Steyerm., Fieldiana Bot. 28(4): 1004. 1957. *J. A. Steyermark 60354*; 20–21 Nov. 1944; Venezuela, Bolívar, Quebrada O-paru-ma; 1,065–1,220 m; F (holo) = *Myrcia albidotomentosa* (Amshoff) McVaugh, 1969.

Aulomyrcia bolivariensis Steyerm., Fieldiana Bot. 28(4): 1004. 1957. *J. A. Steyermark 59534*; 30 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 1,800–2,100 m; F (holo) = *Myrcia bolivarensis* (Steyerm.) McVaugh, 1969.

Aulomyrcia karuaiensis Steyerm., Fieldiana Bot. 28(4): 1005. 1957. *J. A. Steyermark 60702*; 28 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,200 m; F (holo) = *Marlierea karuaiensis* (Steyerm.) McVaugh, 1958.

Aulomyrcia parvifolia Steyerm., Fieldiana Bot. 28(4): 1006. 1957. *J. A. Steyermark 60285*; 15–17 Nov. 1944; Venezuela, Bolívar, between Ptari-tepui & Sororopan-tepui; 1,615 m; F (holo) = *Myrcia rotundata* (Amshoff) McVaugh, 1969.

Aulomyrcia ptariensis Steyerm., Fieldiana Bot. 28(4): 1006. 1957. *J. A. Steyermark 59724*; 1 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,700–1,800 m; F (holo) = *Myrcia ptariensis* (Steyerm.) McVaugh, 1969.

Aulomyrcia salticola Steyerm., Fieldiana Bot. 28(4): 1007. 1957. *J. A. Steyermark 60213*; 15 Nov. 1944; Venezuela, Bolívar, Salto de Iwaracaru-meru, W end of Sororopan-tepui; 1,615 m; F (holo) = *Myrcia salticola* (Steyerm.) McVaugh, 1969.

Aulomyrcia vinacea Steyerm., Fieldiana Bot. 28(4): 1008. 1957. *J. A. Steyermark 62375*; 28 Apr. 1945; Venezuela, Sucre, Cocollar Valley; 820 m; F (holo).

Calycolpus calophyllus (H.B.K.) Berg var. *angustifolius* Steyerm., Ann. Missouri Bot. Gard. 71: 330. 1984. *J. A. Steyermark & F. Delascio 129391*; 5 Apr. 1983; Venezuela, T.F. Amazonas, Dept. Atabapo, Salto Matushi, Río Cununcunuma; VEN (holo).

Calycolpus roraimensis Steyerm., Fieldiana Bot. 28(4): 1009. 1957. *A. S. Pinkus 92*; 30 Dec. 1938; Venezuela, Bolívar, Distr. Mt. Roraima, near Arabupu; 1,300 m; F (holo).

Calyptranthes aquilarii Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 128. 1944. *J. Aguilar 810*; 1942; Guatemala, Dept. Quiché; F (holo) = *C. hondurensis* Standl., 1963.

Calyptranthes macrantha Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 127. 1944. *P. C. Standley 90532*; 1 Apr. 1941; Guatemala, Dept. Alta Verapaz, Río Frio, ca. 8 km below Tactic; 1,400 m; F (holo).

Calyptranthes meridensis Steyerm., Fieldiana Bot. 28(4): 1009. 1957. *J. A. Steyermark 56589*; 18 May 1944; Venezuela, Mérida, above Tabay; 2,285–2,745 m; F (holo).

Eugenia amanuensis Steyerm., Fieldiana Bot. 28(4): 1010. 1957, nom. nov.

Eugenia cacuminum Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 22(5): 357. 1940. *J. A. Steyer-*

mark 30903; 31 Oct. 1939; Guatemala, Dept. Chiquimula, Montaña Nube (Montaña Volcáncitos), between Socorro Mt. & Cerro Brujo, SE of Concepción de las Minas; 1,500–1,700 m; F (holo).

Eugenia caurensis Steyerm., Fieldiana Bot. 28(4): 1010. 1957. *Ll. Williams 11505*; 12 Mar. 1939; Venezuela, Bolívar, Medio Caura, en la playa del Salto de Para; 170 m; F (holo) = *E. biflora* (L.) DC., 1969.

Eugenia cervina Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 128. 1943. *J. A. Steyermark 44691*; 5 Mar. 1942; Guatemala, Dept. Alta Verapaz, near Río Icvolay, near Hacienda Yaxcabnal, 5 mi. NW of Cubilquitz; 250–350 m; F (holo).

Eugenia chiquimulana Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 22(5): 358. 1940. *J. A. Steyermark 31453*; 8 Nov. 1939; Guatemala, Dept. Chiquimula, near summit of Volcán de Quezaltepeque; 2,000 m; F (holo) = *E. pachychlamys* Donn. Sm., 1963.

Eugenia chinajensis Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 129. 1944. *J. A. Steyermark 45142*; 20 Mar. 1942; Guatemala, Dept. Alta Verapaz, S Cerro Chinajá; 150–180 m; F (holo).

Eugenia crebrifolia Steyerm., Fieldiana Bot. 28(4): 1011. 1957. *J. A. Steyermark 57204*; 14 July 1944; Venezuela, Táchira, 2 km above Betania & 7 km above Villapaez, in Paramito between Quebrada de Palmas & Quebrada de Paramito; 2,500 m; F (holo).

Eugenia jutiapensis Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 129. 1944. *J. R. Johnston 1480*; 21 Dec. 1938; Guatemala, Dept. Jutiapa, Jutiapa; F (holo).

Eugenia llewelynii Steyerm., Fieldiana Bot. 28(4): 1011. 1957. *Ll. Williams 14962*; 15 Apr. 1942; Venezuela, T.F. Amazonas, Puerto Ayacucho; 120 m; F (holo).

Eugenia mcvaughii Steyerm. & Lasser, Brittonia 33:25. 1981. *P. E. Berry 670*; 3 Nov. 1979; Venezuela, Distr. Federal, hills of Bot. Gard., Caracas; 920 m; MICH, VEN (holo).

Eugenia meridensis Steyerm., Fieldiana Bot. 28(4): 1012. 1957. *J. A. Steyermark 56251*; 3 May 1944; Venezuela, Mérida, between La Cumbre, San José & Mucutuy; 1,820–2,590 m; F (holo).

Eugenia musarum Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 22(5): 358. 1940. *J. A. Steyermark 39165*; 8 Apr. 1940; Guatemala, Dept. Izabal, Río Juyamá, SE of Cheyenne, ca. 15 mi. SW of Bananera; 50–100 m; F (holo) = *Psidium musarum* (Standl. & Steyerm.) McVaugh, 1962.

Eugenia papalensis Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 130. 1944. *J. A. Steyermark 50964*; 19 Aug. 1942; Guatemala, Dept. Huehuetenango, Cumbre Papal; 1,800–3,000 m; F (holo).

Eugenia patalensis Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 130. 1944. *P. C. Standley 69568*; 30 Mar. 1939; Guatemala, Dept. Baja Verapaz, region of Patal; 1,600 m; F (holo) = *E. guatemalensis* Donn. Sm., 1963.

Eugenia ptariensis Steyerm., Fieldiana Bot. 28(4): 1013. 1957. *J. A. Steyermark 60599*; 27 Nov. 1944; Venezuela, Bolívar, above Río Karuai, Ptari-tepui; 1,220–1,375 m; F (holo) = *E. anastomosans* DC., 1969.

Eugenia rheedioides Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23: 131. 1944. *J. I. Aguilar 1757*; 1942; Guatemala, Dept. Quiché, without locality; F (holo) = *E. myrtifolia* Sims, 1961.

Eugenia rondonensis Steyerm., Fieldiana Bot. 28(4): 1013. 1957. *J. A. Steyermark 58956*; 30 Sep. 1944; Venezuela, Bolívar, Mt. Roraima; 2,040–2,255 m; F (holo) = *Myrcianthes* species ?, 1969 fide McVaugh.

Eugenia sasoana Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 131. 1944. *J. A. Steyermark 31327*; 6 Nov. 1939; Guatemala, Chiquimula, Montaña Castilla, vicinity of Montaña Cebollas, along Río Santa Lucía Saso; 1,200–1,500 m; F (holo).

Eugenia savannarum Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 132. 1944. *J. A. Steyermark 45710*; 6 Apr. 1942; Guatemala, Dept. Alta Verapaz, base of Cerro Chinajá; 150–180 m; F (holo).

Eugenia simiarum Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 22(5): 359. 1940. *J. A. Steyermark 38274*; 28 Mar. 1940; Guatemala, Dept. Izabal, between Bananera & La Presa, Montaña del Mico; 40–300 m; F (holo) = *E. choapamensis* Standl., 1963.

Eugenia tachirensis Steyerm., Fieldiana Bot. 28(4): 1014. 1957. *J. A. Steyermark 57170*; 12 July 1944; Venezuela, Táchira, base of Páramo de Tamá; 2,300–2,430 m; F (holo).

Eugenia tamaensis Steyerm., Fieldiana Bot. 28(4): 1015. 1957. *J. A. Steyermark 57172a*; 13 July 1944; Venezuela, Táchira, Montaña of Río Táchira at base of Páramo de Tamá; 2,430 m; F (holo).

Eugenia tepuiensis Steyerm., Fieldiana Bot. 28(4): 1015. 1957. *J. A. Steyermark 60248*; 15–17 Nov. 1944; Venezuela, Bolívar, between Ptari-tepui & Sororopan-tepui; 1,615 m; F (holo).

Eugenia turumiquirensis Steyerm., Fieldiana Bot. 28(4): 1015. 1957. *J. A. Steyermark 62548*; 5 May 1945; Venezuela, Sucre, SW of Cocollar, Cerro Turumiquire; 2,100–2,200 m; F (holo).

Gomidesia bonnetiasylvestris Steyerm., Fieldiana Bot. 28(4): 1016. 1957. *J. A. Steyermark 59768*; 2 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 2,000–2,200 m; F (holo) = *Myrcia bonnetiasylvestris* (Steyerm.) Steyerm., 1984.

Myrcia sanisidrensis Steyerm., Fieldiana Bot. 28(4): 1018. 1957. *J. A. Steyermark 56551*; 14 May 1944; Venezuela, Mérida, above San Isidro Alto; 1,820 m; F (holo).

Myrcia sororopanensis Steyerm., Fieldiana Bot. 28(4): 1019. 1957. *J. A. Steyermark 60102*; 14 Nov. 1944; Venezuela, Bolívar, Sororopan-tepui; 2,255 m; F (holo).

Myrcia tepuiensis Steyerm., Fieldiana Bot. 28(4): 1019. 1957. *J. A. Steyermark 60284*; 15–17 Nov. 1944; Venezuela, Bolívar, between Ptari-tepui & Sororopan-tepui; 1,615 m; F (holo).

Myrciaria caurensis Steyerm., Fieldiana Bot. 28(4): 1020. 1957. *Ll. Williams 11691*; 3 Mar. 1939; Venezuela, Bolívar, Medio Caura, La Prisión; 120 m; F (holo) = *M. dubia* (H.B.K.) McVaugh, 1969.

Myrtus myricoides H.B.K. var. *turumiquirensis* Steyerm., Fieldiana Bot. 28(4): 1022. 1957. *J. A. Steyermark 62628*; 6 May 1945; Venezuela, Sucre, Cerro Turumiquire; 2,200 m; F (holo) = *Ugni myricoides* (H.B.K.) Berg.

Plinia fruticosa Steyerm., Fieldiana Bot. 28(4): 1023. 1957. *J. A. Steyermark 62611*; 6 May 1945; Venezuela, Sucre, Cerro Turumiquire; 2,500 m; F (holo) = *Siphoneugena densiflora* Berg, 1969.

Siphoneugena densiflora Berg var. *tepuiensis* Steyerm., Fieldiana Bot. 28(4): 1024. 1957. *J. A. Steyermark 59711*; 1 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,700–1,800 m; F (holo) = *S. densiflora* Berg var. *densiflora*, 1969. (= *S. dussii* (Berg) Proenca, ined.).

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Guapira amacurensis Steyerm., Ann. Missouri Bot. Gard. 74: 615. 1987. *L. Marcano Berti 551*; 12 Jan. 1965; Venezuela, Bolívar, E of Río Grande, ENE of El Palmar, near limits of T.F. Amacuro; MO (2670763, 2775683), NY, VEN (holo).

Guapira ayacuchae Steyerm., Ann. Missouri Bot. Gard. 74: 615. 1987. *J. A. Steyermark & O. Huber 113856*; 4 May 1977; Venezuela, T.F. Amazonas, Tobogán de la Selva, 35 km S of Puerto Ayacucho; 85 m; MO (2775745), VEN (holo).

Guapira bolivarensis Steyerm., Ann. Missouri Bot. Gard. 74: 616. 1987. *R. L. Liesner & B. K. Holst 20800*; 11 May 1986; Venezuela, Bolívar, Dept. Piar, summit of Amaruay-tepui, S side, E half; 950–1,100 m; MO (holo), VEN.

Guapira davidsei Steyerm., Ann. Missouri Bot. Gard. 74: 617. 1987. *G. Davidse & A. González 16382*; 28 Mar.–2 Apr. 1979; Venezuela, T.F. Amazonas, Dept. Tucupita, 5–14 km ESE of Los Castillos de Guayana; 50–2,000 m; MO, VEN (holo).

Guapira glabriflora Steyerm., Ann. Missouri Bot. Gard. 74: 617. 1987. *L. Marcano Berti & P. Salcedo 54-979*; 17 Mar. 1979; Venezuela, T.F. Amazonas, Dept. Río Negro, between San Carlos and El Solano; MER (holo), MO (3423162).

Guapira marcano-bertii Steyerm., Ann. Missouri Bot. Gard. 74: 618. 1987. *L. Marcano Berti 209*; 26 May 1964; Venezuela, T.F. Amacuro, E of Río Grande, ENE of El Palmar, near limits of Edo. Bolívar; MO (2701699, 2680864), VEN (holo).

Guapira neblinensis Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *B. Maguire et al. 42068*; 14–16 Nov. 1957; Venezuela; MO (3291201), NY (holo).

Guapira sancarlosiana Steyerm., Ann. Missouri Bot. Gard. 74: 618. 1987. *H. L. Clark & P. Maquirino 7794*; 8 Jan. 1981; Venezuela, T.F. Amazonas, 4.3 km NNE from San Carlos on Solano Road, IVIC study site; 119 m; MO (holo—2991814).

Guapira sipapoana Steyerm., Ann. Missouri Bot. Gard. 74: 620. 1987. *C. Blanco 1158*; May 1971; Venezuela, T.F. Amazonas, Reserva Forestal Sipapo, left margin of Río Sipapo, Bloque 1; VEN (holo).

Mirabilis pulchella Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(1): 5. 1943. *P. C. Standley 73841*; Oct. 1940; Guatemala, Dept. Zacapa, road between Zacapa and Chuquimula; 500–660 m; F (holo).

Neea amaruayensis Steyerm., Ann. Missouri Bot. Gard. 74: 623. 1987. *R. L. Liesner & B. K. Holst 20514*; 2 May 1986; Venezuela, Bolívar, Amaruay-tepui, W side, steep slopes; MO (holo—3395522), VEN.

Neea bernardii Steyerm., Ann. Missouri Bot. Gard. 74: 623. 1987. *L. Bernardi 6746*; 23 Apr. 1957; Venezuela, Bolívar, de Santa Elena de Uairen al sur-este; 800–900 m; MER (holo), MO (2406055), NY.

Neea bracteosa Steyerm., Ann. Missouri Bot. Gard. 74: 624. 1987. *R. L. Liesner & A. González 11277*; 4–5 Apr. 1981; Venezuela, Bolívar, Represa Guri, 55 km NE of Ciudad Piar; 250–300 m; MO (3100093), VEN (holo).

Neea brevipedunculata Steyerm., Ann. Missouri Bot. Gard. 74: 624. 1987. *J. A. Steyermark et al. 122366*; 12 May 1980; Venezuela, T.F. Amazonas, between Paso El Diablo and Caño de Culebra, 25–30 km SE of Puerto Ayacucho; 100 m; MO, VEN (holo).

Neea cedensis Steyerm., Ann. Missouri Bot. Gard. 74: 625. 1987. *B. Stergios et al. 8611*; 16 Apr. 1984; Venezuela, Bolívar, Dept. Cedeño, bosque de galeria del Caño Chaviripa, Carretera Caicara—El Burro; MO (holo—3395524), PORT.

Neea clarkii Steyerm., Ann. Missouri Bot. Gard. 74: 625. 1987. *H. L. Clark 6980*; n.d.; Venezuela, T.F. Amazonas, 4.3 km NNE on Solano Road; 119 m; NY (holo).

Neea davidsei Steyerm., Ann. Missouri Bot. Gard. 74: 627. 1987. *G. Davidse & A. González 16558*; 4–6 Apr. 1979; Venezuela, T.F. Amacuro, Dept. Tucupita, ca. 13 km by road ESE of town of Sierra Imata; 400 m; MO (3395516), VEN (holo).

Neea grandis Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *N. T. Silva & U. Brazao 60606*; 14 Dec. 1965; Brazil, Serra da Neblina, Rio Negra, Rio Cauaburi, Rio Maturacá, from Igarape Anta up slopes to Pico da Neblina; 1,350–2,000 m; MO (3291199), NY (holo).

Neea guaiquinimae Steyerm., Ann. Missouri Bot. Gard. 74: 627. 1987. *J. A. Steyermark et al. 117971*; 9 Apr. 1979; Venezuela, Bolívar, Cerro Guaiquinima, summit, NE sector; 1,650 m; MO (2774805), VEN (holo).

Neea huachamacarae Steyerm., Ann. Missouri Bot. Gard. 74: 628. 1987. *R. L. Liesner 18403*; 7 Mar. 1985; Venezuela, T.F. Amazonas, Río Cunucunuma, base of trail to Cerro Huachamacari; 220 m; MO (3395518), VEN (holo).

Neea ignicola Steyerm., Ann. Missouri Bot. Gard. 74: 628. 1987. *O. Huber & J. Cerda 1456*; 26 Jan. 1978; Venezuela, T.F. Amazonas, 11 km N of Puerto Ayacucho, toward El Burro; 90 m; VEN (holo).

Neea liesneri Steyerm., Ann. Missouri Bot. Gard. 74: 629. 1987. *R. L. Liesner 16502*; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro de la Neblina, 0.4 km W of base camp on Río Mawarinuma; 140 m; MO (3395523), VEN (holo).

Neea mapourioides Steyerm., Ann. Missouri Bot. Gard. 74: 630. 1987. *R. L. Liesner 4096*; 1 Dec. 1977; Venezuela, T.F. Amazonas, 0.5–1.5 km E of San Carlos; 120 m; MO (3029616), VEN (holo).

Neea marahuacae Steyerm., Ann. Missouri Bot. Gard. 74: 631. 1987. *R. L. Liesner 18428*; 8–9 Mar. 1985; Venezuela, T.F. Amazonas, Cerro Marahuaca, 1–2 km N of Sima Camp; 1,100 m; MO (3395521), VEN (holo).

Neea neblinensis Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *B. Maguire et al. 42072*; 14–16 Nov. 1957; Venezuela, T.F. Amazonas, Cerro de la Neblina, Río Yatua, just S of Camp 3; 700 m; MO (3291200), NY (holo).

Neea parimensis Steyerm., Ann. Missouri Bot. Gard. 74: 631. 1987. *J. A. Steyermark 106982*; 18 Apr.–23 May 1973; Venezuela, T.F. Amazonas, Sierra Parima, Simarawochi, Río Matacuni, 6–7 km W of Venezuelan–Brazilian border; 795–830 m; MO (2669239), NY, VEN (holo).

Neea robusta Steyerm., Ann. Missouri Bot. Gard. 74: 632. 1987. *O. Huber 1693*; 14–28 Feb. 1978; Venezuela, T.F. Amazonas, third savanna at W base of Cerro Yapacana; 100 m; VEN (holo).

Neea sebastianii Steyerm., Ann. Missouri Bot. Gard. 74: 633. 1987. *R. L. Liesner & H. Clark 8959*; 31 Jan. 1980; Venezuela, T.F. Amazonas, Isla Sebastian, Río Casiquiare above Chapezón, between Boca and Solano; 120 m; MO (3395520), VEN (holo).

Neea subglabrata Steyerm., Ann. Missouri Bot. Gard. 74: 633. 1987. *J. A. Steyermark et al. 117615*; 15

Dec. 1978; Venezuela, Bolívar, between Betania and Santa Elena de Uairen, 40 km W of Santa Elena; 900 m; MO (2774451), NY, VEN (holo).

Neea tepuiensis Steyerm., Ann. Missouri Bot. Gard. 74: 634. 1987. *J. A. Steyermark & J. J. Wurdack 1104*; 23 Feb. 1955; Venezuela, Bolívar, Chimantá Massif, Torono tepui, summit, S-facing forested slopes above valley of South Caño; 1,955–2,090 m; F, MO, NY, VEN (holo).

Salpianthus standleyi Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 22(3): 139. 1940. *Y. Mexia 8783*; 11 Nov. 1937; Mexico, Guerrero, Barranca del Consuelo, Sierra Madre del Sur, N of Río Balsas, Distr. Adama; F (holo).

OCHNACEAE

Adenanthe Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 10(4): 19. 1961, gen. nov.

Adenanthe bicarpellata Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 10(4): 19. 1961. *J. A. Steyermark & J. J. Wurdack 377*; 3 Feb. 1955; Venezuela, Bolívar, Chimantá Massif; 1,940 m; MO (2011680), NY (holo).

Adenanthe bicarpellata Maguire, Steyerm. & Wurd. var. *chimantensis* Steyerm., ined.?. *J. A. Steyermark et al. 128637*; 2–5 Feb. 1983; Venezuela; MO (iso—3231620).

Ouratea asisae Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *J. Hoyos & G. Morillo 90*; 7 May 1973; Venezuela, T.F. Amazonas, Serranía Parú, Cerro Asisa (La Momia); 1,210 m; VEN (holo).

Ouratea ayacuchae Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *O. Huber & J. Cerda 1447*; 16 Jan. 1978; Venezuela, T.F. Amazonas, Dept. Atures, Puerto Ayacucho; 90 m; VEN (holo).

Ouratea brevicalyx Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *R. Cowan & J. J. Wurdack 31462*; 15 Feb. 1951; Venezuela, T.F. Amazonas, base of Cerro Parú, Serranía Parú; 100 m; NY (holo).

Ouratea brevipedicellata Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *B. Maguire et al. 41909*; 15 Oct. 1957; Venezuela, T.F. Amazonas, Río Guainía between Maroa and Guzman Blanco; 130 m; NY (holo).

Ouratea croizatii Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *L. Croizat 624*; 15 Sep. 1951; Venezuela, T.F. Amazonas, Raudal Bobadilla, alto Orinoco; NY (holo).

Ouratea culmenicola Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *J. A. Steyermark et al. 117393*; 23–24 May 1978; Venezuela, Cerro Guaiquinima, 1 km Río del Salto Szczerbanari; 730–750 m; MO (holo), VEN.

Ouratea deminuta Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *O. Huber 2504*; 23 Aug. 1978; Venezuela, T.F. Amazonas, Dept. Atabapo, Sabana de Minicio; 90 m; VEN (holo).

Ouratea discophora Ducke subsp. *pervenulosa* Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *B. Maguire et al. 36657*; 27 Nov. 1953; Venezuela, 50 km above mouth of Pacimoni; 120 m; NY (holo).

Ouratea duidae Steyerm., Fieldiana Bot. 28(2): 369. 1952. *J. A. Steyermark 58284*; 2 Sep. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,025–1,200 m; F (holo), NY.

Ouratea evoluta Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *B. Maguire et al. 29253*; 17 Oct. 1950; Venezuela, T.F. Amazonas, 15 km above San Fernando de Atabapo; 100 m; NY (holo).

Ouratea fasciculata Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *Forest Dept. Record No. 7227* (*Field No. G251*); 28 Sep. 1952; Guyana, 6 mi. E of Onoro Creek; NY (holo).

Ouratea gillyana (Dwyer) Sandw. & Maguire subsp. *pachypoda* Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *B. Maguire & D. B. Fanshawe 32629*; 16 Nov. 1951; Guyana, Sagaraimadoi Savanna, upper Mazaruni River, Pakaraima Mountains; NY (holo).

Ouratea guaiquinimae Maguire & Steyerm., ined. mss. = *O. guaiquinimensis* Sastre, 1988.

Ouratea huberi Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *O. Huber 1904*; 30 May 1978; Venezuela, T.F. Amazonas, Dept. Atabapo, Río Ventuari; 98 m; VEN (holo).

Ouratea inconformis Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *F. Breteler 4832*; 25 Nov. 1965; Venezuela, T.F. Amazonas, Sipapo River near confluence with Orinoco River; 90 m; NY (holo), VEN.

Ouratea longistyla Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *O. Huber & E. Medina 5763*; 6 Feb. 1981; Venezuela, T.F. Amazonas, Dept. Río Negro, Río Siapo; 125 m; NY (holo), VEN.

Ouratea macurucoensis Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *P. E. Berry 2152*; 25 Mar. 1975; Venezuela, T.F. Amazonas, Piedra Blanca, 1 km Río arriba de Macuruco; 130 m; VEN (holo).

Ouratea marahuacensis Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *J. A. Steyermark & B. K. Holst 130907*; 1 Mar. 1985; Venezuela, T.F. Amazonas, Cerro Marahuaca, along tributary of Caño Negro; 1,140–1,150 m; MO (holo), NY, VEN.

Ouratea medinae Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *E. Medina 534*; Feb. 1971; Venezuela, T.F. Amazonas, Playa Tigre, Río Atabapo, San Fernando de Atabapo; VEN (holo).

Ouratea oligantha Maguire & Steyerm., ined. mss. = *O. soderstromii* Sastre, 1988.

Ouratea ornata Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *B. Maguire & L. Politi 27485*; 1–3 Dec. 1948; Venezuela, T.F. Amazonas, Cerro Sipapo (Paraque); 605–910 m; NY (holo).

Ouratea papillata Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *J. A. Steyermark & G. S. Bunting 103271*; 7 May 1970; Venezuela, T.F. Amazonas, along Río Yatua, base of Cerro Yapacana; 125 m; NY, VEN (holo).

Ouratea paruensis Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *R. Cowan & J. J. Wurdack 31104*; 31 Jan. 1951; Venezuela, T.F. Amazonas, Cerro Parú; 2,000 m; NY (holo).

Ouratea propinqua Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *J. A. Steyermark et al. 109447*; 24 Feb.–7 Mar. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Jaua; 1,800 m; VEN (holo).

Ouratea psammophila Maguire & Steyerm., ined. mss. = *O. steyermarkii* Sastre, 1988.

Ouratea pseudotatei Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *A. S. Pinkus 277*; Jan. 1939; Guyana, Arabaru River (Kako tributary), upper Mazaruni drainage; NY (holo).

Ouratea ptaritepuiensis Steyerm., Fieldiana Bot. 28(2): 370. 1952. *J. A. Steyermark 59642*; 1 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,600 m; F (holo).

Ouratea pumila Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *O. Huber & S. S. Tillett 5481*; 22 July 1980; Venezuela, T.F. Amazonas, Dept. Atabapo, 5 mi. S of Laguna Yagua; 100 m; VEN (holo).

Ouratea pumila Maguire & Steyerm. var. *heterodoxa* Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *O. Huber & S. S. Tillett 5536*; 27 July 1980; Venezuela, T.F. Amazonas, Dept. Azures, 2 km N of Río Guayapo Medio; VEN (holo).

Ouratea ramosissima Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *F. Cardona 2204*; Oct. 1947; Venezuela, Bolívar, Cerro de Acopán (Macizo de Chimantá); 900 m; NY, VEN (holo).

Ouratea rotundipetala Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *B. Maguire et al. 30766*; 6 Jan. 1951; Venezuela, T.F. Amazonas, E-W Caño, N of Cerro Yapacana; 130 m; NY (holo).

Ouratea sipapoensis Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *B. Maguire & L. Politi 27631*; 12 Dec. 1948; Venezuela, T.F. Amazonas, Cerro Sipapo; 1,700 m; NY (holo).

Ouratea subamplexicaulis Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *E. Foldats 2784*; 1 Jan. 1957; Venezuela, Bolívar, 105 km de El Dorado hacia Santa Elena; NY (holo).

Ouratea venezuelensis Steyerm., Fieldiana Bot. 28(2): 370. 1952. *Ll. Williams 14152*; 2 Feb. 1942; Venezuela, T.F. Amazonas, del Caño Temi, Yavita; 128 m; F (holo).

Ouratea wurdackiana Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *J. J. Wurdack & L. S. Adderley 42719*; 1 June 1959; Venezuela, T.F. Amazonas, Río Orinoco just above mouth of Río Atabapo; 125 m; NY (holo).

Ouratea yapacanae Maguire & Steyerm., ined. mss. = *O. yapacanae* Sastre, 1988.

Perissocarpa Steyerm. & Maguire, Ann. Missouri Bot. Gard. 71: 319. 1984, gen. nov.

Perissocarpa steyermarkii (Maguire) Steyerm. & Maguire subsp. *tachirensis* Steyerm. & Maguire, Ann. Missouri Bot. Gard. 71: 320. 1984. *J. A. Steyermark & B. Manara 125174*; 21 June 1981; Venezuela, Táchira, along Río San Buena, area of Presa Las Cuevas, ca. 10 km E of La Fundación; 550–600 m; VEN (holo).

Perissocarpa umbellifera Steyerm. & Maguire, Ann. Missouri Bot. Gard. 71: 320. 1984. *B. Maguire et al. 29529*; 18 Nov. 1950; Venezuela, T.F. Amazonas, Cerro Duida, Río Cunucunuma; 1,400 m; NY, VEN (holo).

Poecilandra pumila Steyerm., Fieldiana Bot. 28(2): 371. 1952. *J. A. Steyermark 59342*; 26 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,220 m; F (holo).

Sauvagesia L. sect. *Spatulatae* Steyerm., Fieldiana Bot. 28(2): 376. 1952, sect. nov.

Sauvagesia duidae Steyerm., Fieldiana Bot. 28(2): 372. 1952. *J. A. Steyermark 58021*; 26 Aug. 1944; Venezuela, T.F. Amazonas, near Caño Negro; 1,400 m; F (holo).

Sauvagesia guianensis (Eichl.) Sastre subsp. *aracamuniensis* Steyerm., Ann. Missouri Bot. Gard.: in press. 1989. *R. L. Liesner & F. Delascio 22075*; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp; 1,550 m; MO (holo), VEN.

Sauvagesia guianensis (Eichl.) Sastre subsp. *guaiquinimensis* Steyerm., Ann. Missouri Bot. Gard. 74: 101. 1987. *J. A. Steyermark et al. 117498*; Venezuela, T.F. Amazonas, Cerro Guaiquinima; 1,540 m; MO (holo), VEN.

Sauvagesia guianensis (Eichl.) Sastre subsp. *Sipapoensis* Steyerm., Ann. Missouri Bot. Gard. 74: 101. 1987. *J. A. Steyermark et al. 124530*; Venezuela, T.F. Amazonas, Serranía Sipapo; 1,500 m; MO (holo), VEN.

Sauvagesia imthurniana (Oliver) Dwyer subsp. *chimantensis* Maguire, Steyerm. & Wurd., Mem. New York Bot. Gard. 10(4): 17. 1961. *J. J. Wurdack 34201*; 26 Jan. 1953; Venezuela, Bolívar, Churi-tepui (Murutepui); 2,250–2,300 m; F, NY (holo).

Sauvagesia longipes Steyerm., Fieldiana Bot. 28(2): 374. 1952. *J. A. Steyermark 60215*; 15 Nov. 1944; Venezuela, Bolívar, Salto de Iwaracaru-meru, Sororopan-tepui; 1,615 m; F (holo), MO (1313407).

Sauvagesia marahuacensis Steyerm., Ann. Missouri Bot. Gard. 74: 98. 1987. *R. L. Liesner 17677a*; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca, Río Yameduaka arriba; MO (holo), VEN.

Sauvagesia marahuacensis Steyerm. subsp. *neblinensis* Steyerm., Ann. Missouri Bot. Gard.: in press. 1987. *R. L. Liesner 16809*; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro de la Neblina, Camp IV; 780 m; MO (holo), VEN.

Sauvagesia miniata Steyerm., Fieldiana Bot. 28(2): 376. 1952. *J. A. Steyermark 58467*; 8 Sep. 1944; Venezuela, T.F. Amazonas, vicinity of Sanariapo; 100 m; F (holo), MO (324780).

Tyleria breweriana Steyerm., Ann. Missouri Bot. Gard. 71: 322. 1984. *J. A. Steyermark et al. 124326*; 14 Feb. 1981; Venezuela, Bolívar, Dept. Sucre, Meseta de Jaua; 2,020 m; VEN (holo).

Tyleria phelpsiana Maguire & Steyerm., Mem. New York Bot. Gard. 23: 866. 1972. *J. A. Steyermark 98049*; 22–27 Mar. 1967; Venezuela, Bolívar, Meseta de Jaua, Cerro Jaua; 1,922–2,100 m; NY (holo), VEN.

OLACACEAE

Dulacia redmondii Steyerm., Phytologia 38(3): 217. 1978. *J. A. Steyermark & P. Redmond 112829*; 28 Dec. 1976; Venezuela, T.F. Amazonas, Canaripo, lado sur del Río Ventuari; 125 m; US, VEN (holo).

Heisteria olivae Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 453. 1966. *J. A. Steyermark 92077*; 15–19 Nov. 1963; Venezuela, Distr. Federal, Cerro Naiguata; 1,000–1,300 m; NY, S, US, VEN (holo) = *H. latifolia* Standl., 1984.

Liriosma tepuiensis Steyerm., Bol. Soc. Venez. Ci. Nat. 32: 328. 1976. *J. A. Steyermark et al. 109041*; 13 Feb. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Sarisariñama; 1,320 m; F, K, L, NY, VEN (holo) = *Dulacia tepuiensis* (Steyerm.) Sleumer & Steyerm., 1984.

Schoepfia clarkii Steyerm., Ann. Missouri Bot. Gard. 75: 1061. 1988. *H. L. Clark 8111*; 16 Aug. 1987; Venezuela, T.F. Amazonas, 10.8 km NE of San Carlos on Solano road; 119 m; MO (holo).

Schoepfia tepuiensis Steyerm., Bol. Soc. Venez. Ci. Nat. 32: 331. 1976. *J. A. Steyermark 93413*; 5 May 1964; Venezuela, Bolívar, Auyan-tepuy; 1,850 m; K, NY, P, S, U, US, VEN (holo).

OLEACEAE

Fraxinus bicolor Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 73. 1944. *P. C. Standley 80408*; Dec. 1940; Guatemala, Dept. Guatemala, near Fiscal; 1,100 m; F (holo).

Fraxinus cavekiana Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 74. 1944. *A. F. Skutch 1660*; Nov. 1934; Guatemala, Dept. Quiché, Nebaj; 1,860 m; F (holo).

Fraxinus vellerea Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 74. 1944. *P. C. Standley 76162*; Oct.–Nov. 1940; Guatemala, Dept. Jutiapa, near Jutiapa; 850 m; F (holo).

Linociera avilensis Steyerm., Brittonia 30: 45. 1978. *E. Delgado 233*; 9 May 1939; Venezuela, Distr. Federal, Cerro Avila; VEN (holo).

Menodora coulteri A. Gray var. *minima* Steyerm., Ann. Missouri Bot. Gard. 19: 121. 1932. *J. E. Kirkwood 20*; June 1908; Mexico, Zacatecas, Cedros, near Arroyos; F, MO (holo).

Menodora decemfida (Gill.) A. Gray var. *longifolia* Steyerm., Ann. Missouri Bot. Gard. 19: 143. 1932. *E. Palmer 429*; Apr., Aug. 1896; Mexico, Durango, Santiago, Papasquiara; MO (holo).

Menodora helianthemoides Humb. & Bonpl. var. *engelmannii* Steyerm., Ann. Missouri Bot. Gard. 19: 119. 1932. *J. Gregg 44*; 7 May 1948; Mexico, Coahuilla, near Saltillo; GH, MO (holo).

Menodora helianthemoides Humb. & Bonpl. var. *humilis* Steyerm., Ann. Missouri Bot. Gard. 19: 118. 1932. *C. C. Parry & E. Palmer 571pp*; 1878; Mexico, San Luis Potosí, region of San Luis Potosí; 1,849 2,439 m; F, G, MO (holo).

Menodora helianthemoides Humb. & Bonpl. var. *magniflora* Steyerm., Ann. Missouri Bot. Gard. 19: 118. 1932. *C. C. Parry & E. Palmer 570pp*; 1878; Mexico, San Luis Potosí, region of San Luis Potosí; 1,829–2,439 m; F, GH, MO (holo).

Menodora heterophylla Moric. ex DC. var. *australis* Steyerm., Ann. Missouri Bot. Gard. 19: 127. 1932. *Pegler 950*; Aug. 1903; South Africa, Transvaal, near Rustenburg; 1,220 m; B (holo).

Menodora intricata Brandg. var. *purpusii* Steyerm., Ann. Missouri Bot. Gard. 19: 150. 1932. *C. A. Purpus 1318*; June 1905; Mexico, Puebla, Tehuacan; F, GH, MO (holo), NY.

Menodora pinnatisecta Steyerm., Ann. Missouri Bot. Gard. 19: 133. 1932. *Jörgensen 2643*; 9 Nov. 1917; Argentina, Terr. del Chaco, Las Palmas; GH (holo).

Menodora scabra Engelm. ex A. Gray var. *longituba* Steyerm., Ann. Missouri Bot. Gard. 19: 141. 1932. *Smart 213*; 5 May 1867; U.S.A., Arizona, Massatzal Mountains; GH (holo).

Menodora scabra Engelm. ex A. Gray var. *ramosissima* Steyerm., Ann. Missouri Bot. Gard. 19: 139. 1932. *E. J. Palmer 31083*; 19 June 1926; U.S.A., Texas, El Paso Co., near El Paso; MO (holo).

Menodora spinescens A. Gray var. *mohavensis* Steyerm., Ann. Missouri Bot. Gard. 19: 155. 1932. *S. B. Parish 9795*; 23 Apr. 1915; U.S.A., California, San Bernardino Co., Mojave Desert, 14 mi. NE of Barstow; CAS (holo).

ONAGRACEAE

Fuchsia adpressipilis Steyerm., Fieldiana Bot. 28(2): 438. 1952. *J. A. Steyermark 55381*; 8 Feb. 1944; Venezuela, Lara, between Santo Domingo and Los Quebraditos, S of Las Sabanetas; 2,430–2,475 m; F (holo).

Fuchsia meridensis Steyerm., Fieldiana Bot. 28(2): 439. 1952. *J. A. Steyermark 56162*; 27 Apr. 1944; Venezuela, Mérida, between La Azulita and La Trampa; 1,280–2,225 m; F (holo).

Fuchsia verrucosa Hartw. var. *tamaensis* Steyerm., Fieldiana Bot. 28(2): 440. 1952. *J. A. Steyermark 57175*; 13 July 1944; Venezuela, Táchira, base of Páramo de Tamá, between Betania and Tamá; 2,430 m; F (holo).

"Ludvigia" alternifolia L. var. *pubescens* Palmer & Steyerm., Ann. Missouri Bot. Gard. 25: 772. 1938. *E. J. Palmer & J. A. Steyermark 41450*; 11 July 1933; U.S.A., Missouri, 4 mi. W of Charleston; GH, MO (holo) = *Ludwigia alternifolia* L. var. *alternifolia*, 1963.

Oenothera pilosella Raf. f. *laevigata* Palmer & Steyerm., Brittonia 10: 116. 1958. *J. A. Steyermark 78703*; 25 June 1955; U.S.A., Missouri, Howell Co., 4 mi. S of West Plains; F (holo) = *O. pilosella* Raf. var. *pilosella*, 1981.

ORCHIDACEAE

Scaphyglottis michelangeliorum Carnevali & Steyerm., Phytologia 55(5): 289. 1984. *J. A. Steyermark 129650*; 13–14 Oct. 1983; Venezuela, T.F. Amazonas, faldas del Cerro Marahuaca; 1,550 m; VEN (holo).

OXALIDACEAE

Oxalis calcicola Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(3): 118. 1944. *J. A. Steyermark 50258*; 8 Aug. 1942; Guatemala, Dept. Huehuetenango, vicinity Chemal, Sierra de los Cuchumatanes; 3,700 m; F (holo).

Oxalis minarum Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 58. 1944. *J. A. Steyermark 29718*; Oct. 1939; Guatemala, Dept. Zacapa, Sierra de las Minas, Finca Alejandría; 1,000–1,500 m; F (holo).

PASSIFLORACEAE

Dilkea magnifica Steyerm., Acta Bot. Venez. 3: 186. 1968. *J. A. Steyermark 87606*; 18 Nov. 1960; Venezuela, Terr. Delta Amacuro, Cerro La Paloma, Sierra Imataca; 100–200 m; NY (holo).

Passiflora bomareifolia Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 455. 1967. *J. A. Steyermark & J. J. Wurdack 1370*; 11 Mar. 1955; Venezuela, Bolívar, Amuri-tepui, Chimantá Massif; 850–1,275 m; MO (2011386), VEN (holo).

Passiflora nuriensis Steyerm., Acta Bot. Venez. 3: 188. 1968. *J. A. Steyermark 88425*; 14 Jan. 1961; Venezuela, Bolívar, Altiplanicie de Nuria, Agua Linda; 400 m; MO (1803670, 180670), NY (holo).

PIPERACEAE

Peperomia acuminata Ruíz & Pavón f. *rubra* Steyerm., Fl. Venez. 2(2): 33. 1984. *L. Ruíz Terán 6461*; 29 Sep. 1971; Venezuela, Mérida, Dept. Rangel, entre Canada del Padre y El Baho, unos 10 km al E de la Sierra Nevada de Santo Domingo; 2,300–3,340 m; MERF, VEN (holo).

Peperomia aristeguietae Steyerm., Acta Bot. Venez. 6: 83. 1971. *J. A. Steyermark 103733*; 17 Aug. 1970;

Venezuela, Distr. Federal, S of Carvao, Río Aguas Calientes; 50–100 m; VEN (holo).

Peperomia aroensis Steyerm., Fl. Venez. 2(1): 50. 1984. *L. Aristeguieta & F. Pannier 1924*; 6–7 July 1953; Venezuela, Yaracuy, Sierra de Aroa; VEN (holo).

Peperomia atabapoensis Steyerm., Fl. Venez. 2(1): 52. 1984. *S. S. Tillett et al. 743-230*; 23–26 Mar. 1974; Venezuela, T.F. Amazonas, Dept. Atabapo, Caño Pavon, margen derecha del Río Orinoco, arriba de San Fernando de Atabapo; 130 m; VEN (holo).

Peperomia berryi Steyerm., Fl. Venez. 2(1): 53. 1984. *P. E. Berry et al. 3923*; 19 June 1982; Venezuela, Falcón, Urapagual, 'Los Haitoncitos,' ca. 2 km SE de Curimagua, ladera sur de la Sierra de San Luis; 1,200–1,300 m; VEN (holo).

Peperomia boomii Steyerm., Brittonia 38: 220. 1986. *B. Boom & M. Grillo 6417*; 26 Oct. 1985; Venezuela, Bolívar, Distr. Cedeño, vicinity of Panare, village of Corozal, 6 km from Maniapure toward Caicara; 200 m; MYR, NY (holo), VEN.

Peperomia borburatensis Steyerm., Fl. Venez. 2(1): 61. 1984. *J. A. & C. Steyermark 95355*; 30 Mar. 1966; Venezuela, Carabobo, selva siempreverde a lo largo de las cabeceras del Río San Gran, arriba de La Loma, al sur de Borburata; 750–850 m; F, US, VEN (holo).

Peperomia buntingii Steyerm., Acta Bot. Venez. 8: 116. 1973. *J. A. Steyermark & G. S. Bunting 105306*; 28 Nov. 1971; Venezuela, Yaracuy, Río Guayabito; 200–250 m; VEN (holo).

Peperomia caraboboensis Steyerm. & Bunting, Acta Bot. Venez. 6: 81. 1971. *J. A. Steyermark et al. 102431*; 4 Jan. 1970; Venezuela, Carabobo, Río Borburata; 150 m; VEN (holo).

Peperomia carnevalii Steyerm., Fl. Venez. 2(1): 67. 1984. *G. Carnevali & H. Pivat 640*; 2 May 1982; Venezuela, Aragua, cumbre de la carretera Cata–Cuyagua; 400 m; MY, VEN (holo).

Peperomia chapensis Steyerm., Fl. Venez. 2(1): 70. 1984. *J. A. Steyermark & G. S. Bunting 97664*; Venezuela, Yaracuy, Cerro La Chapa, N de Nirgua; 1,200–1,360 m; VEN (holo).

Peperomia choroniana Trel. & Yuncker var. *heterodoxa* Steyerm., Fl. Venez. 2(1): 74. 1984. *G. S. Bunting 4461*; 7 July 1971; Venezuela, Yaracuy, Cerro La Chapa, ca. 5 km N de Nirgua; MY (holo).

Peperomia clavigera Standl. & Steyerm., Fieldiana Bot. 24(3): 240. 1952. *J. A. Steyermark 45738*; Guatemala, Alta Verapaz, between Chajmayic and Sebol; 300–500 m; F (holo).

Peperomia croizatiana Steyerm., Acta Bot. Venez. 6: 85. 1971. *J. A. Steyermark & G. Wessels-Boer 100371a*; Venezuela, Yaracuy, Cerro Negro, Sierra de Aroa; 100 m; VEN (holo).

Peperomia cyclophylla Miq. f. *zulianensis* Steyerm., Fl. Venez. 2(1): 80. 1984. *J. A. Steyermark et al. 122730*; 28 May 1980; Venezuela, Zulia, Distr. Mara, Caño Indio, entre la Hacienda Caño Azul y la base del Cerro Yolanda, 15 km al suroeste del Rancho 505; 200–250 m; VEN (holo), MO.

Peperomia delascioi Steyerm., Brittonia 40: 294. 1988. *F. Delascio 13161*; 25–26 Mar. 1987; Venezuela, Bolívar, Distr. Piar, Kamarkaibaray-tepui, al este del Auyan-tepui; 2,400–2,500 m; VEN (holo), MO.

Peperomia dorstenioides Standl. & Steyerm., Fieldiana Bot. 24(3): 244. 1952. *J. A. Steyermark 49410*; n.d.; Guatemala, Huehuetenango, between Ixcan and Finca San Rafael; 200–800 m; F (holo).

Peperomia falconensis Steyerm., Fl. Venez. 2(1): 95. 1984. *R. L. Liesner et al. 7729*; 21 June 1979; Venezuela, Falcón, Parque Nacional Quebrada de la Cueva del Toro; 600 m; VEN (holo), MO.

Peperomia foveolata Steyerm., Fl. Venez. 2(1): 99. 1984. *B. Maguire et al. 36889*; 24 Dec. 1953; Venezuela, T.F. Amazonas, Cerro de la Neblina, Río Yatua, 3 km al sur del Campamento 3; 900 m; NY (holo).

Peperomia fundacionensis Steyerm., Fl. Venez. 2(1): 101. 1984. *R. L. Liesner & A. González 10555*; 14 Mar. 1981; Venezuela, Táchira, 18 km al suroeste de La Fundación; 950 m; VEN (holo), MO.

Peperomia gentryi Steyerm., Ann. Missouri Bot. Gard. 74: 87. 1987. *R. L. Liesner & B. Stannard 16901*; 21–24 Mar. 1984; Venezuela, T.F. Amazonas, Cerro de la Neblina, Camp V, valley N base of Pico Cardona; MO (holo): 3462075, VEN.

Peperomia glabella (Sw.) A. Dietr. var. *obtusa* Steyerm., Fl. Venez. 2(1): 112. 1984. *J. A. Bautista 5037*; 8 Mar. 1977; Venezuela, Barinas, Distr. Ezequiel Zamora, Mun. Andres Eloy Blanco, Reserva Forestal de Caparo; 100 m; VEN (holo), MER.

Peperomia heterodoxa Standl. & Steyerm., Fieldiana Bot. 24(3): 251. 1952. *J. A. Steyermark 51340*; n.d.; Guatemala, Huehuetenango, Sierra de los Cuchumatanes; 800–900 m; F (holo).

Peperomia honigii Steyerm., Fl. Venez. 2(1): 125. 1984. *S. S. Tillett & K. Honig 746-798*; 27 June–5 July 1974; Venezuela, Zulia, Dept. Perija, Serranía de los Motilones, Sierra de Perija; 3,000 m; VEN (holo).

Peperomia huitzensis Standl. & Steyerm., Fieldiana Bot. 24(3): 253. 1952. *J. A. Steyermark 48613*; n.d.; Guatemala, Huehuetenango, Cerro Huitz; 1,500–2,000 m; F (holo).

Peperomia liesneri Steyerm., Fl. Venez. 2(1): 131. 1984. *J. A. Steyermark & R. L. Liesner 118651*; Venezuela, Táchira, Quebrada Agua Azul, al sur de El Reposo, 14 km al SE de Delicias; 2,150–2,300 m; VEN (holo), MO.

Peperomia manarae Steyerm., Fl. Venez. 2(1): 148. 1984. *B. Manara s.n.*; 20 Mar. 1980; Venezuela, Aragua, justamente por debajo de El Portachuelo, a lo largo de la carretera que desciende hacia Ocumare de la Costa, Parque Nacional Henri Pittier; 950 m; VEN (holo).

Peperomia marahuacensis Steyerm., Ann. Missouri Bot. Gard. 74: 87. 1987. *J. A. Steyermark & B. K. Holst 130742a*; 26–27 Feb. 1985; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca, summit, 'Simas' and SE of summit camp; 2,520–2,620 m; MO (holo), VEN.

Peperomia microreticulata Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 411. 1966. *J. A. Steyermark et al. 92807*; 6–7 Jan. 1964; Venezuela, Bolívar, Cerro Venamo; 1,220–1,275 m; VEN (holo) = *P. alata* Ruíz & Pavón, 1984.

Peperomia minarum Standl. & Steyerm., Fieldiana Bot. 24(3): 258. 1952. *J. A. Steyermark 43747*; n.d.; Guatemala, El Progreso, Sierra de las Minas; F (holo). See following entry.

Peperomia minarum Steyerm., Fl. Venez. 2(1): 158. 1984, non 1952. *J. A. Steyermark et al. 119958*; 11 Nov. 1979; Venezuela, Táchira, cumbre boscosa de Cerro Azul, Cerro las Minas, 18 km SE de Santa Ana; 1,200–1,380 m; MO, VEN (holo).

Peperomia ouabiane C. DC. var. *sanluisensis* Steyerm., Fl. Venez. 2(1): 173. 1984. *H. van der Werff et al.*

237; 18 Jan. 1979; Venezuela, Falcón, bosque nublado, arriba de La Chapa, Sierra de San Luis; 1,100 m; VEN (holo).

Peperomia pariensis Steyerm., Fl. Venez. 2(1): 176. 1984. *J. A. Steyermark & M. Rabe 96216*; 9–12 Aug. 1966; Venezuela, Sucre, Peninsula de Paria, fila de Cuchilla de Cueva de Tigre, de Río Nuevo, Oeste de Cerro de Humo; 750–850 m; VEN (holo), US.

Peperomia portuguesensis Steyerm., Fl. Venez. 2(1): 195. 1984. *J. A. Steyermark et al. 126610*; 29 Oct. 1982; Venezuela, Portuguesa, 15 km al Este de Chabasquen, 67 km al Noroeste de Guanare; 1,450–1,520 m; MER, MO, PORT, VEN (holo).

Peperomia pseudoglabella Steyerm., Fl. Venez. 2(1): 198. 1984. *L. Aristeguieta & F. Pannier 1948*; 6–7 July 1953; Venezuela, Yaracuy, Cafetales, Sierra de La Aroa; VEN (holo), NY.

Peperomia pseudojamesoniana Steyerm., Fl. Venez. 2(1): 199. 1984. *J. A. Steyermark & R. L. Liesner 118338*; 22–23 July 1979; Venezuela, Táchira, Quebrada Agua Azul, Sur de El Reposo, 14 km SE de Delicias; 2,150–2,300 m; VEN (holo), MO.

Peperomia tillettii Steyerm., Fl. Venez. 2(1): 257. 1984. *S. S. Tillett et al. 761-83*; Jan. 1976; Venezuela, Mérida, Dept. Sucre, a lo largo de la Toma de Agua arriba de La Rancheria, entre Estanques y La Victoria hacia La Rancheria y Las Palmas; 1,400 m; VEN (holo).

Peperomia treleasei Standl. & Steyerm., Fieldiana Bot. 24(3): 273. 1952. *J. A. Steyermark 46398*; Guatemala, cultivated 14 May 1942; F (holo) = *P. fraseri* C. DC., 1966.

Peperomia trujilloi Steyerm., Fl. Venez. 2(1): 261. 1984. *B. Trujillo & E. del Castillo 7919*; 30 Mar. 1967; Venezuela, Mérida, El Valle-La Culata; 2,650 m; MY (holo).

Peperomia yatuensis Steyerm., Fl. Venez. 2(1): 275. 1984. *B. Maguire et al. 36891*; 24 Dec. 1953; Venezuela, T.F. Amazonas, Cerro de la Neblina, Río Yatua, 3 km al Sur del Campamento 3; 900 m; VEN (holo).

Peperomia yutajensis Steyerm., Fl. Venez. 2(1): 276. 1984. *B. & C. Maguire 35304*; 17–19 Feb. 1953; Venezuela, T.F. Amazonas, Serranía Yutaje, Río Manapiare; 1,800 m; NY (holo), VEN, US.

Piper agostiniorum Steyerm., Fl. Venez. 2(1): 317. 1984. *G. & T. Agostini 1120*; 3 May 1972; Venezuela, Falcón, Dept. Democracia, Cerro Monte (Montana); 900–1,100 m; VEN (holo).

Piper arieianum C. DC. var. *yaracuyense* (Yuncker) Steyerm. f. *barbulaense* Steyerm., Fl. Venez. 2(1): 343. 1984. *C. Joly 5630*; 20 Sep. 1968; Venezuela, Carabobo, La Florida, Sierra Barbula; 1,100 m; CAR (holo).

Piper arieianum C. DC. var. *yaracuyense* (Yuncker) Steyerm. f. *falconense* Steyerm., Fl. Venez. 2(1): 341. 1984. *H. van der Werff et al. 548*; 7 May 1979; Venezuela, Falcón, Montaña de Paraguariba, Sierra de San Luis, 3 km al ENE del Cerro Galicia; 1,400 m; VEN (holo).

Piper arieianum C. DC. var. *yaracuyense* (Yuncker) Steyerm. f. *nubicolum* Steyerm., Fl. Venez. 2(1): 342. 1984. *A. H. G. Alston 6167*; 8 Jan. 1975; Venezuela, Carabobo, arriba de la Hacienda Cura, entre Valencia y Maracay; 1,600 m; NY (holo), US.

Piper arieianum C. DC. var. *yaracuyense* (Yuncker) Steyerm. f. *puberulum* Steyerm., Fl. Venez. 2(1): 341. 1984. *R. L. Liesner & A. González 10494*; 10–13 Mar. 1981; Venezuela, Táchira, 10 km E de la Fundación, alrededor de la Represa Dorada; 600–1,000 m; VEN (holo), MO.

Piper berryi Steyerm., Fl. Venez. 2(1): 354. 1984. *P. E. Berry & M. D. Robinson 3825*; 10 Apr. 1982; Venezuela, Miranda, Parque Nacional Guatopo, ca. 1.5 km E de la autopista Los Alpes–Altagracia, en el punto sur de la curva; MO (3438655), VEN (holo).

Piper bredemeyeri Jacq. f. *escabridum* Steyerm., Fl. Venez. 2(1): 360. 1984. *E. Conicit 2663*; 11 Nov. 1977; Venezuela, Falcón, Dept. Bolívar, San José, N de San Luis, Sierra de San Luis; VEN (holo).

Piper canovillosum Steyerm., Fl. Venez. 2(1): 362. 1984. *J. A. Steyermark & M. Rabe 97257*; 3–4 Sep. 1966; Venezuela, Trujillo, carretera vieja entre Trujillo y Bocono, entre Urbina y San Rafael, 30 km de Bocono; 2,300–2,500 m; US (holo), VEN.

Piper cernuum Vell. f. *papillatum* Steyerm., Fl. Venez. 2(1): 369. 1984. *J. A. Steyermark 105390*; 23 Jan. 1972; Venezuela, Yaracuy, Quebrada Honda, 17.3 km del pueblo de Aroa; 1,100 m; VEN (holo).

Piper cernuum Vell. var. *araguense* (Trel. & Yuncker) Steyerm. f. *pubens* Steyerm., Fl. Venez. 2(1): 374. 1984. *J. A. Steyermark et al. 114221*; 9 Sep. 1977; Venezuela, Aragua, Parque Nacional Henri Pittier, Portachuelo; 860 m; VEN (holo).

Piper cerronianum Steyerm., Fl. Venez. 2(1): 375. 1984. *R. L. Liesner et al. 8176*; 27 June 1979; Venezuela, Falcón, entre el Edo. Lara y el Edo. Falcón, Cerro Cerron; 1,800–2,000 m; VEN (holo), MO.

Piper cordiforme Steyerm., Fl. Venez. 2(1): 380. 1984. *R. L. Liesner & A. González 9767*; 31 Mar. 1980; Venezuela, Yaracuy, Sierra de Aroa, Cerro Tigre, 10 km al E de Aroa; 800–1,200 m; VEN (holo).

Piper crenulatum Steyerm., Fl. Venez. 2(1): 385. 1984. *J. A. Steyermark et al. 100884*; 13 Jan. 1968; Venezuela, Táchira, Selva nublada, cabeceras del Río Quinimari, 20 km al Sur de San Vicente de la Revancha, 35 km al sur de Alquitrana, Suroeste de Santa Ana; 2,500 m; US (holo), VEN.

Piper cuyunianum Steyerm., Fl. Venez. 2(1): 391. 1984. *J. A. Steyermark 89565*; 28 Aug. 1961; Venezuela, Bolívar, cabeceras del Río Chicanan, 80 km al Suroeste de El Dorado; 500 m; VEN (holo).

Piper deliciasanum Steyerm., Fl. Venez. 2(1): 394. 1984. *G. S. Bunting 2332*; 28 Sep. 1967; Venezuela, Táchira, Carretera Rubio–Las Delicias, en montaña arriba de Aldea de Toronjal, sitio 19 km arriba de Diamante; MY (holo), VEN.

Piper diffamatum Trel. & Yuncker var. *angustius* Steyerm., Fl. Venez. 2(1): 402. 1984. *R. Wingfield 5495*; 27 May 1978; Venezuela, Falcón, Sierra de San Luis, arriba de Santa María; 1,240 m; VEN (holo).

Piper dilatatum L. C. Rich. f. *longipilum* Steyerm., Fl. Venez. 2(1): 412. 1984. *J. A. Steyermark & V. C. Espinosa 105826*; 29 Apr.–1 May 1972; Venezuela, Aragua, Parque Nacional Pittier, cabeceras del Río Grande del Medio entre la Fila Alta de Choroni y la Quebrada Río Hondo al Sur de Tremaria; 1,000–1,500 m; NY, US, VEN (holo).

Piper dunstervilleorum Steyerm., Fl. Venez. 2(1): 418. 1984. *J. A. Steyermark et al. 104454*; 25 Dec. 1970; Venezuela, Bolívar, drenaje del Río Cuyuni, a lo largo del Río Anawa-ray-yaru, vecindades del km 134 y Campamento 134, al Sur de El Dorado; 1,300–1,350 m; VEN (holo).

Piper frioense Standl. & Steyerm., Fieldiana Bot. 24(3):

299. 1952. *P. C. Standley 90328*; n.d.; Guatemala, Alta Verapaz, near Tactic; 1,500 m; F (holo).

Piper fundacionense Steyerm., Fl. Venez. 2(2): 426. 1984. *R. L. Liesner & M. Guariglia 11647*; 1 May 1981; Venezuela, Táchira, 10 km E de la Fundación. 13–23 km por carretera, alrededor de la Represa Dorada; 600–900 m; MO, VEN (holo).

Piper galicianum Steyerm., Fl. Venez. 2(2): 427. 1984. *J. A. Steyermark 98956*; 16 July 1967; Venezuela, Falcón, Sierra de San Luis, Selva Nublada, vecindad del Hotel Parador, al Sur de La Tabla; 1,450 m; US, VEN (holo).

Piper galicianum Steyerm. f. "*hirsutopetiolatum*" Steyerm., Fl. Venez. 2(2): 429. 1984. *H. van der Werff 3642*; 10 Aug. 1979; Venezuela, Falcón, selva nublada, Sierra de San Luis, arriba de La Chapa; 1,200 m; VEN (holo). Note: P.g.f. *hirsutipetiolatum* is the correct spelling.

Piper gentryi Steyerm., Ann. Missouri Bot. Gard. 74: 89. 1987. *A. Gentry & B. Stein 46887*; 23 Apr. 1984; Venezuela, T.F. Amazonas, Cerro Neblina, trail S from Base Camp; 140 m; MO (holo—3462077).

Piper heterobracteum Steyerm., Fl. Venez. 2(2): 439. 1984. *J. A. Steyermark 99933*; 31 Aug. 1967; Venezuela, Zulia, Sierra de Perija, vecinidad de la Quebrada Koshida (Kosida), S de la Misión de Los Angeles de Tokuko (Tocucu); 325–350 m; VEN (holo).

Piper hippocrepiforme Steyerm., Fl. Venez. 2(2): 440. 1984. *J. A. Steyermark et al. 92657*; 3 Jan. 1964; Venezuela, Bolívar, Cerro Venamo; 1,400–1,450 m; VEN (holo).

Piper ixocubvainense Standl. & Steyerm., Fieldiana Bot. 24(3): 305. 1952. *J. A. Steyermark 44987*; n.d.; Guatemala, Alta Verapaz, Montaña Ixocubvain; F (holo).

Piper jauaense Steyerm., Bol. Soc. Venez. Ci. Nat. 32: 319. 1976. *J. A. Steyermark et al. 109689*; 28 Feb.–1, 2, 5 Mar. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerru Jaua; 1,810–1,880 m; VEN (holo).

Piper lanciferum Standl. & Steyerm., Fieldiana Bot. 24(3): 307. 1952. *J. A. Steyermark 46696*; Guatemala, Suchitepéquez, Volcán de Santa Clara; 1,300–2,600 m; F (holo).

Piper liesneri Steyerm., Fl. Venez. 2(2): 467. 1984. *R. L. Liesner 6405*; 9 Apr. 1979; Venezuela, T.F. Amazonas, IVIC Estación de Investigación a 4 km NE de San Carlos de Río Negro, ca. 20 km S de la confluencia del Río Negro y Brazo Casiquiare; 120 m; MO, VEN (holo).

Piper linguliforme Steyerm., Fl. Venez. 2(2): 468. 1984. *R. L. Liesner & A. González 10022*; Venezuela, Yaracuy, Sierra de Aroa, 9 km E de San Felipe (por via aerea), 0–3 km NE por carretera entre Cocorote y Aroa, 15 km NE de Cocorote y 1 km SE de los Cruceros; 100–1,500 m; MO, VEN (holo).

Piper linguliforme Steyerm. var. *adpressipilum* Steyerm., Fl. Venez. 2(2): 469. 1984. *J. A. Steyermark et al. 124771*; 1 Mar. 1981; Venezuela, Sierra de Aroa, extremo SE, fila entre los ríos Tejar y Cocoritico, 14–15 km NE de Urachiche, a 3 km NE del Caserio Buenos Aires; 1,350–1,500 m; VEN (holo).

Piper longiappendiculatum Steyerm., Fl. Venez. 2(2): 469. 1984. *R. L. Liesner & A. González 10891*; 20–21 Mar. 1981; Venezuela, Táchira, ca. 35 km SSE de San Cristóbal, La Buenana, 6–12 km E de la Quebrada Colorado; 600–1,200 m; MO, VEN (holo).

Piper longispicum C. DC. f. *tomentosum* Steyerm., Fl. Venez. 2(2): 474. 1984. *J. A. Steyermark 104978*; 1 Mar. 1971; Venezuela, Trujillo, entre La Peña y Agua de Obispo, 22–28 km de Carache; 2,400–2,500 m; VEN (holo).

Piper marturetense Trel. & Yuncker f. *pilosum* Steyerm., Fl. Venez. 2(2): 485. 1984. *J. A. Steyermark et al. 124826*; 1 Mar. 1981; Venezuela, Yaracuy, Serranía de Aroa, extremo SE, selva nublada, fila entre los rios Tejar y Cocoritico, 14–15 km al NNE de Urachiche; 1,350–1,500 m; VEN (holo).

Piper minarum Standl. & Steyerm., Fieldiana Bot. 24(3): 309. 1952. *J. A. Steyermark 42667*; n.d.; Guatemala, Zacapa, Sierra de las Minas; 2,200–2,400 m; F (holo).

Piper morilloi Steyerm., Fl. Venez. 2(2): 489. 1984. *G. Morillo 5510*; 8 Feb. 1977; Venezuela, T.F. Amazonas, 1–4 km S de Solano, entre el Caño Chola y Solano; 120 m; VEN (holo).

Piper mosaicum Steyerm., Ann. Missouri Bot. Gard.: in press. 1989. *R. L. Liesner & F. Delascio 21968*; 16 Oct. 1987; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp; 1,550 m; MO (holo), VEN.

Piper nubigenum Kunth var. *venezuelense* Steyerm., Fl. Venez. 2(2): 497. 1984. *J. A. Steyermark 104989*; 1 Mar. 1971; Venezuela, Trujillo, entre La Peña y Agua de Obispo, 22–28 km de Carache; 2,400–2,500 m; VEN (holo).

Piper otto-huberi Steyerm., Fl. Venez. 2(2): 503. 1984. *O. Huber 1848*; 29 May 1978; Venezuela, T.F. Amazonas, Dept. Atabapo, E del campamento, alrededores de Canaripo; 98 m; VEN (holo).

Piper otto-huberi Steyerm. var. *eciliatum* Steyerm., Fl. Venez. 2(2): 504. 1984. *P. E. Berry 694*; 22 May 1975; Venezuela, T.F. Amazonas, al lado de la pista de Santa Barbara de Orinoco; VEN (holo).

Piper papilliferum Steyerm., Fl. Venez. 2(2): 507. 1984. *G. Morillo 4136*; 28 Apr. 1978; Venezuela, T.F. Amazonas, alrededores de San Simon Cocuy; VEN (holo).

Piper pavasense Steyerm., Fl. Venez. 2(2): 510. 1984. *J. A. Steyermark et al. 117209*; 22 May 1978; Venezuela, Bolívar, Las Pavas arriba del Salto Para, Río Caura; 250–260 m; VEN (holo).

Piper perijaense Steyerm., Fl. Venez. 2(2): 517. 1984. *J. Jangoux 10193*; 15 Sep. 1974; Venezuela, Zulia, Sierra de Perija, al pie de la montana, Serranía de Abusanqui; 250 m; VEN (holo).

Piper perstipulare Steyerm., Fl. Venez. 2(2): 519. 1984. *S. S. & C. L. Tillett 45501*; 23 Sep. 1960; Guyana, Cuenca del Alto Río Mazaruni, Río Kako, Campamento 3, 0.4 km debajo de las cataratas del Kako; 500 m; NY, VEN (holo).

Piper philodendroides Standl. & Steyerm., Fieldiana Bot. 24(3): 316. 1952. *J. A. Steyermark 41928*; n.d.; Guatemala, Izabal, Cerro San Gil; 300–900 m; F (holo).

Piper pinetorum Standl. & Steyerm., Fieldiana Bot. 24(3): 317. 1952. *J. A. Steyermark 49712*; Guatemala, Huehuetenango, Cerro Victoria, near Barillas, Sierra de los Cuchumatanes; 1,800–2,000 m; F (holo).

Piper politii Yuncker subsp. *toronoense* Steyerm., Fl. Venez. 2(2): 530. 1984. *J. A. Steyermark & J. J. Wurdack 1197*; 27 Feb. 1955; Venezuela, Bolívar, Macizo de Chimantá, Torono-tepui; 1,880–1,970 m; F, NY, VEN (holo).

Piper politii Yuncker subsp. *sipapoense* Steyerm., Fl. Venez. 2(2): 532. 1984. *B. Maguire & L. Politi 28516*; 21 Jan. 1949; Venezuela, T.F. Amazonas, Cerro Sipapo (Paraque), arriba del Caño Grande; 1,500 m; NY (holo).

Piper pseudoacreanum Steyerm., Fl. Venez. 2(2): 539.

1984. *R. L. Liesner 6222*; 5 Apr. 1979; Venezuela, 0.5 km S de San Carlos de Río Negro; 120 m; MO (2734623), VEN (holo).

Piper pseudoaequale Steyerm., Fl. Venez. 2(2): 540. 1984. *J. A. Steyermark 95002*; 4 Mar. 1966; Venezuela, Sucre, Peninsula de Paria, Cerro de Humo, entre la Laguna y Roma, NE de Irapa; 900–1,060 m; VEN (holo).

Piper pseudobredemeyeri Steyerm., Fl. Venez. 2(2): 542. 1984. *J. A. Steyermark 94897*; 2 Mar. 1966; Venezuela, Sucre, Peninsula de Paria, Cerro de Humo; 1,273 m; F, NY, US, VEN (holo).

Piper pseudodivulgatum Steyerm., Fl. Venez. 2(2): 543. 1984. *R. Wingfield & H. van der Werff 6571*; 25 Aug. 1978; Venezuela, Falcón, Sierra de San Luis, selva nublada arriba del Hotel Parador; 1,500 m; VEN (holo).

Piper pseudohastularum Steyerm., Fl. Venez. 2(2): 548. 1984. *J. A. Steyermark et al. 119971*; 11 Nov. 1979; Venezuela, Táchira, en el Cerro Las Minas, 18 km SE de Santa Ana; 1,200–1,380 m; MO, VEN (holo).

Piper pubivaginatum Steyerm., Fl. Venez. 2(2): 549. 1984. *B. Manara s.n.*; 27 Mar. 1971; Venezuela, T.F. Amazonas, 1 km de aeropuerto de San Carlos de Río Negro; VEN (holo).

Piper punctulatum Standl. & Steyerm., Fieldiana Bot. 24(3): 320. 1952. *J. A. Steyermark 43622*; n.d.; Guatemala, Dept. El Progreso, Sierra de las Minas; 1,500–2,600 m; F (holo).

Piper ronaldii Steyerm., Fl. Venez. 2(2): 556. 1984. *R. L. Liesner & M. Guariglia 11873*; 6 May 1981; Venezuela, Táchira, Cerro Minas; 1,200–1,380 m; MO, VEN (holo).

Piper santae-clarae Standl. & Steyerm., Fieldiana Bot. 24(3): 321. 1952. *J. A. Steyermark 46624*; n.d.; Guatemala, Dept. Suchitepéquez, Volcán de Santa Clara; 1,250–2,600 m; F (holo).

Piper sierra-aroense Steyerm., Fl. Venez. 2(2): 563. 1984. *R. L. Liesner & A. González 9699*; 30 Mar. 1980; Venezuela, Yaracuy, Cerro Tigre; 800–1,000 m; MO, VEN (holo).

Piper subsessilifolium C. DC. var. *morii* Steyerm., Fl. Venez. 2(2): 567. 1984. *J. A. Steyermark & R. L. Liesner 126472*; 4 Mar. 1982; Venezuela, Yaracuy, cumbre Gamelotal en El Amparo, 7.5 km N de Salom; 1,250 m; MO (3438654), VEN (holo).

Piper tacariguense Steyerm., Fl. Venez. 2(2): 570. 1984. *J. A. Steyermark et al. 121697*; 23 Feb. 1980; Venezuela, Sucre, Dept. Arismendi, Peninsula de Paria, entre Tacarigua y las cabeceras del Río Tacarigua, E del Cerro de Humo; 750 m; MO, VEN (holo).

Piper tamayoanum Steyerm., Fl. Venez. 2(2): 572. 1984. *J. A. Steyermark & R. L. Liesner 127445*; 1 Dec. 1982; Venezuela, Bolívar, Distr. Roscio, near base of Cerro Ceita; 950 m; MO, VEN (holo).

Piper tepuiense Steyerm., Fl. Venez. 2(2): 575. 1984. *J. A. Steyermark & J. J. Wurdack 1346*; 10 Mar. 1955; Venezuela, Bolívar, Macizo de Chimantá, Amuritepuy; 1,365 m; VEN (holo).

Piper toronotepuiense Steyerm., Fl. Venez. 2(2): 576. 1984. *J. A. Steyermark 75476*; 19–20 May 1953; Venezuela, Bolívar, Macizo de Chimantá, Chimantátepui (Torono-tepui); 1,700 m; VEN (holo).

Piper vaccinum Standl. & Steyerm., Fieldiana Bot. 24(3): 333. 1952. *P. H. Gentle 2264*; n.d.; Belize, El Cayo Distr., Vaca; F (holo), MICH.

Piper venamoense Steyerm., Fl. Venez. 2(2): 589. 1984. *J. A. Steyermark et al. 92631*; 3 Jan. 1964; Venezuela, Bolívar, Cerro Venamo; 1,400–1,450 m; VEN (holo).

Piper veraguense C. DC. var. *venezuelense* Steyerm., Fl. Venez. 2(2): 590. 1984. *F. Breteler 4082*; 11 Aug. 1964; Venezuela, Trujillo, 16 km de Bucono, a lo largo de la carretera a Biscucuy; 1,850 m; MER, VEN (holo).

Piper vitaceum Yuncker var. *venezuelense* Steyerm., Fl. Venez. 2(2): 594. 1984. *J. A. Steyermark & S. Nilsson 176*; 15–17 Apr. 1960; Venezuela, Bolívar, la Fila de La Danta, entre Luepa y Cerro Venamo; 1,200 m; VEN (holo).

Piper wingfieldii Steyerm., Fl. Venez. 2(2): 595. 1984. *R. L. Liesner et al. 8211*; 27 June 1979; Venezuela, Falcón, area disputada entre el Edo. Lara y el Edo. Falcón, Cerro Cerron; 1,800–2,000 m; VEN (holo).

Sarcorhachis venezuelana Steyerm., Pittieria 3: 33. 1971. *J. A. & C. Steyermark 95152*; 27–28 Mar. 1966; Venezuela, Carabobo, del Río San Gian, al Sur de Borburata, arriba de la planta electrica, entre Los Tanques y La Toma; 750 m; US, VEN (holo).

POACEAE

Muhlenbergia brachyphylla Bush f. *aristata* Palmer & Steyerm., Brittonia 10: 110. 1958. *J. A. Steyermark 82921*; 7 Oct. 1956; U.S.A., Missouri, Pike Co., vicinity of Stillhouse Cave, along City Fork of Spencer Creek; F (holo), US.

POLEMONIACEAE

Phlox divaricata L. var. *laphamii* Woodson f. *candida* Palmer & Steyerm., Rhodora 57: 316. 1955. *E. J. Palmer 55411*; 30 Apr. 1953; U.S.A., Missouri, Barton Co., 1 mi. W of Nashville; Palmer Herbarium (holo), F.

POLYGALACEAE

Polygala appressa Benth. var. *kavanayena* Steyerm., Fieldiana Bot. 28(2): 298. 1952. *J. A. Steyermark 59359*; 26 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,220 m; F (holo).

Polygala blakeana Steyerm., Fieldiana Bot. 28(2): 298. 1952. *J. A. Steyermark 59065*; 10 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,065–1,200 m; F (holo).

Polygala rimulicola Steyerm., Ann. Missouri Bot. Gard. 19: 390. 1932. *J. A. Moore & J. A. Steyermark 3515*; 20 July 1931; U.S.A., Texas, Culberson Co., Smith Canyon, Guadalupe Mts.; 1,900 m; GH (holo), MO (1011635).

Polygala sanariapoana Steyerm., Fieldiana Bot. 28(2): 301. 1952. *J. A. Steyermark 59452*; 8 Sep. 1944; Venezuela, T.F. Amazonas, Sanariapo; 100 m; F (holo).

Polygala santanderensis Killip & Steyerm., Fieldiana Bot. 28(2): 301. 1952. *Killip & Smith 16585*; 5–6 Jan. 1927; Colombia, Dept. Santander, Río Surata valley; 2,000–2,300 m; F, US (holo).

PORTULACACEAE

Montia calcicola Standl. & Steyerm., Field. Mus. Nat. Hist., Bot. Ser. 23(2): 48. 1944. *J. A. Steyermark 50308*; 8 Aug. 1942; Guatemala, Dept. Huehuetenango, Cerro Chemal; 3,700–3,800 m; F (holo).

Portulaca insignis Steyerm., Ann. Missouri Bot. Gard. 75: 1058. 1988. *G. Morillo & G. Carnevali 8260*; 26 Feb. 1980; Venezuela, Bolívar, carretera Ciudad

Bolívar–Maripa, 100 km W of Ciudad Bolívar; 100–200 m; VEN (holo).

Portulaca pygmaea Steyerm., Ann. Missouri Bot. Gard. 75: 1058. 1988. *B. Maguire et al. 36188*; 12 Nov. 1953; Venezuela, T.F. Amazonas, 1 km E of Hotel Amazonas, Puerto Ayacucho; 100 m; NY (holo).

PRIMULACEAE

Lysimachia quadriflora Sims f. *albescens* Steyerm., Rhodora 54: 257. 1952. *J. A. Steyermark 68397*; 4 July 1949; U.S.A., Missouri, Carter Co., along route 60 along spring branch tributary to right fork of Carter Creek, 6.7 mi. NE of Van Buren; F (holo).

PROTEACEAE

Euplassa chimantensis Steyerm., Bol. Soc. Venez. Ci. Nat. 25: 77. 1963. *J. A. Steyermark & J. J. Wurdack 1103*; 23 Feb. 1955; Venezuela, Bolívar, Chimantá Massif, Torono-tepui; 1,955–2,090 m; VEN (holo), F, NY.

Euplassa venezuelana Steyerm., Fieldiana Bot. 28(1): 217. 1951. *J. A. Steyermark 60824*; 30 Nov. 1944; Venezuela, Bolívar, NW of Santa Teresita de Kavanayen, along Río Karuai; 1,220 m; F (holo).

Panopsis cuaoensis Steyerm., Ann. Missouri Bot. Gard. 74: 612. 1987. *B. Maguire & L. Politi 28409*; 17 Jan. 1949; Venezuela, T.F. Amazonas, Río Cuao, Río Orinoco; NY (holo).

Panopsis ornatinervia Steyerm., Bol. Soc. Venez. Ci. Nat. 25: 79. 1963. *J. A. Steyermark & J. J. Wurdack 1036*; 21 Feb. 1955; Venezuela, Bolívar, Chimantá Massif; 2,030–2,150 m; F, NY, VEN (holo).

Panopsis parimensis Steyerm., Ann. Missouri Bot. Gard. 74: 612. 1987. *O. Huber 6136*; 12 June 1981; Venezuela, T.F. Amazonas, Dept. Atabapo, Sierra Parima, 25 km NNE de Parima 'B,' cabeceras del Río Ocamo; MO (3295700), NY, VEN (holo).

Panopsis perijensis Steyerm., ined.? *J. A. Steyermark et al. 105677*; 27 Mar. 1972; Venezuela, Zulia, Sierra de Perija, Suroeste de Pishikakao e Iría hacia la Misión de Sucurpo; 1,500–1,800 m; MO (iso—2680841).

Panopsis ptariana Steyerm., Fieldiana Bot. 28(1): 218. 1951. *J. A. Steyermark 59677*; 1 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,600 m; F (holo).

Panopsis tepuiana Steyerm., Fieldiana Bot. 28(1): 219. 1951. *J. A. Steyermark 59988*; 10–11 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,585–1,600 m; F (holo).

Roupala chimantensis Steyerm., Bol. Soc. Venez. Ci. Nat. 25: 81. 1963. *J. A. Steyermark & J. J. Wurdack 1105*; 23 Feb. 1955; Venezuela, Bolívar, Chimantá Massif; 2,090 m; VEN (holo), F, MO (2011335), NY.

Roupala griotii Steyerm., Phytologia 44(5): 321. 1979. *J. A. Steyermark et al. 117920*; 22 Feb. 1979; Venezuela, T.F. Amazonas, vecindades del Río Coro-Coro y del aeropuerto de Yutaje; VEN (holo).

Roupala minima Steyerm., Fieldiana Bot. 28(1): 220. 1951. *J. A. Steyermark 60234*; 15–17 Nov. 1944; Venezuela, Bolívar, between Ptari-tepui and Sororopan-tepui; 1,615 m; F (holo).

Roupala obovata H.B.K. var. *ecuadorensis* Steyerm., Phytologia 9(6): 342. 1964. *J. A. Steyermark 54825*; 20 Oct. 1943; Ecuador, Prov. Loja, along Río Cachiyacu at Tambo Cachiyacu; 2,000 m; F (holo).

Roupala paruensis Steyerm., Ann. Missouri Bot. Gard. 74: 613. 1987. *R. S. Cowan & J. J. Wurdack 31378*; 10 Feb. 1951; Venezuela, T.F. Amazonas, Cerro Parú, S-SE to edge descent to tributary of Caño Asisa, Río Ventuari; 2,000 m; NY (holo).

Roupala sororopana Steyerm., Fieldiana Bot. 28(1): 220. 1951. *J. A. Steyermark 60089*; 13 Nov. 1944; Venezuela, Bolívar, Sororopan-tepui; 2,225–2,255 m; F (holo).

QUIINIACEAE

Froesia venezuelensis Steyerm. & Bunting, Brittonia 27: 175. 1975. *J. A. Steyermark & G. S. Bunting 105237*; 12 Oct. 1971; Venezuela, Yaracuy, entre Nirgua y Las Marias; 1,000–1,200 m; NY, US, VEN (holo).

RANUNCULACEAE

Anemone virginiana L. f. *plena* Palmer & Steyerm., Brittonia 10: 113. 1958. *G. E. Moore s.n.*; 1956; U.S.A., Missouri, St. Louis Co., Rockwoods Reservation; F (holo).

Clematis caleoides Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 52. 1944. *P. C. Standley 58732*; Dec. 1938; Guatemala, Dept. Chimaltenango, Cerro Tecpán, region of Santa Elena; 2,700 m; F (holo).

Clematis versicolor Small ex Rydb. f. *pubescens* Steyerm., Rhodora 40: 71. 1938. *Brinkley 268*; 24 July 1937; U.S.A., Arkansas, Sevier Co., Boggy Springs; F (holo).

Ranunculus nubigenus H.B.K. f. *subintegrus* Steyerm., Fieldiana Bot. 28(1): 232. 1951. *J. A. Steyermark 57481*; 21 July 1944; Venezuela, Mérida, above Los Apartaderos, above Laguna Mucubaji towards Laguna Negra; 3,625–3,655 m; F (holo) = *R. flagelliformis* Smith, 1971.

Thalictrum johnstonii Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 229. 1940. *J. R. Johnston 1643*; 20 June 1940; Guatemala, Dept. Totonicapán, Desconsuelo; F (holo).

Thalictrum standleyi Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 229. 1940. *J. A. Steyermark 36258*; 20 Feb. 1940; Guatemala, Dept. San Marcos, Río Vega, near San Rafael and Guatemala–Mexican boundary Volcán Tacaná; 2,500–3,000 m; F (holo).

RAPATEACEAE

Kunhardtia radiata Maguire & Steyerm., Acta Amazonica 9(2): 267. 1979. *J. A. Steyermark & O. Huber 113851*; 4 May 1977; Venezuela, T.F. Amazonas, 35 km S of Puerto Ayacucho at Tobogán; 85 m; NY (holo), VEN.

Rapatea aracamuniana Steyerm., Ann. Missouri Bot. Gard.: in press. 1989. *R. L. Liesner & F. Delascio 22197*; 20 Oct. 1987; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro Aracamuni; 600 m; MO (holo), VEN.

Rapatea chimantensis Steyerm., Ann. Missouri Bot. Gard. 75: 313. 1988. *J. A. Steyermark 75584*; 24 May 1953; Venezuela, Bolívar, Chimantá Massif, lower southwestern slopes of Chimantá-tepui; 1,000 m; MO, NY, VEN (holo).

Stegolepis albiflora Steyerm., Ann. Missouri Bot. Gard. 74: 609–658. 1987. *J. A. Steyermark et al. 108873*; 10 Feb. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Sarisariâma, NE part; 1,410 m; VEN (holo), NY.

Stegolepis allenii Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 325. 1940. *P. H. Allen 2153*; 23 June

1940; Panama, Prov. Coclé, hills N of El Valle de Anton; 1,000 m; F (holo), MO (1227389) = *Epidryos allenii* (Steyerm.) Maguire, 1962.

Stegolepis gleasoniana Steyerm., Fieldiana Bot. 28(1): 130. 1951. *J. A. Steyermark 58040*; 26 Aug. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,095–1,520 m; F (holo).

Stegolepis huberi Steyerm., Ann. Missouri Bot. Gard. 74: 610. 1987. *O. Huber 9467*; 28 Apr. 1984; Venezuela, Bolívar, Kukenán-tepui; 2,500 m; MO, VEN (holo).

Stegolepis humilis Steyerm., Ann. Missouri Bot. Gard. 74: 611. 1987. *J. A. Steyermark et al. 132006*; 22–24 May 1986; Venezuela, Bolívar, Camarcaibari-tepui, SW-facing shoulder; 1,825 m; MO (holo—3514022, 3393686), VEN.

Stegolepis maguireana Steyerm., Ann. Missouri Bot. Gard. 71: 300. 1984. *J. A. Steyermark et al. 129962*; 14 Feb. 1984; Venezuela, Bolívar, Chimantá Massif, Acopan-tepui; 1,950 m; VEN (holo), NY.

Stegolepis minor Steyerm., Ann. Missouri Bot. Gard. 75: 315. 1988. *J. A. Steyermark 89577*; 28 Aug. 1961; Venezuela, Bolívar, Sierra de Lema, cabeceras del Río Chicanán; NY, VEN (holo).

Stegolepis parvipetala Steyerm., Fieldiana Bot. 28(1): 133. 1951. *J. A. Steyermark 59514*; 29 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 1,810 m; F (holo).

Stegolepis ptaritepuiensis Steyerm., Fieldiana Bot. 28(1): 133. 1951. *J. A. Steyermark 59655*; 1 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,600 m; F (holo).

Stegolepis terramarensis Steyerm., Ann. Missouri Bot. Gard. 71: 301. 1984. *J. A. Steyermark & F. Delascio 129197*; 30 Mar.–1 Apr. 1983; Venezuela, T.F. Amazonas, Cerro Marahuaca; 2,580–2,600 m; VEN (holo).

RHAMNACEAE

Colubrina pittieriana Steyerm., Fieldiana Bot. 28(4): 971. 1957, nom. nov.

Colubrina venezuelensis Steyerm.; Fieldiana Bot. 28(2): 355. 1952. *T. González s.n.*; n.d.; Venezuela, Distr. Federal, alrededores de Caracas; 1,600–1,800 m; F (holo).

Gouania wurdackii Steyerm., Ann. Missouri Bot. Gard. 75: 1065. 1988. *J. J. Wurdack & J. V. Monachino 39810*; 12 Dec. 1955; Venezuela, Bolívar, Distr. Cedeño, Cerro San Borja; 100 300 m; MO (holo), NY, VEN.

Rhamnus acuminata Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *B. Maguire et al. 42496*; 25 Dec. 1957; Venezuela, T.F. Amazonas, Cerro de la Neblina, summit, Cañon Grande; 1,050–1,150 m; MO (3291195), NY (holo).

Rhamnus chimantensis Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 451. 1967. *J. A. Steyermark 75946*; 21–22 June 1953; Venezuela, Bolívar, Apacara-tepui, Chimantá Massif; 2,450–2,500 m; NY (holo).

Rhamnus longipes Steyerm., Ann. Missouri Bot. Gard. 75: 1066. 1988. *R. S. Cowan & J. J. Wurdack 31388*; 10 Feb. 1951; Venezuela, T.F. Amazonas, Serranía Parú; 2,000 m; NY (holo).

Rhamnus marahuacensis Steyerm. & Maguire, Acta Bot. Venez. 14(3): 22. 1984; *J. A. Steyermark et al. 126049*; 2 Feb. 1982; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca; 2,480–2,500 m; NY, VEN (holo).

Rhamnus microreticulata Maguire & Steyerm., ined. mss. = *R. neblinensis* Maguire & Steyerm., 1989.

Rhamnus neblinensis Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *B. Maguire et al. 37040*; 4 Jan. 1954; Venezuela, T.F. Amazonas, Cerro de la Neblina, summit; 1,800 m; MO (3291187), NY (holo).

Rhamnus psilocarpa Maguire & Steyerm., Mem. New York Bot. Gard. 50: in press. 1989. *B. Maguire et al. 37230*; 10 Jan. 1954; Venezuela, T.F. Amazonas, Cerro de la Neblina, summit; 1,700–2,000 m; MO (3291189), NY (holo).

Rhamnus sipapoensis Steyerm., Ann. Missouri Bot. Gard. 75: 1066. 1987. *B. Maguire & L. Politi 28656*; 26–28 Jan. 1949; Venezuela, T.F. Amazonas, Cerro Sipapo (Paraque) rim head of S basin; 1970 m; NY (holo), MO.

Rhamnus subpedunculata Maguire & Steyerm., ined. mss. = *R. acuminata* Maguire & Steyerm., 1989.

RHIZOPHORACEAE

Hypogyneae Steyerm. & Liesner, Ann. Missouri Bot. Gard. 70: 184. 1983, tribe nov.

Sterigmapetalum Kuhlmann subg. *Balsamocaulon* Steyerm. & Liesner, Ann. Missouri Bot. Gard. 70: 190. 1983, subg. nov.

Sterigmapetalum exappendiculatum Steyerm. & Liesner, Ann. Missouri Bot. Gard. 70: 188. 1983. *B. Maguire et al. 46876*; 20–21 Aug. 1962; Venezuela, Bolívar, La Escalera, Alto Río Cuyuni, Río Uiri-Yuk; 1,000 m; NY, VEN (holo).

Sterigmapetalum guianense Steyerm., Fieldiana Bot. 28(2): 422. 1952. *J. A. Steyermark 60658*; 27 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,220 m; F (holo).

Sterigmapetalum guianense Steyerm. subsp. *ichunense* Steyerm. & Liesner, Ann. Missouri Bot. Gard. 70: 188. 1983. *J. A. Steyermark 90428*; 29 Dec. 1961; Venezuela, Bolívar, Sierra Ichun; 500–625 m; NY, US, VEN (holo).

Sterigmapetalum heterodoxum Steyerm. & Liesner, Ann. Missouri Bot. Gard. 70: 192. 1983. *J. A. Steyermark 99409*; 21 July 1967; Venezuela, Falcón, Sierra de San Luis, Montaña de Paraquariba, entre de Hotel Parador y Curimagua; 1,300 m; US, VEN (holo).

Sterigmapetalum resinosum Steyerm. & Liesner, Ann. Missouri Bot. Gard. 70: 190. 1983. *J. A. Steyermark & E. Dunsterville 104569*; 27–28 Dec. 1970; Venezuela, Bolívar, Cerro Uei, km 121.5 S of El Dorado; 1,050 m; US (holo).

Sterigmapetalum tachirense Steyerm. & Liesner, Ann. Missouri Bot. Gard. 70: 190. 1983. *J. A. Steyermark et al. 120032*; 11 Nov. 1979; Venezuela, Táchira, Cerro Azul, at Cerro Las Minas, 18 km SE of Santa Ana; 1,200–1,380 m; MO (3466058), VEN (holo).

ROSACEAE

Amelanchier canadensis (L.) Medic. f. *nuda* Palmer & Steyerm., Ann. Missouri Bot. Gard. 25: 772. 1938. *E. J. Palmer & J. A. Steyermark 40317*; 5 July 1933; U.S.A., Missouri, Mercer Co., 5 mi. S of Linesville; GH (holo).

Rosa setigera Michx. f. *alba* Steyerm., Rhodora 54: 254. 1952. *J. A. Steyermark 72011*; 7 July 1951; U.S.A., Missouri, Reynolds Co., 4 mi. SE of Bunker, along Bee Fork; F (holo), GH, MO.

Rosa setigera Michx. f. *inermis* Palmer & Steyerm.,

Ann. Missouri Bot. Gard. 22: 569. 1935. *E. J. Palmer 39039*; 26 Apr. 1931; U.S.A., Missouri, Bollinger, Patton; GH (holo).

Rosa setigera Michx. var. *serena* Palmer & Steyerm., Ann. Missouri Bot. Gard. 22: 569. 1935. *E. J. Palmer & J. A. Steyermark 41642*; 2 July 1933; U.S.A., Missouri, Ripley Co., Ponder; GH (holo).

Rubus flagellaris Willd. var. *occidualis* Bailey f. *roseus* Steyerm., Rhodora 62: 130. 1960. *J. A. Steyermark 84212*; 8 May 1957; U.S.A., Missouri, Bollinger Co., in valley of creek tributary to Castor River, NW of Buchanan Post Office; UMO (holo).

Rubus flagellaris Willd. f. *roseo-plenus* Palmer & Steyerm., Brittonia 10: 114. 1958. *E. J. Palmer 59655*; 3 May 1955; U.S.A., Missouri, Barton Co., 0.5 mi. SE of Libera; F (holo) = *R. flagellaris* var. *occidualis* Bailey f. *roseo-plenus* (Palmer & Steyerm.) Steyerm., 1960.

Rubus hadrocarpus Standl. & Steyerm., Fieldiana Bot. 24(4): 477. 1946. *P. C. Standley 86270*; 6 Feb. 1941; Guatemala, Dept. San Marcos, Barranco Eminencia; 2,500–2,700 m; F (holo).

Rubus hadrocarpus Standl. & Steyerm. f. *adenophorus* Standl. & Steyerm., Fieldiana Bot. 24(4): 478. 1946. *J. A. Steyermark 49859*; 31 July 1942; Guatemala, Dept. Huehuetenango, Cruz de Limón; 2,600–3,000 m; F (holo).

Rubus pensilvanicus Poir. f. *albinus* Palmer & Steyerm., Brittonia 10: 114. 1958. *J. A. Steyermark 78868*; 23 July 1955; U.S.A., Missouri, Howell Co., 6 mi. NE of West Plains, 5 mi. SSE of White Church; F (holo), GH, MO, US.

RUBIACEAE

Alibertia acuminata (Benth.) Sandw. var. *obtusiuscula* Steyerm., Mem. New York Bot. Gard. 12(3): 223. 1965. *L. Aristeguieta 5264*; 30 Jan. 1950; Venezuela, Bolívar, Ciudad Bolívar; VEN (holo).

Alibertia davidsei Steyerm., Ann. Missouri Bot. Gard. 66: 903. 1979. *G. Davidse & A. González 12910*; 8–9 May 1977; Venezuela, Apure, Distr. Pedro Camejo, 11 km E of Paso de San Pablo, 2 km ENE of Fundo Picachón, along Río Capanapano; 45 m; MO (268781), VEN (holo).

Alibertia latifolia Benth. var. *paragueniana* Steyerm., Mem. New York Bot. Gard. 12(3): 225. 1965. *J. J. Wurdack & J. Monachino 39784*; 10 Dec. 1955; Venezuela, Bolívar, Río Paragueni; 90 m; NY (holo).

Alibertia myrciifolia (Spruce) K. Schum. var. *tepuiensis* Steyerm., Mem. New York Bot. Gard. 12(3): 226. 1965. *B. & C. K. Maguire 40009*; 22 Nov. 1954; Brazil, Terr. Rio Branco, Serra Tepequem; 800 m; NY (holo).

Alibertia triloba Steyerm., Mem. New York Bot. Gard. 12(3): 227. 1965. *S. S. Tillett et al. 45180*; 7 Aug. 1960; Guyana, upper Mazaruni River basin, Mt. Ayanganna; 900–1,100 m; NY (holo).

Alseis microcarpa Standl. & Steyerm., Fieldiana Bot. 28(3): 565. 1953. *J. A. Steyermark 62232*; 19 Apr. 1945; Venezuela, Monagas, Montaña de Aguacate, along Quebrada de Pajarral; 600–900 m; F (holo).

Alseis trichocarpa Standl. & Steyerm., Fieldiana Bot. 28(3): 566. 1953. *J. A. Steyermark 57713*; 31 July–1 Aug. 1944; Venezuela, Bolívar, 1–10 km NW of Upata on road to San Felix; F (holo) = *A. labatiodes* Karst. ex Schumann, 1974.

Amaioua brevidentata Steyerm., Mem. New York Bot. Gard. 12(3): 216. 1965. *J. A. Steyermark 89802*; 20 Oct. 1961; Venezuela, Aragua, Parque Nacional Henri Pittier, Rancho Grande Biology Station, towards Pico Guacamayo; 1,500–1,700 m; VEN (holo).

Amaioua guianensis Aublet var. *macrantha* Steyerm., Mem. New York Bot. Gard. 12(3): 216. 1965. *B. Maguire et al. 42025*; 11 Nov. 1957; Venezuela, T.F. Amazonas, Cerro de la Neblina, Camp 3; 700 m; NY (holo).

Amphidasya intermedia Steyerm., Mem. New York Bot. Gard. 23(1): 319. 1972. *F. R. Fosberg & N. C. Fassett 21825*; 20 Apr. 1944; Colombia, Dept. Santander, E of Cimatara, 17 km WNW of Landazuri; 230–330 m; US (holo), NY.

Amphidasya neblinae Steyerm., Mem. New York Bot. Gard. 23(1): 320. 1972. *B. Maguire et al. 60295*; 1 Dec. 1965; Brazil; Amazonas, Rio Negro, Rio Cauaburi, Rio Tucano, base of Serra de Neblina; MO (2029484), NY (holo), VEN.

Aphanocarpus Steyerm., Mem. New York Bot. Gard. 12(3): 263. 1965, gen. nov.

Aphanocarpus steyermarkii (Standl.) Steyerm. f. *elongatus* Steyerm., Ann. Missouri Bot. Gard. 71: 331. 1984. *O. Huber & J. A. Steyermark 6945*; 26–29 Jan. 1983; Venezuela, Bolívar, Piar, Macizo de Chimantá; 2,000 m; VEN (holo).

Aphanocarpus steyermarkii (Standl.) Steyerm. f. *glabrior* Steyerm., Ann. Missouri Bot. Gard. 71: 330. 1984. *J. A. Steyermark et al. 115968*; 25 Feb. 1978; Venezuela, Bolívar, cumbre de Aprada-tepui; 2,460–2,500 m; VEN (holo).

Appunia longiloba Steyerm., Mem. New York Bot. Gard. 17(1): 358. 1967. *A. C. Smith 2384*; 1–4 Nov. 1937; Guyana, basin of Rupununi River, near mouth of Charwair Creek; NY (holo) = *Morinda longiloba* (Steyerm.) Steyerm., 1972.

Appunia sparsiflora Steyerm., Mem. New York. Bot. Gard. 17(1): 356. 1967. *Forest Dept. Field No. CAP 41*; 16 Feb. 1946; Guyana, Mazaruni Station; NY (holo) = *Morinda sparsiflora* (Steyerm.) Steyerm., 1972.

Appunia tenuiflora (Benth.) Jacks. & Hook. var. *leiophylla* Steyerm., Mem. New York Bot. Gard. 17(1): 358. 1967. *Forest Dept. Field No. WB 500*; Nov. 1948; Guyana, Iramaipang, Kanuku Mountains; 150 m; NY (holo) = *Morinda tenuiflora* (Benth.) Steyerm. var. *leiophylla* (Steyerm.) Steyerm., 1972.

Appunia venezuelensis Steyerm., Mem. New York Bot. Gard. 17(1): 356. 1967. *J. A. Steyermark 88277*; 10 Jan. 1961; Venezuela, Bolívar, Altiplanicie de Nuria; 400 m; VEN (holo) = *Morinda venezuelensis* (Steyerm.) Steyerm., 1972.

"*Arachnothrix*" *calycophylla* Steyerm., Mem. New York Bot. Gard. 17(1): 257. 1967. *J. A. Steyermark 57136*; 12 July 1944; Venezuela, Táchira, between Las Delicias and Paraquita, Río Táchira; 1,675–1,980 m; VEN (holo). Note: *Arachnothyrx* is the correct spelling.

"*Arachnothrix*" *costanensis* Steyerm., Mem. New York Bot. Gard. 17(1): 259. 1967. *J. A. Steyermark 61424*; 7 Mar. 1945; Venezuela, Anzoátegui, Cerro Peonia (Cerro Coroy); 1,000–1,450 m; VEN (holo).

"*Arachnothrix*" *fosbergii* Steyerm., Mem. New York Bot. Gard. 17(1): 255. 1967. *F. R. Fosberg & M. A. Giler 22964*; 10 Feb. 1945; Ecuador, Loja, Río Salado; NY (holo), US.

"*Arachnothrix*" *lojensis* Steyerm., Mem. New York Bot.

Gard. 17(1): 255. 1967. *F. R. Fosberg & M. A. Giler 23141*; Ecuador, Loja, Río San Francisco, Cordillera de Zamora (El Condor); NY (holo).

"*Arachnothrix*" *reflexa* (Benth.) Planch. var. *breviloba* Steyerm., Mem. New York Bot. Gard. 17(1): 253. 1967. *F. R. Fosberg 21418*; 14 Dec. 1943; Colombia, Norte de Santander, La Camarona; 1,700–1,850 m; NY (holo).

"*Arachnothrix*" *reflexa* (Benth.) Planch. var. *calycina* Steyerm., Mem. New York Bot. Gard. 17(1): 255. 1967. *J. Cuatrecasas & R. Romero Castañeda 24332*; 22 Sep. 1959; Colombia, Magdalena, Sierra Nevada de Santa Marta, Hoya del Río Donachui; 1,350–1,500 m; VEN (holo).

"*Arachnothrix*" *reflexa* (Benth.) Planch. var. *glandulifera* Steyerm., Mem. New York. Bot. Gard. 17(1): 253. 1967. *J. A. Steyermark 61317*; 1–2 Mar. 1945; Venezuela, Anzoátegui, along Río Zumbador, near base of Piedra Blanca; 800–1,000 m; VEN (holo).

"*Arachnothrix*" *reflexa* (Benth.) Planch. var. *meridensis* Steyerm., Mem. New York Bot. Gard. 17(1): 253. 1967. 1st cited: *L. Bernardi 985*; 21 Sep. 1953; Venezuela, Mérida, Santo Domingo; 1,600 m; depository not designated.

"*Arachnothrix*" *rugulosa* (Standl.) Steyerm. var. *tachirensis* Steyerm., Acta Bot. Venez. 6: 110. 1971. *L. Cardenas de Guavara 805*; 29 Dec. 1968; Venezuela, Táchira, Distr. Lobatera, Parque Río Conejo-Borota; MY (holo).

"*Arachnothrix*" *venezuelensis* Steyerm., Mem. New York Bot. Gard. 17(1): 256. 1967. *C. E. Chardon 179*; 26 Oct. 1940; Venezuela, Aragua, Carretera a Choroni; 1,300 m; VEN (holo).

Arcytophyllum nitidum (H.B.K.) Schlecht. subsp. *caracasanum* (H.B.K.) Steyerm. var. *culmenicolum* Steyerm., Acta Bot. Venez. 6: 119. 1971. *F. Tamayo 4509*; Sep. 1961; Venezuela, Mérida, teleferico de Mérida; VEN (holo).

Arcytophyllum nitidum (H.B.K.) Schlecht. f. *hispidum* Steyerm., Acta Bot. Venez. 6: 117. 1971. *J. A. Steyermark et al. 98558*; 20–23 May 1967; Venezuela, Táchira, Páramo de Tamá; 2,750–2,950 m; depository not designated.

Arcytophyllum vareschii Steyerm., Acta Bot. Venez. 6: 113. 1971. *V. Vareschi & K. Magdefrau 6850*; 3 Apr. 1958; Venezuela, Mérida, Pico Bolívar, Laguna Anteojos; 4,100 m; VEN (holo).

Arcytophyllum venezuelanum Steyerm., Acta Bot. Venez. 6: 120. 1971. *J. A. Steyermark & T. Koyama 102360*; 17 Dec. 1969; Venezuela, Mérida, estación La Aguada, between Mérida and Pico Espejo; 3,475 m; VEN (holo).

Bertiera aequaliramosa Steyerm., Mem. New York Bot. Gard. 17(1): 319. 1967. *G. P. Cooper 586*; Jan.–Mar. 1928; Panama, Prov. Bocas del Toro, Almirante, Buena Vista Camp on Chiriquí trail; 380 m; NY (holo).

Bertiera diversiramea Steyerm., Mem. New York Bot. Gard. 17(1): 319. 1967. *H. S. Irwin et al. 55299*; 1 Sep. 1963; Suriname, West Rivier, 4 km S Juliana Top, Wilhelmina Gebergte; 700 m; NY (holo).

Bertiera guianensis Aublet var. *glabriflora* Steyerm., Mem. New York Bot. Gard. 17(1): 318. 1967. *R. Spruce 4109*; 1855–1856; Perú, Prope Tarapoto; NY (holo).

Bertiera guianensis Aublet var. *leiophylla* Steyerm., Mem. New York Bot. Gard. 17(1): 318. 1967. *H. Pittier 5178*; Jan. 1912; Panamá, Prov. Chiriquí, vicinity of San Felix; 0–120 m; NY (holo).

Bertiera guianensis Aublet subsp. *pubiflora* Steyerm., Mem. New York Bot. Gard. 17(1): 318. 1967. *G. Klug 2164*; May–July 1931; Perú, Loreto, Río Zubineta mouth, Florida, Río Putpumayo; 180 m; NY (holo).

Borojoa duckei Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 478. 1966. *A. Ducke 1141*; 3 Oct. 1942; Brazil, Amazonas, Esperanca (Boca de Javary); NY, US (holo).

Borojoa universitatis Steyerm., Acta Bot. Venez. 3: 193. 1968. *L. Aristeguieta et al. 6466*; Nov. 1966; Venezuela, Miranda, Parque Naciónal de Guatopo; 650 m; VEN (holo).

Borojoa venezuelensis Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 475. 1966. *J. Garcia 128*; 8 Aug. 1951; Venezuela, Aragua, Rancho Grande; 1,130 m; VEN (holo).

Borreria aristeguietaeana Steyerm., Bol. Soc. Venez. Ci. Nat. 29: 22. 1971. *E. Castellanos 46*; 4 Sep. 1965; Venezuela, Guárico, Estación Biologica de Los Llanos, Calabozo; VEN (holo).

Borreria bolivarensis Steyerm., Mem. New York Bot. Gard. 23: 819. 1972. *J. A. Steyermark 87964*; 12 Dec. 1960; Venezuela, Bolívar, Sierra Imataca, Río Toro (Río Grande); 200–250 m; VEN (holo), NY.

Borreria capitata (Ruíz & Pavón) DC. f. *glabra* Steyerm., Mem. New York Bot. Gard. 23: 823. 1972. *L. Aristeguieta 4250*; July 1960; Venezuela, Guárico, Sabanas, Estación Biologica de Los Llanos; VEN (holo).

Borreria cataractarum Steyerm., Mem. New York Bot. Gard. 23: 813. 1972. *B. Maguire et al. 4612*; 7 Sep. 1961; Guyana, S Pakaraima Mountains, base of Chimpau Falls; depository not designated.

Borreria confertifolia Steyerm., Mem. New York Bot. Gard. 23: 828. 1972. *J. J. Wurdack & L. S. Adderley 42701*; 30 May 1959; Venezuela, T.F. Amazonas, Río Orinoco 2 km below mouth of Río Atabapo, Sabanita Morocto; 125–150 m; NY (holo), VEN.

Borreria intricata Steyerm., Mem. New York Bot. Gard. 23: 828. 1972. *J. J. Wurdack & L. S. Adderley 42988*; 12 June 1959; Colombia, opposite Manacal on Río Atabapo; 125–140 m; NY (holo), VEN.

Borreria jangouxii Steyerm., Fl. Venez. 9(3): 165. 1974. *J. Jangoux 10157*; 20 Apr. 1974; Venezuela, T.F. Amazonas, 8–10 km E of Caño Parucito, E of Hato Yavi, N of Caño Majagua, S of Cerro Corobita; 150 m; VEN (holo).

Borreria laevis (Lam.) Griseb. var. *edentata* Steyerm., Acta Bot. Venez. 6: 196. 1971. *H. Pittier 9829*; 18 Sep. 1921; Venezuela, Upper Cotiza, around Caracas; 800–1,000 m; NY (holo), VEN.

Borreria macrocephala Standl. & Steyerm., Fieldiana Bot. 28(3): 566. 1953. *Ll. Williams 13853*; 19 Jan. 1943; Venezuela, T.F. Amazonas, banks of Caño Rana, Río Atabapo; 280 m; F (holo).

Borreria oligodonta Steyerm., Mem. New York Bot. Gard. 23: 826. 1972. *G. H. H. Tate 1147*; Dec. 1937–Jan. 1938; Venezuela, Bolívar, Auyan-tepui; NY (holo).

Borreria pygmaea Spruce var. *robusta* Steyerm., Mem. New York Bot. Gard. 23: 812. 1972. *B. Maguire et al. 29242a*; 24 Oct. 1950; Venezuela, T.F. Amazonas, Puerto Ayacucho, E of Hotel Amazonas; 150 m; NY (holo).

Borreria wurdackii Steyerm., Mem. New York Bot. Gard. 23: 812. 1972. *J. J. Wurdack & L. Adderley 42915*; 10 June 1959; Venezuela, T.F. Amazonas, Río Ata-

bapo, Yavita–Pimichin trail near Yavita; 125–140 m; NY (holo), VEN.

Borreria vegeta Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 21. 1943. *P. C. Standley 76007*; Nov. 1940; Guatemala, Dept. Jutiapa, between Jutiapa and La Burrera; 800 m; F (holo).

Botryarrhena venezuelensis Steyerm., Ann. Missouri Bot. Gard. 70(1): 207. 1983. *G. Davidse et al. 17427*; 8 May 1979; Venezuela, T.F. Amazonas, Dept. Atabapo, SE bank of middle part of Caño Yagua at Cucurbital de Yagua; 120 m; MO (2769061), VEN (holo).

Bouvardia nubigena Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 382. 1940. *J. A. Steyermark 31901*; 18 Nov. 1939; Guatemala, Dept. Jutiapa, Volcán Suchitán, NW of Asunción Mita; 2,050 m; F (holo) = *B. laevis* Mart. & Gal., 1975.

Bouvardia pachecoana Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 22. 1943. *P. C. Standley 86226*; Feb. 1941; Guatemala, Dept. San Marcos, Barranco Eminencia, road between San Marcos and San Rafael Pie de la Cuesta; 2,500–2,700 m; F (holo) = *B. dictyoneura* Standl., 1975.

Bouvardia salvadorensis Steyerm., Ceiba 4: 302. 1955. *J. M. Tucker 1368*; 12 May 1942; El Salvador, Dept. Sonsonate, steep bank of Río Acachapa; 630 m; F (holo) = *B. multiflora* (Cav.) Schult., 1975.

Calycophyllum intonsum Steyerm., Mem. New York Bot. Gard. 10(5): 186. 1963. *S. S. Tillett & C. L. Tillett 45567*; 30 Sep. 1960; Guyana, Karow-tipu, upper Mazaruni river basin, Kako River; 950 m; NY (holo), VEN.

Calycophyllum merumense Steyerm., Mem. New York Bot. Gard. 23(1): 228. 1972. *S. S. Tillett et al. 44837*; 6 July 1960; Guyana, Partang River, SE ridge of Merume Mt.; 1,140 m; NY (holo).

Calycophyllum spectabile Steyerm., Mem. New York Bot. Gard. 10(5): 188. 1963. *B. Maguire & D. B. Fanshawe 32219*; 23 Oct. 1951; Guyana, between Imbaimadai airstrip and Mt. Yamanaik, upper Mazaruni River; 1,200 m; NY (holo), VEN.

Calycophyllum venezuelense Steyerm., Mem. New York Bot. Gard. 10(5): 189. 1963. *J. A. Steyermark & L. Aristeguieta 4*; 6 Mar. 1962; Venezuela, Bolívar, Cerro Paují; 800 m; NY, VEN (holo).

Capirona wurdackii Steyerm., Mem. New York Bot. Gard. 10(5): 190. 1963. *J. J. Wurdack & L. S. Adderley 43383*; 10 July 1959; Venezuela, T.F. Amazonas, near left bank of Caño Duquiapo, Río Cassiquiare, 2 km above Solano; 100 m; NY (holo), VEN.

Cephaëlis bolivarensis Standl. & Steyerm., Fieldiana Bot. 28(3): 567. 1953. *J. A. Steyermark 60185*; 15 Nov. 1944; Venezuela, Bolívar, Sororopan-tepui; 2,130 2,250 m; F (holo) = *Psychotria bolivarensis* (Standl. & Steyerm.) Steyerm., 1972.

Cephaëlis cacuminis Steyerm., Acta Bot. Venez. 2: 335. 1967. *J. A. Steyermark 93564*; 7 May 1964; Venezuela, Bolívar, Auyan-tepui; 1,800 m; VEN (holo) = *Psychotria cacuminis* (Steyerm.) Steyerm., 1972.

Cephaëlis sandwithiana Steyerm., Mem. New York Bot. Gard. 17(1): 428. 1967. *B. Maguire et al. 53562*; 3 Sep. 1962; Venezuela, Bolívar, along Río Franela, Cerro Piton, Cordillera Epicara, Alto Río Cuyuni, Río Chicanan; 400 m; VEN (holo) = *Psychotria sandwithiana* (Steyerm.) Steyerm., 1972.

Cephaëlis tepuiensis Steyerm., Mem. New York Bot. Gard. 17(1): 430. 1967. *B. Maguire et al. 46864*; 20–21 Aug. 1962; Venezuela, Bolívar, La Escalera, Río Uiriyuk, Alto Río Cuyuni; 1,000 m; MO (2389390), VEN (holo) = *Psychotria tepuiensis* (Steyerm.) Steyerm., 1972.

Cephaëlis tinctoria Standl. & Steyerm., Fieldiana Bot. 28(3): 568. 1953. *J. A. Steyermark 55256*; 4 Feb. 1944; Venezuela, Lara, Palojosco above Los Aposentos, above Humocaro Bajo; 2,530–2,680 m; F (holo) = *Psychotria eciliata* Steyerm., nom. nov., 1972.

Cephalodendron Steyerm., Mem. New York Bot. Gard. 23(1): 228. 1972, gen. nov.

Cephalodendron aracamuniensis Steyerm., Ann. Missouri Bot. Gard.: in press. 1989. *R. L. Liesner & F. Delascio 22064*; 17 Oct. 1987; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp; 1,550 m; MO (holo), VEN.

Cephalodendron globosum Steyerm., Mem. New York Bot. Gard. 23(1): 228. 1972. *B. Maguire et al. 42467*; 24 Dec. 1957; Venezuela, T.F. Amazonas, Cerro de la Neblina; 1,100 m; NY (holo), VEN.

Chalepophyllum guianense Hook. f. var. *cuneatum* Steyerm., Mem. New York Bot. Gard. 10(5): 193. 1963. *B. Maguire 33700*; 30 Mar. 1952; Venezuela, Bolívar, near Kavanayen; 1,300 m; NY (holo).

Chalepophyllum longilobum Steyerm., Mem. New York Bot. Gard. 10(5): 193. 1963. *B. Maguire et al. 40637*; 7–8 Feb. 1955; Guyana, between Ayanganna and Chinowieng, Mt. Ayanganna, Pakaraima Mountains; 100–1,200 m; NY (holo).

Chalepophyllum pungens Standl. & Steyerm., Fieldiana Bot. 28(3): 568. 1953. *Ll. Williams 12970*; 18 May 1940; Venezuela, T.F. Amazonas, Puerto Ayacucho; 100 m; F (holo) = *Acanthella sprucei* Hook. f., 1973.

Chimarrhis bathysoides Steyerm., Mem. New York Bot. Gard. 12(3): 181. 1965. *B. Maguire & L. Politi 28626*; 25 Jan. 1949; Venezuela, T.F. Amazonas, Cerro Sipapo, near Base Camp; 125 m; NY (holo).

Chimarrhis brevipes Steyerm., Mem. New York Bot. Gard. 12(3): 179. 1965. *B. Maguire & L. Politi 27971*; 25 Dec. 1948; Venezuela, T.F. Amazonas, Cerro Sipapo, near Base Camp; 125 m; NY (holo).

Chimarrhis cubensis Steyerm., Mem. New York Bot. Gard. 12(3): 184. 1965, nom. nov.

Chimarrhis decurrens Steyerm., Ceiba 3: 18. 1952. *P. H. Allen 3566*; 28 June 1946; Panama, Prov. Coclé, El Valle; 600 m; F (holo), MO = *Allenanthus erythrocarpus* Standl., 1965.

Chimarrhis microcarpa Standl. var. *speciosa* Steyerm., Mem. New York Bot. Gard. 12(3): 183. 1965. *T. Garcia 147*; 18 Sep. 1951; Venezuela, Aragua, Rancho Grande; VEN (holo).

Chimarrhis perijaënsis Steyerm., Acta Bot. Venez. 8: 248. 1973. *J. A. Steyermark et al. 105658*; 25 Mar. 1972; Venezuela, Zulia, Sierra Perija, Río Omira-Kuna (Tumuriasa); 1,470–1,560 m; MO (2250725), VEN (holo). Note: No. 105655 is a paratype, collected at the same locality.

Chimarrhis venezuelensis Standl. & Steyerm., Fieldiana Bot. 28(3): 570. 1953. *J. A. Steyermark 55408*; 8 Feb. 1944; Venezuela, Lara, mountain between Santo Domingo and Los Quebraditos, S of Las Sabanetas; 2,430–2,475 m; F (holo) = *Dioicodendron dioicum* (K. Schum. & K. Krause) Steyerm., 1974.

Chiococca alba (L.) A. Hitchc. subsp. *parvifolia* (Wullsch. ex Griseb.) Steyerm. var. *micrantha* (Johnston) Steyerm. f. *pilosa* Steyerm., Acta Bot. Venez. 6: 141.

1971. *J. Saer 4*; 1923; Venezuela, Lara, cercanias de Barquisimento; VEN (holo).

Chiococca auyantepuiensis Steyerm., Mem. New York Bot. Gard. 23(1): 374. 1972. *J. A. Steyermark 93652*; 10 May 1964; Venezuela, Bolívar, Auyan-tepui; 1,800 m; VEN (holo).

Chiococca lucens Standl. & Steyerm., Fieldiana Bot. 28(3): 571. 1953. *J. A. Steyermark 60184*; 15 Nov. 1944; Venezuela, Bolívar, Sororopan-tepui; 2,130–2,250 m; F (holo).

Chiococca multipedunculata Steyerm., Mem. New York Bot. Gard. 23(1): 373. 1972. *B. A. Whitton 120*; 20 Aug. 1959; Guyana, Potaro Distr., Mt. Kanaima; 485 m; NY (holo).

Chiococca naiguatensis Steyerm., Acta Bot. Venez. 6: 135. 1971. *J. A. Steyermark 97475*; 8 Oct. 1966; Venezuela, Distr. Federal, Cerro Naiguata; 1,400 m; MO (2270191), NY, VEN (holo).

Chiococca nitida Benth. var. *chimantensis* Steyerm., Mem. New York Bot. Gard. 23(1): 376. 1972. *J. A. Steyermark 75406*; 15 May 1953; Venezuela, Bolívar, Chimantá Massif, Chimantá-tepui (Torono-tepui); MO (2012043, 2011333), NY, US, VEN (holo).

Chiococca semipilosa Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 278. 1940. *J. A. Steyermark 31406*; 7 Nov. 1939; Guatemala, Dept. Chiquimula, Caracol Mt., 1.5 mi. N of Quezaltepeque; 1,200–1,400 m; F (holo).

Chione guatemalensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(3): 174. 1940. *J. A. Steyermark 39375*; 14 Apr. 1940; Guatemala, Dept. Izabal, Río Dulce near Livingston; sea level; F (holo).

Chione panamensis Steyerm., Ceiba 3: 19. 1952. *C. & W. von Hagen 2137*; 1 July 1940; Panama, Prov. Chiriquí, Cerro Horqueta, Boquete region; 2,167 m; F (holo), MO.

Chomelia delascioi Steyerm., Mem. Soc. Ci. Nat. La Salle 40(113): 83. 1980. *F. Delascio et al. 8471*; Aug. 1979; Venezuela, Bolívar, Distr. Roscio, San Martín de Turumban, Suroeste de Tumeremo, Río Cuyuni; VEN (holo), LA SALLE.

Chomelia glabricalyx Steyerm., Ann. Missouri Bot. Gard. 74: 657. 1987. *G. Morillo 6811*; May 1982; Venezuela, Bolívar, Río Caura, 5–10 km S of Las Pavas (Salto Para); 240 m; VEN (holo).

Chomelia glabriuscula Steyerm., Mem. New York Bot. Gard. 23(1): 372. 1972. *Oldeman & Sastre 209*; 12 Feb. 1968; French Guiana, Grand Tamouri, Riviere Camopi; P (holo).

Chomelia monachinoi Steyerm., Mem. New York Bot. Gard. 17(1): 336. 1967. *J. J. Wurdack & J. Monachino 40970*; 26 Dec. 1955; Venezuela, Bolívar, W of El Carmen, Río Parguaza; 110 m; NY (holo).

Chomelia ramiae Steyerm., Fl. Venez. 9(2): 854. 1974. *M. Ramia & R. Montes 5254*; 22 May 1973; Venezuela, Apure, cercanias a Mantecal, alto Apure; 80 m; VEN (holo).

Chomelia schomburgkii Steyerm., Mem. New York Bot. Gard. 17(1): 339. 1967. *R. Schomburgk 924*; 1841; Guyana; NY (holo).

Chomelia stergiosii Steyerm., Ann. Missouri Bot. Gard. 74: 105. 1987. *B. Stergios & G. Aymard 2804*; 20 Aug. 1981; Venezuela, Bolívar, Anacoco, Río Ciyuni, entre puesto de la Guardia Nacional Acarabisi and Anacoco; Port, VEN (holo).

Chomelia venezuelensis Steyerm., Mem. New York Bot. Gard. 17(1): 336. 1967. *E. Rohl 103*; 1939; Venezuela, Distr. Federal, Los Castillitos, near Caracas; VEN (holo).

Chondrococcus Steyerm., Mem. New York Bot. Gard. 23(1): 403. 1972, gen. nov. = *Coccochondra* Rauschert, 1982.

Chondrococcus laevis Steyerm., Mem. New York Bot. Gard. 23(1): 405. 1972. *R. S. Cowan & J. J. Wurdack 31130*; 2 Feb. 1951; Venezuela, T.F. Amazonas, Río Ventuari, Caño Asisa, Río Parú, Serranía Parú; 2,000 m; NY (holo), VEN = *Coccochondra laevis* (Steyerm.) Rauschert, 1982.

Cinchona henleana Karst. var. *trichophylla* Steyerm., Acta Bot. Venez. 8: 247. 1973. *J. A. & C. Steyermark 95374*; 31 Mar. 1966; Venezuela, Carabobo, Río San Gian, E Los Tanques, S Borburata; 750–1,100 m; VEN (holo).

Coccocypselum apurense Steyerm., Ann. Missouri Bot. Gard. 74: 398. 1987. *G. Davidse & A. C. González 15825*; 27 Feb. 1979; Venezuela, Apure, Dept. Pedro Camejo, Caño El Cabello, between the Río Meta and Río Cinaruco; 75 m; MO (holo—2746721), VEN.

Coccocypselum brevipetiolatum Steyerm., Mem. New York Bot. Gard. 17(1): 304. 1967. *F. W. Pennell 1676*; 4 Sep. 1917; Colombia, Cundinamarca, Buenavista to Pipiral, SE of Quetame; 1,000–1,200 m; NY (holo).

Coccocypselum croatii Steyerm., Ann. Missouri Bot. Gard. 74: 106. 1987. *T. B. Croat 54112*; 25 July 1982; Venezuela, Bolívar, vicinity of Icabarú; 600 m; MO (holo—3327537).

Coccocypselum guianense (Aublet) Schumann var. *patens* Steyerm., Mem. New York Bot. Gard. 17(1): 303. 1967. *T. Lasser 1417*; 25 Apr. 1946; Venezuela, Bolívar, Alto Caroni; VEN (holo).

Coccocypselum huberi Steyerm., Ann. Missouri Bot. Gard. 74: 657. 1987. *O. Huber 9123*; 1 Mar. 1984; Venezuela, Bolívar, Distr. Roscio, Serranía del Caco, 25 km NW of San Ignacio de Yuruani 2.5 km ESE of Wanarú; 1,150–1,200 m; MO (3327365), VEN (holo).

Coccocypselum trinitense Steyerm., Mem. New York Bot. Gard. 17(1): 300. 1967. *J. A. Steyermark 90919*; 3 July 1962; Trinidad, Aripa Savanna, Long Stretch Forest Reserve; VEN (holo).

Coryphothamnus Steyerm., Mem. New York Bot. Gard. 12(3): 264. 1965, gen. nov.

Coussarea amapaensis Steyerm., Mem. New York Bot. Gard. 17(1): 366. 1967. *J. Murca Pires et al. 50285*; 31 July 1961; Brazil, Amapa, Serra do Navio, on Rio Amapari; NY (holo).

Coussarea bernardii Steyerm., Mem. New York Bot. Gard. 17(1): 371. 1967. *L. Bernardi 2325*; June 1955; Venezuela, Mérida, Pueblos del Sur; 1,600–2,200 m; NY (holo).

Coussarea darienensis Steyerm., Ceiba 3: 20. 1952. *P. H. Allen 4576*; 9–11 June 1947; Panamá, Prov. Darién, along Río Chico, vicinity of Yaviza; 33 m; F (holo), MO.

Coussarea evoluta Steyerm., Ann. Missouri Bot. Gard. 75: 334. 1988. *R. L. Liesner & D. Bell 17493*; 4 Dec. 1984; Venezuela, T.F. Amazonas, Cerro de la Neblina; 140–340 m; MO (holo—3524658), VEN.

Coussarea fanshawei Steyerm., Mem. New York Bot. Gard. 17(1): 365. 1967. *B. Maguire & D. B. Fanshawe 23072*; 28 Apr. 1944; Guyana, Potaro River Gorge; NY (holo).

Coussarea hallei Steyerm., Mem. New York Bot. Gard. 23(1): 387. 1972. *F. Halle 1018*; 30 Jan. 1965; French Guiana, Route du lac des Americains; P (holo).

Coussarea hirticalyx Standl. var. *glabrior* Steyerm., Mem. New York Bot. Gard. 17(1): 363. 1967. *R. E. Schultes & G. A. Black 8156*; 11–18 Sep. 1946; Colombia, Amazonas, near Sergipe, Putumayo (Ica) River; 100 m; US (holo).

Coussarea klugii Steyerm., Mem. New York Bot. Gard. 17(1): 363. 1967. *G. Klug 2362*; Oct.–Nov. 1931; Peru, Loreto, mouth of Río Zubineta Río Putumayo, Florida; 180 m; F (holo).

Coussarea lasseri Steyerm., Mem. New York Bot. Gard. 17(1): 366. 1967. *T. Lasser 1682*; 27 May 1946; Venezuela, Bolívar, Río Uairen; VEN (holo).

Coussarea liesneri Steyerm., Ann. Missouri Bot. Gard.: in press. 1989. *R. L. Liesner & F. Delascio 22262*; 21 Oct. 1987; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro Aracamuni, Quebrada Camp; 600 m; MO, VEN (holo).

Coussarea mediocris Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 248. 1947. *J. A. Steyermark 48732*; 15 July 1942; Guatemala, Dept. Huehuetenango, vicinity Maxbal, Sierra de los Cuchumatanes; 1,500 m; F (holo).

Coussarea pittieri Steyerm., Bol. Soc. Venez. Ci. Nat. 25(106): 70. 1963. *J. A. Steyermark 91518*; 5 July 1963; Venezuela, Aragua, Parque Nacional Pittier, halfway up Fila de Paraiso; 1,400 m; VEN (holo).

Coussarea revoluta Steyerm., Mem. New York Bot. Gard. 17(1): 369. 1967. *J. J. Wurdack & L. Adderley 43078*; 20 June 1959; Venezuela, T.F. Amazonas, Río Orinoco, just below mouth of Río Cunucunuma; 150 m; NY (holo).

Coussarea terepaimensis Steyerm., Acta Bot. Venez. 8: 250. 1973. *R. F. Smith V-6649*; 14 Apr. 1971; Venezuela, Lara, La Fila, 6 km SE de Terepairma; VEN (holo).

Cuatrecasasiodendron Standl. & Steyerm., Acta Bot. Venez. 4(1): 29. 1964, gen. nov.

Cuatrecasasiodendron colombianum Standl. & Steyerm., Acta Bot. Venez. 4(1): 30. 1964. *J. Cuatrecasas 13694*; 19 Dec. 1942; Colombia, Dept. del Valle, Cordillera Occidental, Hoya del Río Anchicaya, Quebrada del Retiro; 300 m; F (holo).

Cuatrecasasiodendron spectabile Steyerm., Acta Bot. Venez. 4(1): 33. 1964. *J. Cuatrecasas 17165*; 21–30 Apr. 1944; Colombia, Dept. del Valle, Costa del Pacifico, Río Cajambre, Barco; 5–80 m; US (holo), VEN.

Declieuxia dasyphylla Schumann ex Steyerm. f. *ciliata* Steyerm., Los Angeles Co. Mus. Contr. Sci. 21: 26. 1958. *E. Y. Dawson 14163a*; 13 Apr. 1956; Brazil, Goiás, Chapada dos Veadeiros; F, R (holo) = *D. dasyphylla* Schumann ex Steyerm. var. *dasyphylla*, 1976.

Dendrosipanea revoluta Steyerm., Mem. New York Bot. Gard. 10(5): 196. 1963. *B. Maguire et al. 37592*; 7 Feb. 1954; Venezuela, T.F. Amazonas, right bank of Río Pacimoni; 100–140 m; NY (holo).

Dendrosipanea wurdackii Steyerm., Mem. New York Bot. Gard. 10(5): 198. 1963. *B. Maguire & J. J. Wurdack 3558*; 14 Apr. 1953; Venezuela, T.F. Amazonas, Sabana El Venado on left bank of Caño Pimichin, above Pimichin, Río Guainía; 140 m; NY (holo).

Deppea amaranthina Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 281. 1940. *J. A. Steyermark 30926*; 1 Nov. 1939; Guatemala, Dept. Chiquimula, Cerro Brujo, vicinity of Río Negro, below Montaña Montenegro, near Brujo; 1,500–2,000 m; F (holo).

Deppea inaequalis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 385. 1940. *J. A. Steyermark 37974*; 16 Mar. 1940; Guatemala, Dept. San Marcos, above Finca El Porvenir, along Río Cabús, Volcán Tajumulco; 1,300–1,500 m; F (holo).

Diodia angustata Steyerm., Los Angeles Co. Mus. Contr. Sci. 21: 26. 1958. *E. Y. Dawson 14672*; 24 Apr. 1956; Brazil, Goiás, Chapada dos Veadeiros, 14 km S of Veadeiros; F, LAM, R (holo), US.

Diodia hyssopifolia (Willd.) Cham. & Schl. var. *leiocarpa* Steyerm., Mem. New York Bot. Gard. 23: 797. 1972. *J. A. Steyermark & C. K. Maguire 60125*; 7 Nov. 1965; Brazil, Amazonas, Rio Negro, along Rio Cauaburi; depository not designated.

Diodia hyssopifolia (Willd.) Cham. & Schlecht. var. *linearis* (Willd.) Steyerm. f. *glabriuscula* Steyerm., Mem. New York Bot. Gard. 23: 796. 1972. *H. H. Bartlett 8300*; Oct. 1904; Guyana, Cuyuni River, Tinamu Falls; NY (holo).

Diodia hyssopifolia (Willd.) Cham. & Schlecht. f. *psiloclada* Steyerm., Mem. New York Bot. Gard. 23: 795. 1972. *J. A. Steyermark 90798*; 15 Jan. 1962; Venezuela, Bolívar, Río Paragua, Raudal de Guaiquinima, base of Cerro Guaiquinima; 475 m; VEN (holo).

Diodia radula (Willd. & Hoffmanns.) Cham. & Schlecht. subsp. *venezuelensis* Steyerm., Acta Bot. Venez. 6: 181. 1971. *F. J. Breteler 4095*; 12 Aug. 1964; Venezuela, Trujillo, 22 km from Boconó along road to Trujillo; 1,900 m; VEN (holo).

Diodia teres Walter var. *angustata* (A. Gray) Steyerm. f. *latior* Steyerm., Acta Bot. Venez. 6: 184. 1971. *H. H. Smith 2628*; 1,898–1,899 m; Colombia, Dept. Magdalena, Santa Marta; NY (holo).

Diodia teres Walter subsp. *prostrata* (Swartz) Steyerm. f. *latifolia* Steyerm., Acta Bot. Venez. 6: 186. 1971. *J. Blydenstein 250*; 16 Aug. 1961; Venezuela, Guárico, Alto Llano, Hato El Carmen, Estación Biologica de Los Llanos; VEN (holo).

Diodia teres Walter subsp. *prostrata* (Swartz) Steyerm. f. *leiocarpa* Steyerm., Acta Bot. Venez. 6: 187. 1971. *F. J. Breteler 4204*; 4 Sep. 1964; Venezuela, Barinas, 14 km from Barinas along road to Guanare; 200 m; VEN (holo).

Dioicodendron Steyerm., Bol. Soc. Venez. Ci. Nat. 25: 24. 1963, gen. nov.

Dioicodendron cuatrecasasii Steyerm., Bol. Soc. Venez. Ci. Nat. 25: 27. 1963. *J. Cuatrecasas 15192*; 19–28 Aug. 1943; Colombia, Dept. del Valle, Cordillera Occidentale, Hoja del Río Digua, Piedra de Moler; 900–1,180 m; F, US, VEN (holo).

Duroia amapana Steyerm., Mem. New York Bot. Gard. 12(3): 209. 1965. *J. Murca Pires et al. 51601*; 9 Oct. 1961; Brazil, Terr. Amapa, Camp 13, Rio Araguari; NY (holo).

Duroia bolivarensis Steyerm., Mem. New York Bot. Gard. 12(3): 206. 1965. *F. Cardona 819*; 2–15 Aug. 1943; Venezuela, Bolívar, Alto Río Paragua, orillas del Río Tonoro; F, VEN (holo).

Duroia eriopila L.f. var. *brevidentata* Steyerm., Mem. New York Bot. Gard. 12(3): 203. 1965. *A. Ducke 1332*; 31 Aug. 1943; Brazil, Rio Branco, Serra Grande; NY (holo).

Duroia eriopila L.f. f. *glabra* Steyerm., Mem. New York

Bot. Gard. 12(3): 203. 1965. *A. C. Smith 2792*; 15–24 Dec. 1937; Guyana, near mouth of Onoro Creek, basin of Essequibo River; NY (holo).

Duroia eriopila L.f. var. *tafelbergensis* Steyerm., Mem. New York Bot. Gard. 12(3): 203. 1965. *B. Maguire 24393*; 16 Aug. 1944; Suriname, Tafelberg, between savannas 4 and 5; 535 m; NY (holo).

Duroia genipifolia Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(3): 186. 1940. *J. A. Steyermark 39382*; 14 Apr. 1940; Guatemala, Dept. Izabal, Río Dulce, near Livingston; sea level; F (holo).

Duroia gransabanensis Steyerm., Mem. New York Bot. Gard. 12(3): 205. 1965. *F. Tamayo 3133*; 15 Mar. 1946; Venezuela, Bolívar, Gran Sabana, Uari; VEN (holo).

Duroia hirsutissima Steyerm., Brittonia 33: 385–400. *G. T. Prance et al. 7606*; 27 Sep. 1968; Brazil, Acre, Mun. Sena Madueira, 4 km E of Sena Madueira; NY, VEN (holo).

Duroia kotchubaeoides Steyerm., Mem. New York Bot. Gard. 12(3): 201. 1965. *J. Silverio Level 147*; 12 Sep. 1954; Venezuela, T.F. Amazonas, Río Orinoco, Caño Tama-Tama; 150 m; NY (holo).

Duroia maguirei Steyerm., Mem. New York Bot. Gard. 23(1): 343. 1972. *B. Maguire et al. 60071*; 4 Nov. 1965; Brazil, Amazonas, Río Cauaburi, base of Cachoeria Caranguejo; NY (holo), VEN.

Duroia maguirei Steyerm. var. *patentinervia* Steyerm., Mem. New York Bot. Gard. 23(1): 345. 1972. *J. A. Steyermark & G. S. Bunting 102939*; 22 Apr. 1970; Venezuela, T.F. Amazonas, 7–9 km from Yavita on road to Pimichin; NY, VEN (holo).

Duroia merumensis Steyerm., Mem. New York Bot. Gard. 12(3): 207. 1965. *S. S. Tillett et al. 44835*; 6 July 1960; Guyana, SE ridge of Merume Mt., upper Mazaruni river basin, Partang River, Merume Mountains; 1,140 m; NY (holo).

Duroia nitida Steyerm., Mem. New York Bot. Gard. 12(3): 208. 1965. *A. Ducke 799*; 28 Sep. 1941; Brazil, Amazonas, Cachoeira Iracema, Rio Irubu; NY, US (holo).

Duroia paruensis Steyerm., Mem. New York Bot. Gard. 12(3): 206. 1965. *R. Cowan & J. J. Wurdack 31447*; 13 Feb. 1951; Venezuela, T.F. Amazonas, Serranía Parú; NY (holo).

Duroia prancei Steyerm., Mem. New York Bot. Gard. 23(1): 345. 1972. *G. T. Prance et al. 59234*; 2 Oct. 1964; Brazil, Mato Grosso, 3 km from Garapu; NY (holo).

Duroia retrorsipila Steyerm., Mem. New York Bot. Gard. 12(3): 208. 1965. *J. A. Steyermark & S. Nilsson 382*; 20–22 Apr. 1960; Venezuela, Bolívar, vicinity Cerro Uei, vicinity road campamento 125, between Luepa & Cerro Venamo; 1,100 m; VEN (holo).

Duroia strigosa Steyerm., Mem. New York Bot. Gard. 12(3): 204. 1965. *B. Maguire et al. 53676*; 9–11 Sep. 1962; Venezuela, Bolívar, Río Chicanan, Cordillera Epicara, Cerro Piton; 400 m; VEN (holo).

Elaeagia alterniramosa Steyerm., Acta Bot. Venez. 4(1): 39. 1964. *J. Cuatrecasas 23870*; 27 Mar. 1947; Colombia, Dept. del Valle, Cordillera Occidental, Hoya del Río Digua, Río San Juan; US (holo), VEN.

Elaeagia barbata Steyerm., Mem. New York Bot. Gard. 12(3): 191. 1965. *J. M. Duque 1559*; n.d.; Colombia, Dept. del Valle, Cordillera Occidental, Cali; 1,800 m; US (holo).

Elaeagia cuatrecasasii Steyerm., Acta Bot. Venez. 4(1): 38. 1964. *J. Cuatrecasas 21682*; 24 July 1946; Colombia, Dept. del Valle, Cordillera Occidental, Hoya del Río Cali; 2,500 m; US (holo), VEN.

Elaeagia ecuadorensis Steyerm., Bol. Soc. Venez. Ci. Nat. 96: 242. 1960. *J. A. Steyermark 54305*; 10 Sep. 1943; Ecuador, Prov. Santiago-Zamora, on trail between Pailas and El Pan; 30–50 ft.; F (holo).

Elaeagia laxiflora Standl. & Steyerm., Fieldiana Bot. 28(3): 574. 1953. *J. A. Steyermark 61373*; 5 Mar. 1945; Venezuela, Anzoátegui, NE of Bergatín, along headwaters of tributary to Río Neverí; 800–1,200 m; F (holo).

Elaeagia magniflora Steyerm., Bol. Soc. Venez. Ci. Nat. 96: 240. 1960. *L. Aristeguieta 1989*; Aug. 1953; Venezuela, Aragua, Parque Nacional Henri Pittier, Rancho Grande; VEN (holo).

Elaeagia maguirei Standl. var. *pubens* Steyerm., Mem. New York Bot. Gard. 12(3): 190. 1965. *J. A. Steyermark & L. Aristeguieta 102*; 6–11 Mar. 1962; Venezuela, Bolívar, NE of Luepa, vicinity of km 143 S of El Dorado, Río Aponguao drainage; 800–1,200 m; VEN (holo).

Elaeagia microcarpa Steyerm., Mem. New York Bot. Gard. 12(3): 189. 1955. *B. A. Krukoff 10650*; 27–31 July 1939; Bolivia, Dept. La Paz, Prov. S Yungas, Asunta (near Evenay), Basin of Río Bopi; NY, US (holo).

Elaeagia multinervia Steyerm., Acta Bot. Venez. 4(1): 40. 1964. *J. Cuatrecasas 11515*; 31 Dec. 1940; Colombia, Comisario del Putumaya; 2,200–2,400 m; US (holo).

Elaeagia ruiz-teranii Steyerm., Pittieria 4: 15. 1972. *L. Ruíz Terán & M. Lopez Figueiras 441*; n.d.; Venezuela, Mérida, Los Pinos, Distr. Sucre, Mun. Estanques, unos 600 m antes del El Portachuelo (El Ramal), paramo de Las Colorados, entre Santa Cruz de Mora y el Molino; 2,800 m; depository not designated.

"*Emmeorrhiza*" *umbellata* (Spreng.) Schumann subsp. *septentrionalis* Steyerm., Mem. New York Bot. Gard. 23: 786. 1976. *J. A. Steyermark & S. Nilsson 767*; 25 Apr. 1960; Venezuela, Bolívar, between Luepa and Cerro Venamo; 1,300 m; NY (holo), VEN. Note: *Emmeorhiza* is the correct spelling.

"*Emmeorrhiza*" *umbellata* (Spreng.) Schumann subsp. *septentrionalis* Steyerm. var. *pubens* Steyerm., Mem. New York Bot. Gard. 23: 787. 1972. *L. Aristequieta & M. Saldiva 555*; 20 Mar. 1951; Venezuela, Aragua, Trayecto Guamitas–La Mesa; VEN (holo).

Faramea anisocalyx Poepp. & Endl. var. *schwackei* (Schumann & Krause) Steyerm. f. *dentata* Steyerm., Mem. New York Bot. Gard. 17(1): 375. 1967. *O. Buchtien 1719*; 26 Nov. 1926; Bolivia, Mapiri region, San Carlos bei Sarampiuni; 600 m; NY (holo).

Faramea berryi Steyerm., Pittieria 9: 5. 1981. *P. E. Berry & L. Chesney 2096*; 26 Feb.–2 Mar. 1976; Venezuela, T.F. Amazonas, Estación Exp. de Sta. Barbara del Orinoco, 1–2 km al Sur de Trapichote; 130 m; MO, VEN (holo).

Faramea boomii Steyerm., Ann. Missouri Bot. Gard. 75: 335. 1988. *B. Boom & A. Weitzman 5278*; 4 Dec. 1984; Venezuela, T.F. Amazonas, Cerro de la Neblina, Base Camp; 140 m; AAU, B, BR, COL, GH, INPA, K, MG, MO (holo—3393678), NY, P, PORT, U, US, VEN.

Faramea brevipes Steyerm., Mem. New York Bot. Gard. 17(1): 381. 1967. *Forest Dept. Field No. Fanshawe 877*; 10 July 1942; Guyana, Keriti Creek; K (holo).

Faramea cardonae Standl. & Steyerm., Fieldiana Bot.

28(3): 574. 1953. *F. Cardona P. 1115*; 10 July 1944; Venezuela, Bolívar, Cerro Guaiquinima, Alto Río Paragua; 1,200 m; F (holo), US.

Faramea cazaderensis Steyerm., Ann. Missouri Bot. Gard. 74: 398. 1987. *H. van der Werff & R. Ortiz 5457*; 22 July 1983; Venezuela, Táchira, Dept. Lobertera, La Cazadera; 2,000 m; MO (holo), VEN.

Faramea costata Steyerm., Mem. New York Bot. Gard. 17(1): 389. 1967. *J. & P. A. Florschutz 1180*; 5 Feb. 1951; Suriname, Saramacca River, upstream of Awana Falls; NY (holo).

Faramea fanshawei Steyerm., Mem. New York Bot. Gard. 17(1): 380. 1967. *B. Maguire & D. B. Fanshawe 32329*; 26 Oct. 1951; Guyana, Kamarang Station, upper Mazaruni River; 500 m; NY (holo).

Faramea garciae Steyerm., Bol. Soc. Venez. Ci. Nat. 25(106): 72. 1963. *J. Garcia 80*; 21 June 1951; Venezuela, Aragua, Rancho Grande; 1,100 m; VEN (holo).

Faramea irwinii Steyerm., Mem. New York Bot. Gard. 17(1): 379. 1967. *Forest Dept. Field No. G569*; 9 Nov. 1952; Guyana, Sierra Irikoume, Acari Mountains; NY (holo).

Faramea larensis Steyerm., Mem. New York Bot. Gard. 17(1): 382. 1967. *B. Trujillo 2763*; 22 Aug. 1954; Venezuela, Lara, Morterito, Estación Experimental de Sanare; 1,600 m; MY (holo).

Faramea lourteigiana Steyerm., Bradea 1(16): 147. 1972, nom. nov.

Faramea maguirei Steyerm., Mem. New York Bot. Gard. 17(1): 396. 1967. *B. Maguire & D. B. Fanshawe 32357*; 29 Oct.–4 Nov. 1951; Guyana, Membaru–Kurupang trail; 1,000 m; NY (holo).

Faramea morilloi Steyerm., Ann. Missouri Bot. Gard. 75: 337. 1988. *G. Morillo 6716*; 17 Nov. 1977; Venezuela, T.F. Amazonas, Parcela Fénologica, 16 km de Cruce con la carretera a Puerta Ayacucho–Sanariapo; 100 m; VEN (holo).

Faramea multiflora A. Rich. var. *epedunculata* Steyerm., Mem. New York Bot. Gard. 17(1): 392. 1967. *H. Pittier 10948*; n.d.; Venezuela, Zulia, Selvas de Río Lora; VEN (holo).

Faramea neblinae Steyerm., Mem. New York Bot. Gard. 17(1): 395. 1967. *B. Maguire et al. 42515*; 25 Dec. 1957; Venezuela, T.F. Amazonas, Cerro de la Neblina, Caño Grande; 1,050–1,100 m; MO (1811401), NY (holo).

Faramea occidentalis (L.) A. Rich. var. *brachycalyx* Steyerm., Mem. New York Bot. Gard. 17(1): 385. 1967. *H. Curran s.n.*; Apr.–May 1916; Colombia, Bolívar, Island of Mompos, Lands of Loba; US (holo).

Faramea occidentalis (L.) A. Rich. subsp. *lonchocalyx* Steyerm., Mem. New York Bot. Gard. 17(1): 385. 1967. *O. Haught 3068*; 6 Feb. 1940; Ecuador, Manabí, near Guale; 250 m; US (holo).

Faramea occidentalis (L.) A. Rich. var. *meridionalis* Steyerm., Mem. New York Bot. Gard. 17(1): 384. 1967. *H. Pittier 12192*; 16 Aug. 1926; Venezuela, Carabobo, Canaobito near Urama; VEN (holo).

Faramea paludicola Steyerm., Ann. Missouri Bot. Gard. 75: 338. 1988. *R. L. Liesner 16960*; 26 Mar. 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, upper Caño Baria; 130 m; MO (holo), NY, VEN.

Faramea parvibractea Steyerm., Mem. New York Bot. Gard. 17(1): 376. 1967. *J. Silverio Level 145*; 12 Sep. 1954; Venezuela, Amazonas, Caño Tama-Tama, Río Orinoco; 150 m; NY (holo).

Faramea pseudospathacea Steyerm., Mem. New York Bot. Gard. 17(1): 383. 1967. *L. Schlim 531*; May 1846–1852; Colombia, Prov. Ocana, Pericos; 1,210 m; F (holo).

Faramea silvae Steyerm., Mem. New York Bot. Gard. 23(1): 389. 1972. *N. T. Silva & U. Brazao 60700*; 21 Dec. 1965; Brazil, Amazonas, Serra de Neblina; 400–600 m; NY (holo), VEN.

Faramea yavitensis Steyerm., Ann. Missouri Bot. Gard. 75: 338. 1988. *Ll. Williams 14026*; 28 Jan. 1942; Venezuela, T.F. Amazonas, Yavita; F (holo), VEN.

Faramea yutajensis Steyerm., Ann. Missouri Bot. Gard. 75: 339. 1988. *R. L. Liesner & B. K. Holst 21640*; 4 Mar. 1987; Venezuela, T.F. Amazonas, 8 km NW of Yutajé, W of Serranía de Yutajé; 1,500–1,760 m; MO (holo—3482984), VEN.

Ferdinandusa boomii Steyerm., Ann. Missouri Bot. Gard. 75: 339. 1988. *B. Boom & A. Weitzman 5274*; 8 Dec. 1984; Venezuela, T.F. Amazonas, Cerro de la Neblina, Base Camp; BR, COL, GH, INPA, K, MO (holo—3393679), NY, PORT, U, VEN.

Ferdinandusa duckei Steyerm., Mem. New York Bot. Gard. 23(1): 284. 1972. *A. Ducke 1167*; 19 Jan. 1943; Brazil, Amazonas, Rio Taruma-miry, Manaos; NY (holo), US.

Ferdinandusa goudotiana Schumann var. *eciliata* Steyerm., Mem. New York Bot. Gard. 23(1): 281. 1972. *R. Schomburgk 955*; n.d.; Venezuela, Bolívar, Roraima; K (holo).

Ferdinandusa goudotiana Schumann var. *psilocarpa* Steyerm., Mem. New York Bot. Gard. 23(1): 281. 1972. *S. S. Tillett et al. 45184*; 7 Aug. 1960; Guyana, Mt. Ayanganna; 900–1,000 m; NY (holo).

Ferdinandusa neblinensis Steyerm., Mem. New York Bot. Gard. 23(1): 283. 1972. *B. Maguire et al. 36800*; 22 Dec. 1953; Venezuela, T.F. Amazonas, Río Yatua, Cerro de la Neblina; 200 m; NY (holo), VEN.

Ferdinandusa schultesii Steyerm., Mem. New York Bot. Gard. 23(1): 279. 1972. *R. E. Schultes & I. Cabrera 14475*; 28 Sep. 1951; Colombia, Amazonas–Vaupés, Río Apaporis, Río Kananan, Cerro Isibukuri; US (holo).

Galium canescens H.B.K. f. *alstonii* Steyerm., Acta Bot. Venez. 8: 253. 1973. *A. H. G. Alston 6533*; 23 Jan. 1939; Venezuela, Mérida, between Timotes & Chachopo; 2,150–2,400 m; NY (holo).

Genipa americana L. var. *caruto* (H.B.K.) K. Schum. f. *jorgensenii* Steyerm. Mem. New York Bot. Gard. 23(1): 350. 1972. *P. Jörgensen 3694*; July 1931; Paraguay, Villarrica; NY (holo).

Genipa spruceana Steyerm., Mem. New York Bot. Gard. 23(1): 353. 1972. *J. Murca Pires & P. B. Cavalcante 52451*; 10 Aug. 1962; Brazil, Amapá, Terr. Amapa, Lago Cujubim; NY (holo).

Geophila cordifolia Miq. var. *peruviana* Steyerm., Mem. New York Bot. Gard. 23(1): 393. 1972. *E. P. Killip & A. C. Smith 26780*; 20–21 July 1929; Perú, Dept. Junin, Cahuapanas, on Río Pichis; 340 m; NY (holo), US.

Geophila croatii Steyerm., Phytologia 35(6): 401. 1977. *T. B. Croat 6647*; 3 Oct. 1968; Panama Canal Zone, Barro Colorado Island, Zetek trail; MO (holo).

Geophila harleyi Steyerm., ined.? *R. M. Harley et al. 15006*; 10 Jan. 1974; Brazil, Bahía, Itabuna, in the grounds of Centro de Pesquisas do Cacau; MO (iso—2417113).

Geophila orbicularis (Muell. Arg.) Steyerm. var. *neblinae* Steyerm., Mem. New York Bot. Gard. 23(1): 398.

1972. *B. Maguire et al. 36975*; 29 Dec. 1953; Venezuela, T.F. Amazonas, Río Yatua, Cerro de la Neblina; 650 m; NY (holo), VEN.

Geophila prancei Steyerm., Mem. New York Bot. Gard. 23(1): 393. 1972. *G. T. Prance et al. 8985*; 29 Nov. 1968; Brazil, Terr. Rondonia, Serro do Tres Irmãos; NY (holo), VEN.

Gleasonia duidana Standl. var. *latifolia* Steyerm., Mem. New York Bot. Gard. 17(1): 239. 1967. *B. Maguire & C. K. Maguire 35344*; 27 Feb. 1953; Venezuela, T.F. Amazonas, Cerro Yutaje, Camp Yutaje; 1,300 m; GH, NY (holo), U, VEN.

Gleasonia duidana Standl. var. *oblanceolata* Steyerm., Mem. New York Bot. Gard. 17(1): 239. 1967. *F. Cardona 1610*; 26 June 1946; Venezuela, Bolívar, Cerro Apacara, Caroni; 800–900 m; NY, VEN (holo) = *G. duidana* Standl. var. *duidana*, 1984.

Gonzalagunia ciliata Steyerm., Acta Bot. Venez. 6: 123. 1971. *J. Saer 635*; Aug. 1930; Venezuela, Lara, Distr. Cabudare, Serranias de Terepaima; 800–1,000 m; VEN (holo).

Gonzalagunia dicocca Cham. & Schlecht. var. *guianensis* Steyerm., Mem. New York Bot. Gard. 23(1): 315. 1972. *B. Maguire & D. B. Fanshawe 32456*; 8 Nov. 1951; Guyana, Paruima Falls to Paruima Mission; 600 m; NY (holo), VEN.

Gonzalagunia dicocca Cham. & Schlecht. subsp. *venezuelensis* Steyerm., Mem. New York Bot. Gard. 23(1): 315. 1972. *A. Allart 225*; Nov. 1924; Venezuela, Miranda, Quebrada de las Comadres; 800 m; VEN (holo).

Guettarda bernardii Steyerm., Acta Bot. Venez. 6: 128. 1971. *L. Bernardi 2011*; 21. Feb. 1955; Venezuela, Barinas, Mun. Pedraza, Alto de Aguada-Los Piedrones; 1,200 m; NY (holo).

Guettarda crispiflora Vahl var. *venezuelensis* Steyerm., Acta Bot. Venez. 6: 129. 1971. *H. Pittier 9967*; 25 Dec. 1921; Venezuela, Aragua, Colonia Tovar; 1,900–2,000 m; VEN (holo).

Guettarda fanshawei Steyerm., Mem. New York Bot. Gard. 23(1): 359. 1972. *D. B. Fanshawe 1255* (*Rec.* 3991); 21 Apr. 1943; Guyana, Groete Creek, Lower Essequibo River; NY (holo).

Guettarda leiantha Steyerm., Ann. Missouri Bot. Gard. 71: 1175. 1984. *J. A. Steyermark et al. 122318*; 12 May 1980; Venezuela, T.F. Amazonas, along road between Paso El Diablo and Caño de Culebra, 20–30 km SE of Puerto Ayachcho; 100 m; MO, VEN (holo).

Guettarda steyermarkii Standl. f. *latior* Standl. & Steyerm., Fieldiana Bot. 28(3): 578. 1953. *J. A. Steyermark 55965*; 20 Apr. 1944; Venezuela, Mérida, Hacienda El Joque of Dr. Ricardo Sargent, above Jaji; 2,195 m; F (holo) = *G. steyermarkii* Standl. f. *steyermarkii*, 1972.

Guettarda steyermarkii Standl. f. *pilosior* Steyerm., Acta Bot. Venez. 6: 131. 1971. *E. L. Little 15372*; 22 July 1953; Venezuela, Mérida, 40 km ESE of Tabay, 5 km E of San Juan Bautista; VEN (holo).

Henriquezia nitida Spruce ex Benth. var. *subcuneata* Steyerm., Mem. New York Bot. Gard. 10(5): 207. *R. L. Fróes 22885*; 18 Nov. 1947; Brazil, Rio Negro, Preto, Campina; NY (holo), US = *H. nitida* Spruce var. *macrophylla* (Ducke) Steyerm., 1984.

Henriquezia verticillata Spruce ex Benth. in Hook. var. *apiculata* Steyerm., Mem. New York Bot. Gard. 10(5): 204. 1963. *A. Ducke 81*; 19 Dec. 1935; Brazil, Amazonas, Manaos; A, F, MO, NY, R, US (holo) = *H. verticillata* Spruce var. *verticillata*, 1984.

Hillia bonoi Steyerm., Ernstia 42: 5. 1987. *J. Bono 3797*; 2 Apr. 1984; Venezuela, Táchira, Dept. Junín, Rubio y Las Delicias; 2,000 m; VEN (holo).

Hillia costanensis Steyerm., Mem. New York Bot. Gard. 23(1): 293. 1972. *J. A. Steyermark 99274*; 20 July 1967; Venezuela, Falcón, Sierra de San Luis; 800–900 m; VEN (holo).

Hillia foldatsii Steyerm., Mem. New York Bot. Gard. 23(1): 290. 1972. *E. Foldats 7192*; 17 Aug. 1968; Venezuela, Bolívar, Auyantepuy, Valle de Orquideas; 1,200 m; VEN (holo).

Hillia irwinii Steyerm., Mem. New York Bot. Gard. 23(1): 287. 1972. *W. A. Egler & H. S. Irwin 46683*; 26 Aug. 1961; Brazil, Terr. Amapá, near Cachoeira Macacoara, Rio Jari; 200 m; NY (holo).

Hillia macrocarpa Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 23. 1943. *J. A. Steyermark 33667*; Jan. 1940; Guatemala, Dept. Quezaltenango, Volcán Santa María, between Santa María de Jesús and Calahuache; 1,300-1,500 m; F (holo).

Hillia maguirei Steyerm., Mem. New York Bot. Gard. 10(5): 209. 1963. *B. Maguire & C. K. Maguire 35287*; 17–19 Feb. 1953; Venezuela, T.F. Amazonas, Serranía Yutaje, Río Manapiare; 1,750 m; NY (holo).

Hillia marcano-bertii Steyerm., Pittieria 9: 6. 1986. *L. Marcano Berti & L. Pena 519-979*; 5 Dec. 1979; Venezuela, Táchira, Mun. Lobatera, Parque 'Cazadero', carretera Palo Grande–Minas de Barbon de Lobatera; MER, VEN (holo).

Hillia microcarpa Steyerm., Mem. New York Bot. Gard. 23(1): 292. 1972. *J. A. Steyermark 56591*; 18 May 1944; Venezuela, Mérida, above Tabay; 2,285–2,745 m; F (holo), VEN.

Hillia psammophila Steyerm., Mem. New York Bot. Gard. 10(5): 211. 1963. *J. A. Steyermark & S. Nilsson 392*; 20 Apr. 1960; Venezuela, Bolívar, vicinity of camp 125 at km 125 between Luepa and Cerro Venamo, vicinity of Cerro Uei; 1,100 m; NY, VEN (holo).

Hillia schultesii Steyerm., Mem. New York Bot. Gard. 23(1): 286. 1972. *R. E. Schultes & I. Cabrera 13075*; 18 July 1951; Colombia, Amazonas-Vaupés, mouth of Pacoa, Río Apaporis; 250 m; US (holo).

Hillia wurdackii Steyerm., Mem. New York Bot. Gard. 23(1): 294. 1972. *P. C. Hutchinson & J. K. Wright 6799*; 8 Oct. 1964; Perú, Dept. Amazonas, Prov. Bongara, 5 km N of N end of Pomacocha (lake) on road to Rioja; 2,000 m; VEN (holo).

Hillia zuliaensis Steyerm., Ann. Missouri Bot. Gard. 71: 1176. 1984. *J. A. Steyermark et al. 122876*; 29 May 1980; Venezuela, Zulia, Mara, vicinity of Río Guasare, between Rancho 505 and Cerro Yolanda; 200–270 m; MO, VEN (holo).

Hindsia Benth. ex Lindl. sect. *Brevicalyx* Steyerm., Brittonia 30: 34. 1978, sect. nov.

Hindsia irwinii Steyerm., Brittonia 30: 34. 1978. *H. S. Irwin et al. 23537*; 19 Feb. 1969; Brazil, Minas Gerais, ca. 15 km W of Grão Mogol, Serra do Espinhaco; 950 m; MO (2817604), NY, UB (holo), VEN.

Hippotis grandiflora Steyerm., Acta Bot. Venez. 1(1): 92. 1965. *O. Haught 5400*; 28 Dec. 1946; Colombia, Dept. Cauca, Valle de San Juan de Micay; 100 m; US (holo).

Hippotis lasseri Steyerm., Acta Bot. Venez. 1(1): 89. 1965. *H. Pittier 14103*; 8, 29 Aug. 1937; Venezuela,

Aragua, selvas nubladas de valle de Ocumare, cerca de Rancho Grande; 1,000 m; VEN (holo).

Hippotis latifolia Steyerm., Acta Bot. Venez. 1(1): 94. 1965. *J. J. Wurdack 1817*; 3–4 Sep. 1962; Perú, Dept. Amazonas, Prov. de Bagua, Valle del Río Marañon arriba de las Cascadas de Mayasi cerca del Campamento stte Montenegro; 450 m; US (holo).

Hippotis subelongata Steyerm., Acta Bot. Venez. 1(1): 90. 1965. *G. Klug 3084*; May 1933; Peru, Dept. Loreto, Balsapuerto; 220 m; US (holo).

Hippotis wurdackii Steyerm., Acta Bot. Venez. 1(1): 96. 1965. *J. J. Wurdack 2089*; 4–7 Oct. 1962; Peru, Dept. Loreto, Prov. de Alto Amazonas, del Río Marañon cerca de Temente Punglo, justamente arriba de Pongo de Manseriche; 250–300 m; US, VEN (holo).

Hoffmannia aroensis Steyerm., Pittieria 4: 17. 1972. *J. A. Steyermark & G. Wessels-Boer 100400*; 13 Nov. 1967; Venezuela, Yaracuy, Cerro Negro, Sierra de Aroa, arriba de San Felipe; 1,100–1,250 m; VEN (holo).

Hoffmannia bernardii Steyerm., Pittieria 4: 20. 1972. *A. L. Bernardi 3180*; 12 May 1956; Venezuela, Mérida, Portachuelo a lo largo del Cacique; 950–1,100 m; NY (holo).

Hoffmannia bernardii Steyerm. var. *aracalensis* Steyerm., Pittieria 4: 20. 1972. *B. Trujillo & G. S. Bunting 7594*; 30 May 1967; Venezuela, Yaracuy, Aracal; 600–800 m; NY (holo).

Hoffmannia costensis Standl. & Steyerm., Fieldiana Bot. 28(3): 578. 1953. *J. A. Steyermark 62542*; 5 May 1945; Venezuela, Sucre, above La Trinidad; 2,100–2,200 m; F (holo) = *H. triosteoides* Standl. & Steyerm. subsp. *costensis* (Standl. & Steyerm.) Steyerm., 1972.

Hoffmannia huehueteca Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 249. 1947. *J. A. Steyermark 51697*; 31 Aug. 1942; Guatemala, Dept. Huehuetenango (Sierra de los Cuchumatanes), Cerro Negro; 1,600–2,000 m; F (holo).

Hoffmannia larensis Steyerm., Pittieria 4: 20. 1972. *J. A. Steyermark et al. 103322*; 3 Aug. 1970; Venezuela, Lara, Distr. Palavecino, Terepaima, 20 km S de Cabudare; 1,200–1,300 m; VEN (holo).

Hoffmannia parvifolia Steyerm., Bol. Soc. Venez. Ci. Nat. 25(107): 231. 1964. *J. J. Wurdack 911*; 19 July 1962; Peru, Dept. Amazonas, Prov. Bongara, NW of Pomacocha; 2,300–2,700 m; US, VEN (holo).

Hoffmannia pauciflora Standl. subsp. *venezuelensis* Steyerm., Pittieria 4: 25. 1972. *F. Breteler 3463*; 20 Dec. 1963; Venezuela, Mérida, La Mucuy, 15 mi. NE of Mérida; 2,350 m; VEN (holo).

Hoffmannia quadrifolia Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 250. 1947. *J. A. Steyermark 42600*; 12–13 Jan. 1942; Guatemala, Dept. Zacapa, Sierra de las Minas, Monte Virgen; 2,400 m; F (holo).

Hoffmannia racemifera Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 249. 1947. *J. A. Steyermark 41910*; 25 Dec. 1941; Guatemala, Dept. Izabal, Cerro San Gil; 300–900 m; F (holo).

Hoffmannia stenocarpa Steyerm., Pittieria 4: 21. 1972. *J. A. Steyermark & G. Wessels-Boer 100402*; 13 Nov. 1967; Venezuela, Yaracuy, Sierra de Aroa, Cerro Negro, arriba de San Felipe; 1,100–1,250 m; depository not designated.

Hoffmannia terepaimensis Steyerm., Pittieria 4: 24. 1972. *J. A. Steyermark et al. 103352*; 14 Aug. 1970; Venezuela, Laro, La Toma, Loma Redonda, S of Terepaima, 23 km S of Babudare; 1,100 m; VEN (holo).

Hoffmannia tuerckheimii Donn. Sm. var. *glabra* Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 250. 1947. *J. A. Steyermark 43806*; 10 Feb. 1942; Guatemala, Dept. El Progresso, Sierra de las Minas, Montaña Canahuí; 1,600–2,300 m; F (holo).

Hoffmannia vulcanicola Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 251. 1947. *J. A. Steyermark 47931*; 20 June 1942. Guatemala, Dept. Sololá, S Volcán Atitlán, above Finca Moca; 1,000–1,250 m; F (holo).

Holstianthus Steyerm., Ann. Missouri Bot. Gard. 73: 495. 1986, gen. nov.

Holstianthus barbigularis Steyerm., Ann. Missouri Bot. Gard. 73: 495. 1986. *J. A. Steyermark & B. K. Holst 130637*; 23–24 Feb. 1985; Venezuela, T.F. Amazonas, Dept. Atabapo, above Caño Negro, Cerro Marahuaca; 1,220–1,350 m; MO (holo), VEN.

Houstonia pusilla Schoepf. f. *rosea* Steyerm., Rhodora 41: 585. 1939. *J. A. Steyermark 4599a*; 17 Apr. 1937; U.S.A., Missouri, Pulaski Co., along road D, 4 mi. W of Jerome; F (holo), MO.

Isertia haenkeana DC. var. *mirandensis* Steyerm., Mem. New York Bot. Gard. 17(1): 298. 1967. *J. A. Steyermark 87079*; 11 Sep. 1960; Venezuela, Miranda, Parque Nacional de Guatopo; 500 m; VEN (holo).

Isertia parviflora Vahl var. *hirta* Steyerm., Mem. New York Bot. Gard. 17(1): 295. 1967. *Forest Dept. Field No. WB388*; Oct. 1948; Guyana, Wabuwak, Kanuku Mountains; 605 m; NY (holo).

Isertia wilhelminensis Steyerm., Mem. New York Bot. Gard. 17(1): 296. 1967. *H. S. Irwin et al. 54949*; 22 Aug. 1963; Suriname, Wilhelmina Gebergete, Frederik Top, 3 km SE of Juliana Top; 1,050 m; NY (holo).

Ixora agostiniana Steyerm., Acta Bot. Venez. 1(2): 75. 1966. *J. A. Steyermark & G. Agostini 91120*; 19 July 1962; Venezuela, Sucre, Cerro Patao; 800–825 m; VEN (holo).

Ixora aluminicola Steyerm., Mem. New York Bot. Gard. 17(1): 343. 1967. *B. Maguire 40799*; 12 Mar. 1955; Suriname, Nassau Mountains, Marowijne River, Plateau C; 400–550 m; NY (holo).

Ixora amapaënsis Steyerm., Mem. New York Bot. Gard. 23(1): 386. 1972. *J. Murca Pires et al. 51210*; 25 Sep. 1961; Brazil, Amapá, Rio Araguari, Serra do Navio; VEN (holo).

Ixora intropilosa Steyerm., Mem. New York Bot. Gard. 17(1): 352. 1967. *S. S. & C. Tillett et al. 45085*; 10 Aug. 1960; Guyana, Base Camp to Thompson Camp, Mt. Ayanganna; 760–1,400 m; NY (holo).

Ixora piresii Steyerm., Mem. New York Bot. Gard. 17(1): 384. 1967. *J. Murca Pires et al. 50632*; 1 Sep. 1961; Brazil, Amapá, Rio Araguari; NY (holo).

Ixora potaroensis Steyerm., Mem. New York Bot. Gard. 17(1): 348. 1967. *D. B. Fanshawe 1147* (Field. No.): 26 Jan. 1943; Guyana, Kakaralli-Clump Eagle Mt., Potaro River; K (holo).

Ixora sandwithiana Steyerm., Mem. New York Bot. Gard. 17(1): 344. 1967. *R. Spruce 937*; June 1850; Brazil, Pará, Tapajoz, Santarem; K (holo).

Ixora yavitensis Steyerm., Mem. New York Bot. Gard. 23(1): 386. 1972. *J. A. Steyermark & G. S. Bunting 102858*; 21 Apr. 1970; Venezuela, along road between Yavita and Pimichin, 1 km from Yavita; 125 m; NY, VEN (holo).

Joosia subg. *Sectocalyx* Steyerm., Brittonia 27: 252. 1975, subg. nov.

Joosia aequatoria Steyerm., Brittonia 27: 257. 1975.

J. A. Steyermark 54506; 9 Oct. 1943; Ecuador, Santiago-Zamora, Quebrada Achupallas; F (holo), US.

Joosia macrocalyx Standl. ex Steyerm., Brittonia 27: 259. 1975. *Ownbey 2739*; 25 Mar. 1944; Ecuador, Napo-Pastaza, ridge S of Río Pano, Cordillera de Guacamayos, Archidona-Tena region; 1,605 m; F (holo), NY, US.

Joosia standleyana Steyerm., Brittonia 27: 257. 1975. *J. A. Steyermark 54558*; 10 Oct. 1943; Ecuador, Santiago-Zamora, Quebrada Honda, vicinity Rancho Achupallas; 2,500–2,700 m; F (holo), NY, US.

Joosia ulei Steyerm., Brittonia 27: 255. 1975. *E. Ule 6795*; Mar. 1903; Peru, Loreto, Pampas de Ponasa; 1,200 m; G, HBG (holo).

Joosia umbellifera Karst. var. *caucana* Steyerm., Brittonia 27: 254. 1944. *Core 1367*; 27 Sep. 1944; Colombia, Cauca, Río Pinche, near headwaters, NW of Argelia; 1,060 m; NY, US (holo).

Joosia umbellifera Karst. subsp. *macarensis* Steyerm., Brittonia 27: 254. 1975. *Philipson et al. 2072*; 10 Jan. 1950; Colombia, Int. Meta, N Ridge, Central Mountains, Serranía de la Macarena; 1,500 m; F, US (holo).

Joosia umbellifera Karst. var. *occidentalis* Steyerm., Brittonia 27: 254. 1975. *J. Cuatrecasas 14827*; 4 Aug. 1943; Colombia, Valle, Cordillera Occidental, Hoya del Río Anchicaya, El Prado; US (holo).

"*Kotchubaea*" *duckei* Steyerm., Mem. New York Bot. Gard. 10(5): 216. 1963. *A. Ducke 1557*; 5 Apr. 1944; Brazil, Amazonas, São Paulo de Olivenca; F, NY, US (holo). Note: *Kutchubaea* is the correct spelling.

"*Kotchubaea*" *longiloba* Steyerm., Mem. New York Bot. Gard. 10(5): 218. 1963. *J. A. Steyermark 75544*; 24 May 1953; Venezuela, Bolívar, near Río Tirica, lower slopes Chimantá-tepui (Torono-tepui), Chimantá Massif; 1,000 m; F, NY, VEN (holo).

"*Kotchubaea*" *micrantha* Steyerm., Mem. New York Bot. Gard. 10(5): 215. 1963. *E. Foldats 3758*; 7 Sep. 1960; Venezuela, T.F. Amazonas, de Alto Río Atacavi; NY, VEN (holo).

"*Kotchubaea*" *montana* Steyerm., Mem. New York Bot. Gard. 10(5): 217. 1963. *G. Klug 3452*; Dec. 1933; Peru, Dept. San Martín, Zepelacio, near Moyobamba, 1,200–1,600 m; NY (holo).

"*Kotchubaea*" *morilloi* Steyerm., Acta Bot. Venez. 9: 287. 1974. *J. Hoyas & G. Morillo 46*; 7 May 1973; Venezuela, T.F. Amazonas, Cerro Asisa (La Momia), Serranía Parú; 1,310 m; MO (2250699), VEN (holo).

"*Kotchubaea*" *neblinensis* Steyerm., Mem. New York Bot. Gard. 10(5): 216. 1963. *B. Maguire et al. 42084*; 17 Nov. 1957; Venezuela, T.F. Amazonas, Cerro de la Neblina, just N of Camp 3; 650–700 m; NY (holo).

Ladenbergia buntingii Steyerm., Acta Bot. Venez. 6: 99. 1971. *G. S. Bunting 4509*; 31 July 1971; Venezuela, Yaracuy, Cerro La Chapa; MO (holo—3399535), MY, VEN.

Ladenbergia puberula Steyerm., Mem. New York Bot. Gard. 23(1): 270. 1972. *B. Maguire et al. 42493*; 25 Dec. 1957; Venezuela, T.F. Amazonas, Cerro de la Neblina; 1,050–1,100 m; NY (holo).

Ladenbergia venamoensis Steyerm., Mem. New York Bot. Gard. 23(1): 271. 1972. *J. A. Steyermark & S. Nilsson 426*; 21 Apr. 1960; Venezuela, Bolívar, Cerro Venamo; 1,140 m; VEN (holo).

Maguireocharis Steyerm., Mem. New York Bot. Gard. 23(1): 230. 1972, gen. nov.

Maguireocharis neblinae Steyerm., Mem. New York Bot. Gard. 23(1): 230. 1972. *N. T. Silva & U. Brazao 60898*; 26 Jan. 1966; Venezuela, T.F. Amazonas, Sierra Pirapucu; 1,300 m; NY (holo), VEN.

Maguireothamnus Steyerm., Mem. New York Bot. Gard. 10(5): 220. 1963, gen. nov.

Maguireothamnus jauaensis (Steyerm.) Steyerm. var. *breweri* Steyerm., Fl. Venez. 9(1): 311. 1974. *J. A. Steyermark et al. 109765*; 4 Mar. 1974; Venezuela, Bolívar, Cerro Jaua, Meseta del Jaua; 1,750 m; VEN (holo).

Maguireothamnus speciosus (N.E. Br.) Steyerm. subsp. *jauaensis* Steyerm., Mem. New York Bot. Gard. 23: 883. 1972. *J. A. Steyermark 97837*; 22–27 Mar. 1967; Venezuela, Bolívar, Cerro Jaua; VEN (holo) = *M. jauaensis* (Steyerm.) Steyerm., 1974.

Malanea auyantepuiensis Steyerm., Mem. New York Bot. Gard. 12(3): 256. 1965. *J. A. Steyermark 94103*; 18 May 1964; Venezuela, Bolívar, valle de Kamarata, Auyan-tepui; 1,530–1,800 m; NY, US, VEN (holo).

Malanea chimantensis Steyerm., Mem. New York Bot. Gard. 12(3): 259. 1965. *J. A. Steyermark 75166*; 19 Apr. 1953. Venezuela, Bolívar, Chimantá Massif, Abacapa-tepui; 1,400 m; NY (holo).

Malanea ciliolata Steyerm., Mem. New York Bot. Gard. 12(3): 258. 1965. *S. S. Tillett et al. 45081*; 10–12 Aug. 1960; Guyana, upper Mazaruni River basin, Mt. Ayanganna, above Thompson Camp; 1,418–1,525 m; NY (holo).

Malanea cruzii Steyerm., Mem. New York Bot. Gard. 12(3): 253. 1965. *J. S. de la Cruz 2164*; 22 Sep. 6 Oct. 1922; Guyana, upper Mazaruni River; NY (holo).

Malanea egleri Steyerm., Mem. New York Bot. Gard. 12(3): 260. 1965. *A. Egler & J. Murca Pires et al. 47729*; 22 Aug. 1960; Brazil, Terr. Amapá, 0.5 km E of confluence with Rio Oiapoque; NY (holo).

Malanea guaiquinimensis Steyerm., Mem. New York Bot. Gard. 12(3): 253. 1965. *F. Cardona 1117*; 10 July 1944; Venezuela, Bolívar, Alto Río Paraqua, Cerro Guaiquinima; 1,200 m; F, US (holo), VEN.

Malanea hypoleuca Steyerm., Mem. New York Bot. Gard. 12(3): 251. 1965. *J. A. Steyermark & L. Aristeguieta 5*; 6–11 Mar. 1962; Venezuela, Bolívar, vicinity of km 110, S of El Dorado; 800–1,200 m; VEN (holo).

Malanea jauaensis Steyerm., Mem. New York Bot. Gard. 23: 885. 1972. *J. A. Steyermark 97857*; 22–27 Mar. 1967; Venezuela, Bolívar, Cerro Jaua; 1,922–2,100 m; VEN (holo).

Malanea macrophylla Bartl. f. *cuneata* Steyerm., Mem. New York Bot. Gard. 12(3): 250. 1965. *A. C. Smith 2618*; 21–26 Nov. 1937; Guyana, ca. 150 mi. from mouth, basin of Kuyuwini River (Essequibo tributary); NY (holo).

Malanea microphylla Standl. & Steyerm., Fieldiana Bot. 28(3): 582. 1953. *J. A. Steyermark 60875*; 7 Dec. 1944; Venezuela, Bolívar, Carrao-tepui; 2,130–2,430 m; F (holo).

Malanea pariensis Steyerm., Mem. New York Bot. Gard. 12(3): 248. 1965. *J. A. Steyermark & G. Agostini 91126*; 19 July 1962; Venezuela, Sucre, Peninsula de Paria, NE de Guiria, N de Puerto de Hierro, Cerro Patao; 800–825 m; VEN (holo).

Malanea ptariensis Steyerm., Mem. New York Bot. Gard. 12(3): 255. 1965. *J. A. Steyermark 59548*; 30 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 2,285–2,405 m; F (holo), NY, US, VEN.

Malanea sanluisensis Steyerm., Acta Bot. Venez. 6: 133. 1971. *J. A. Steyermark 99363*; 21 July 1967; Ven-

ezuela, Falcón, Sierra de San Luis; 1,300 m; VEN (holo).

Malanea sarmentosa Aublet f. *sparsipilosa* Steyerm., Mem. New York Bot. Gard. 12(3): 257. 1965. *A. C. Smith 3066*; 15–17 Feb. 1938; Guyana, Parabaru Savanna, between Rupununi & Kuyuwini rivers; NY (holo).

Malanea sarmentosa Aublet f. *tomentosa* Steyerm., Mem. New York Bot. Gard. 12(3): 258. 1965. *B. Maguire 24874*; 30 Sep. 1944; Suriname, Saramacca River headwaters, between camps 3 and 2; NY (holo).

Malanea schomburgkii Steyerm., Mem. New York Bot. Gard. 12(3): 261. 1984, nom. nov.

Malanea setulosa Steyerm., Mem. New York Bot. Gard. 12(3): 260. 1965. *J. A. Steyermark 58558*; 24 Sep. 1944; Venezuela, Bolívar, stream tributary to Río Kukenan at base of Mt. Roraima; 1,185–1,280 m; F, NY (holo), VEN.

Malanea sipapoensis Steyerm., Mem. New York Bot. Gard. 12(3): 252. 1965. *B. Maguire & L. Politi 28743*; 2 Feb. 1949; Venezuela, T.F. Amazonas, Cerro Sipapo (Paraque), near Intermediate Camp; 600 m; NY (holo).

Malanea subtruncata Steyerm., Mem. New York Bot. Gard. 12(3): 258. 1965. *A. Ducke 1943*; 29 Apr. 1946; Brazil, Pará, Belem Bosque Municipal; NY (holo), US.

Malanea tafelbergensis Steyerm., Mem. New York Bot. Gard. 12(3): 251. 1965. *B. Maguire 24530*; 28 Aug. 1944; Suriname, Tafelberg, Savanna No. 8; 776 m; NY (holo).

Malanea ueiensis Steyerm., Mem. New York Bot. Gard. 12(3): 255. 1965. *J. A. Steyermark & S. Nilsson 385*; 20–22 Apr. 1960; Venezuela, Bolívar, between Luepa and Cerro Venamo, vicinity of road campamento 125, vicinity of Cerro Uei; 1,100 m; VEN (holo).

Manettia Mutis ex L. sect. *Irwinianthus* Steyerm., Brittonia 30: 36. 1978, sect. nov.

Manettia badilloi Steyerm., Mem. New York Bot. Gard. 23(1): 248. 1972. *V. Badillo 3126*; 4 July 1952; Venezuela, Aragua, Alto de Choroní; MAY (holo), VEN.

Manettia bernardii Steyerm., Acta Bot. Venez. 6: 104. 1971, also Mem. New York Bot. Gard. 23(1): 245. 1972. *L. Bernardi 611*; 14 June 1953; Venezuela, Mérida, Sierra Nevada de Mérida; 2,200 m; NY (holo).

Manettia breteleri Steyerm., Acta Bot. Venez. 6: 103. 1971, also Mem. New York Bot. Gard. 23(1): 244. 1972. *F. J. Breteler 4089*; 11 Aug. 1964; Venezuela, Trujillo, Boconó along road to Biscucuy; 1,850 m; MO (2417037), VEN (holo).

Manettia coccocypseloides Wernham var. *glabrior* Steyerm., Acta Bot. Venez. 6: 107. 1971, also Mem. New York Bot. Gard. 23(1): 248. 1972. *J. A. Steyermark & M. Rabe 97071*; 31 Aug. 1966; Venezuela, Mérida, E of Jaji & SE of La Carbonera; 1,900–2,100 m; VEN (holo).

Manettia honigii Steyerm., Phytologia 31(6): 483. 1975. *S. S. Tillett & K. W. Hönig 738-366*; 23 Aug. 1973; Venezuela, Mérida, Distr. Rivas Davila, 2 km above Las Tapias, S of Bailladores, Sierra de Tovar, Cordillera de Mérida; 2,275 m; VEN (holo).

Manettia irwinii Steyerm., Brittonia 30: 36. 1978. *H. S. Irwin et al. 18688*; 17 Jan. 1968; Brazil, Minas Gerais, 15 km N of Corumba de Goiás on road to Niquelandea; 1,150 m; MO (2817602), NY, UB (holo), VEN.

Manettia lindenii Sprague f. *appendiculata* Steyerm., Acta Bot. Venez. 6: 102. 1971, also Mem. New York Bot. Gard. 23(1): 243. 1972. *J. A. Steyermark & M. Rabe 97239*; 3–4 Sep. 1966; Venezuela, Trujillo, 30 km from Boconó; 2,300–2,500 m; MO (2270190), VEN (holo).

Manettia paramorum Steyerm., Acta Bot. Venez. 6: 104. 1971, also Mem. New York Bot. Gard. 23(1): 245. 1972. *L. Bernardi 1248*; 16 May 1954; Venezuela, Mérida, Páramo de los Conojos; 3,100 m; NY (holo).

Manettia tachirensis Steyerm., Acta Bot. Venez. 6: 105. 1971, also Mem. New York Bot. Gard. 23(1): 246. 1972. *J. A. Steyermark & M. Rabe 96736*; 28 Aug. 1966; Venezuela, Táchira, E of Zumbador; 1,700 m; VEN (holo).

Manettia tamaensis Steyerm., Acta Bot. Venez. 6: 106. 1971, also Mem. New York Bot. Gard. 23(1): 247. 1972. *J. A. Steyermark et al. 98298*; 15–16 May 1967; Venezuela, Táchira, entre Bramon y Las Delicias; 1,750 m; VEN (holo).

Manettia tillettii Steyerm., Phytologia 31(6): 484. 1975. *S. S. Tillett & K. W. Hönig 746-501*; 24–26 June 1974; Venezuela, Zulia, Distr. Perijá, Sierra de Perijá, Serranía de los Motilones, headwaters of Río Tocuco, Campamento Frontier I; 1,900–2,000 m; VEN (holo).

Meruma Steyerm., Mem. New York Bot. Gard. 23(1): 232. 1972, gen. nov.

Meruma coccocypseloides Steyerm., Mem. New York Bot. Gard. 23(1): 233. 1972. *B. Maguire & L. Politi 28243*; 8 Jan. 1949; Venezuela, Amazonas, Cerro Sipapo (Paraque); 1,600 m; NY (holo), VEN.

Meruma plicata Steyerm., Mem. New York Bot. Gard. 23(1): 235. 1972. *S S. Tillett et al. 43944*; 1 July 1960; Guyana, Merume Mountains, Merume Mt., upper Mazaruni River basin, Partang River; 1,140 m; NY (holo), VEN.

Mitracarpus frigidus (Willd.) Schumann var. *andinus* Steyerm., Mem. New York Bot. Gard. 23: 779. 1972. *O. Kuntze 1643*; 21 May 1874; Venezuela, Distr. Federal, Silla de Caracas; NY (holo).

Mitracarpus frigidus (Willd.) Schumann var. *orinocensis* Steyerm., Mem. New York Bot. Gard. 23: 780. 1972. *J. J. Wurdack & L. Adderley 42698*; 30 May 1959; Venezuela, T.F. Amazonas, Río Orinoco, Sabanita Morocoto; 125–150 m; NY (holo), VEN.

Mitracarpus frigidus (Willd.) Schumann var. *peruvianus* Steyerm., Mem. New York Bot. Gard. 23: 780. 1972. *E. L. Evinger 513*; 21 Aug. 1943; Peru, Dept. Amazonas, 10 km E of Balzas; 2,300 m; NY (holo), US, VEN.

Mitracarpus pusillus Steyerm., Brittonia 30: 36. 1978. *H. S. Irwin et al. 27120*; 7 Mar. 1970; Brazil, Minas Gerais, Serra do Cabral, ca. 8 km W of Joaquim Felicio; 1,200 m; NY, UB (holo).

Morinda longipedunculata Steyerm., Ann. Missouri Bot. Gard. 75: 340. 1988. *G. Davidse & J. S. Miller 27327*; 9–14 July 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro de la Neblina, Cañon Grande; 350–400 m; MO (holo), VEN.

Neblinathamnus Steyerm., Mem. New York Bot. Gard. 10(5): 229. 1963, gen. nov.

Neblinathamnus aracamunianus Steyerm., Ann. Missouri Bot. Gard.: in press. 1989. *R. L. Liesner & F. Delascio 22153*; 19 Oct. 1987; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp; 1,550 m; MO (holo), VEN.

Neblinathamnus argyreus Steyerm., Mem. New York Bot. Gard. 10(5): 229. 1963. *B. Maguire et al. 42120*;

16 Nov. 1957; Venezuela, T.F. Amazonas, Cerro de la Neblina; NY (holo).

Neblinathamnus brasiliensis Steyerm., Mem. New York Bot. Gard. 23(1): 309. 1972. *N. T. Silva & U. Brazao 60907*; 26 Jan. 1966; Brazil, Amazonas, Serra Pirapucú; 1,300 m; NY (holo).

Neblinathamnus glabratus Steyerm., Mem. New York Bot. Gard. 10(5): 231. 1963. *B. Maguire et al. 37011*; 30 Dec. 1953; Venezuela, T.F. Amazonas, Cerro de la Neblina; NY (holo).

Pagamea acrensis Steyerm., Brittonia 33: 385. 1981. *N. A. Rosa 706*; 10 Feb. 1976. Brazil, Acre, Cruziero do Sul, Projecto RADAM-Ponto 10-SB-18-2D; IAN, VEN (holo).

Pagamea anisophylla Standl. & Steyerm., Fieldiana Bot. 28(3): 584. 1953. *J. A. Steyermark 58461*; 8 Sep. 1944; Venezuela, T.F. Amazonas, Sanariapo; 100 m; F (holo).

Pagamea auyantepuiensis Steyerm., Fieldiana Bot. 28: 584. 1953. *G. H. H. Tate 1365*; Dec. 1937–Jan. 1938; Venezuela, Bolívar, Mt. Auyan-tepui; 2,200 m; F (holo) = *Coryphothamnus auyantepuiensis* (Steyerm.) Steyerm., 1967.

Pagamea brevipedunculata Steyerm., Mem. New York Bot. Gard. 12(3): 283. 1965. *B. Maguire 33070*; 10–12 Jan. 1952; Venezuela, Bolívar, Cerro Guaiquinima, North Valley; 1,600–1,700 m; NY (holo).

Pagamea capitata Benth. subsp. *conferta* (Standl.) Steyerm. f. *breviloba* Steyerm., Mem. New York Bot. Gard. 12(3): 281. 1965. *B. Maguire et al. 29573*; 20 Nov. 1950; Venezuela, T.F. Amazonas, Cerro Duida, Río Cunucunuma, above Culebra; 1,400 m; NY (holo).

Pagamea coriacea Spruce var. *acuta* Steyerm., Mem. New York Bot. Gard. 12(3): 273. 1965. *R. E. Schultes & I. Cabrera 19367*; 14 May 1953; Colombia, Vaupés, Río Vaupés, between Mitu and Jauarete, Yutica; US (holo).

Pagamea coriacea Spruce var. *pubescens* Steyerm., Mem. New York Bot. Gard. 12(3): 273. 1965. *A Ducke 683*; 22 Mar. 1941; Brazil, Amazonas, Rio Negro inferior, Acajutaba; NY, US (holo).

Pagamea diceras Steyerm., Mem. New York Bot. Gard. 12(3): 281. 1965. *R. S. Cowan & J. J. Wurdack 31241*; 4 Feb. 1941; Venezuela, T.F. Amazonas, Serranía Parú; 2,000 m; NY (holo).

Pagamea duidana Standl. & Steyerm., Fieldiana Bot. 28(3): 586. 1953. *G. H. H. Tate 567*; 1 Jan. 1929; Venezuela, T.F. Amazonas, Mt. Duida, Central Camp; 1,600 m; F (holo), NY.

Pagamea dudleyi Steyerm., Phytologia 31(2): 226. 1975. *T. R. Dudley 13543*; 31 July 1969; Perú, Dept. Huanuco, SW slope of Río Llulla Pichas watershed, on ascent of Cerros del Sira; 1,850 m; NA, VEN (holo).

Pagamea guianensis Aublet var. *macrocarpa* Steyerm., Mem. New York Bot. Gard. 12(3): 278. 1965. *E. L. & R. R. Little, Jr. 9533*; 4 Mar. 1945; Colombia, Comisario de Caqueta, 8 km SE of Tres Esquinas, Solano, on Río Caqueta below mouth of Río Orteguaza; 200 m; NY (holo), US.

Pagamea harleyi Steyerm., Kew Bull. 38(2): 317. 1983. *R. Harley et al. 17069*; Jan.–Apr. 1974; Brazil, Bahia; CEPEC (holo), MO (2397731).

Pagamea jauaensis Steyerm., Mem. New York Bot. Gard. 23: 883. 1972. *J. A. Steyermark 97928*; 22–27 Mar. 1967; Venezuela, Bolívar, Cerro Jaua; 1,922–2,100 m; VEN (holo).

Pagamea magniflora Steyerm., Mem. New York Bot. Gard. 12(3): 285. 1965. *B. Maguire 33427*; 15 May 1952; Venezuela, Bolívar, Ilu-tepui, between N Peak and Central Plateau; 2,450–2,550 m; NY (holo).

Pagamea pauciflora Standl. & Steyerm., Fieldiana Bot. 28(3): 588. 1953. *J. A. Steyermark 60888*; 7 Dec. 1944; Venezuela, Bolívar, Carrao-tepui; 2,470–2,500 m; F (holo).

Pagamea plicata Spruce var. *multinervia* Steyerm., Mem. New York Bot. Gard. 12(3): 274. 1965. *L. Bernardi 1690*; 5 Sep. 1954; Venezuela, Bolívar, region de Uriman; 340–380 m; VEN (holo).

Pagamea plicatiformis Steyerm., Mem. New York Bot. Gard. 12(3): 274. 1965. *Ll. Williams 14190*; 9 Feb. 1942; Venezuela, T.F. Amazonas, Alto Río Negro, Guainía, selva de Maroa; 127 m; F (holo).

Pagamea puberula Steyerm., Mem. New York Bot. Gard. 12(3): 276. 1965. *A. Ducke 8462* (*RB22951*); 21 Aug. 1907; Brazil, Pará, Campos do Chicodaca; US (holo).

Pagamea reducta Steyerm., Mem. New York Bot. Gard. 12(3): 283. 1965. *K. D. Phelps & C. B. Hitchcock 366*; 1–15 Feb. 1948; Venezuela; Bolívar, Uaipan-tepui; 1,900 m; NY (holo), VEN.

Pagamea standleyana Steyerm., Fieldiana Bot. 28(3): 589. 1953. *J. A. Steyermark 59634*; 1 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,600 m; F (holo).

Pagamea uniflora Steyerm., Mem. New York Bot. Gard. 12(3): 284. 1965. *J. A. Steyermark 74877*; 13 Apr. 1953; Venezuela, Bolívar, Chimantá Massif, NW part of Abacapa-tepui; depository not designated.

Pagamea velutina Steyerm., Mem. New York Bot. Gard. 12(3): 275. 1965. *B. Maguire & L. Politi 28536*; 21 Jan. 1949; Venezuela, T.F. Amazonas, Cerro Sipapo (Paraque), near Camp Savannah; 1,500 m; NY (holo).

Pagameopsis Steyerm., Mem. New York Bot. Gard. 12(3): 267. 1965, gen nov.

Pagameopsis maguirei Steyerm., Mem. New York Bot. Gard. 12(3): 267. 1965. *J. A. Steyermark & J. J. Wurdack 1020*; 21 Feb. 1955; Venezuela, Bolívar, Chimantá Massif, Torono-tepui, Caño Mojado; 2,030–2,150 m; NY (holo), VEN.

Pagameopsis maguirei Steyerm. subsp. *neblinensis* Steyerm., Mem. New York Bot. Gard. 12(3): 270. 1965. *B. Maguire et al. 37130*; 6 Jan. 1954; Venezuela, T.F. Amazonas, Cerro de la Neblina, 5 km W of Cumbre Camp, summit; 1,900 m; NY (holo).

Pagameopsis maguirei Steyerm. subsp. *neblinensis* Steyerm. var. *angustifolius* Steyerm., Mem. New York Bot. Gard. 12(3): 270. 1965. *B. Maguire et al. 36948*; 27 Dec. 1953; Venezuela, T.F. Amazonas, Cerro de la Neblina, E of Camp 3; 1,700 m; NY (holo), VEN.

Pagameopsis maguirei Steyerm. subsp. *neblinensis* Steyerm. var. *pirapucuensis* Steyerm., Ann. Missouri Bot. Gard. 74: 108. 1987. *N. T. Silva & U. Brazao 60880*; 20 Jan. 1966; Brazil, Serra Pirapucú; 1,300 m; NY (holo). Note: This specimen is also holotype for *Psychotria canescens* Steyerm., however the dates and elevation differ.

Pagameopsis maguirei Steyerm. subsp. *pusillus* Steyerm., Ann. Missouri Bot. Gard. 74: 106. 1987. *R. L. Liesner 16013*; 16–18 Feb. 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro de la Neblina, Camp III, NW Plateau; 1,750–1,850 m; MO (holo—3327370), VEN.

Pagameopsis maguirei Steyerm. subsp. *pusillus* Steyerm. var. *glabrus* Steyerm., Ann. Missouri Bot. Gard. 74: 108. 1987. *E. Cardona 3096*; 5 Dec. 1972;

Venezuela, T.F. Amazonas, summit of Cerro Avispa, Río Siapa; 1,510 m; NY (holo), VEN.

Palicourea aculeifera Steyerm., Acta Bot. Venez. 2: 331. 1967. *J. A. Steyermark 60377*; 20–21 Nov. 1944; Venezuela, Bolívar, Auyan-tepui; 1,065–1,220 m; F, VEN (holo) = *P. longistipulata* subsp. *chrysorrhachis* (Bremek.) Steyerm., 1972.

Palicourea amapaensis Steyerm., Mem. New York Bot. Gard. 23: 765. 1972. *J. Murca Pires et al. 50386*; 20 Aug. 1961; Brazil, Terr. Amapá, near Rio Araguari between Cachoieras Travessão and Santa Maria; NY (holo).

Palicourea angustifolia H.B.K. var. *glabricaulis* Steyerm., Acta Bot. Venez. 6: 174. 1971, also Mem. New York Bot. Gard. 23: 771. 1972. *L. Ruíz Terán & L. E. Rodriquez Poveda 3746*; 10 Mar. 1967; Venezuela, Lara, Distr. Iribarren, Mun. Juarez, La Cuchilla; 1,500 m; VEN (holo).

Palicourea bostrychostachya Steyerm., Acta Bot. Venez. 6: 158. 1971. *Funck & Schlim 1500*; Nov. 1846; Venezuela, Mérida, San Jacinto; P (holo).

Palicourea buntingii Steyerm., Acta Bot. Venez. 6: 148. 1971. *J. A. Steyermark et al. 101900*; 5 Apr. 1968; Venezuela, Apure, Cerro La Cristalina; 300 m; NY, VEN (holo).

Palicourea buntingii Steyerm. var. *glabrior* Steyerm., Acta Bot. Venez. 6: 151. 1971. *L. Bernardi 7437*; 22 Mar. 1959; Venezuela, Zulia, Río Negro; 1,000 m; MER (holo), MO (2763590).

Palicourea canaguensis Steyerm., Acta Bot. Venez. 6: 157. 1971. Type not designated in the original description. Note: Fl. Venez. cites the type as: *J. A. Steyermark 56412*; n.d.; Venezuela, Mérida, Quebrada de Los Salichales, afluente del Río Canaguá, al SO de Canagua; depository not indicated.

Palicourea cardonae Steyerm., Mem. New York Bot. Gard. 23: 759. 1972. *F. Cardona 1383*; 16–24 Feb. 1946; Brazil, Rio Castanho, afluente de Rio Padauiri que cae al Rio Negro; 100–140 m; US (holo).

Palicourea chimo Standl. & Steyerm., Fieldiana Bot. 28(3): 591. 1953. *J. A. Steyermark 55371*; 6 Feb. 1944; Venezuela, Lara, between Las Sabanetas and ridge top by boundary line of Lara–Trujillo, above Humocaro Bajo; 2,600–2,800 m; F (holo) = *Palicourea demissa* Standl. var. *chimo* (Standl. & Steyerm.) Steyerm., 1971.

Palicourea crocea (Sw.) Roemer & Schultes var. *riparia* (Benth.) Griseb. f. *heterodoxa* Steyerm., Mem. New York Bot. Gard. 23: 739. 1972. *J. Lanjouw & J. C. Lindeman 802*; 12 Oct. 1948; Suriname, km 12.2 Moengo; NY (holo), U.

Palicourea ctenocalyx Steyerm., Acta Bot. Venez. 6: 165. 1971. *J. A. Steyermark et al. 100763*; 12 Jan. 1968; Venezuela, Táchira, cabeceras del Río Quinimari; 2,500–2,800 m; VEN (holo).

Palicourea demissa Standl. var. *chimo* (Standl. & Steyerm.) Steyerm. f. *pubens* Steyerm., Acta Bot. Venez. 6: 163. 1971. *J. A. Steyermark & M. Rabe 96816*; 28 Aug. 1966; Venezuela, Táchira, entre Michelena y Boca del Monte; 2,000–2,400 m; VEN (holo).

Palicourea dunstervilleorum Steyerm., Acta Bot. Venez. 6: 175. 1971. *J. A. Steyermark et al. 98810*; 22–24 May 1967; Venezuela, Táchira, Páramo de Tamá; 2,300–2,450 m; VEN (holo).

Palicourea ensiformis Steyerm., Acta Bot. Venez. 6: 172. 1971. *J. A. Steyermark 57192*; 13 July 1944; Venezuela, Táchira, Montaña of Río Táchira at base of Páramo de Tamá; 2,430 m; VEN (holo).

Palicourea flexiramea Steyerm., Acta Bot. Venez. 6: 159. 1971. *R. Velasco & M. Ramia 627*; 2 Apr. 1950; Venezuela, Mérida, entre La Azulita y Ejido; MY (holo).

Palicourea foldatsii Steyerm., Mem. New York Bot. Gard. 23: 777. 1972. *E. Foldats 3670*; 4 Sep. 1960; Venezuela, T.F. Amazonas, Santa Cruz, Río Atabapo; NY, VEN (holo).

Palicourea garciae Steyerm., Acta Bot. Venez. 6: 167. 1971. *F. Garcia 55*; 12 May 1951; Venezuela, Aragua, Fila del Paraiso, Rancho Grande; 1,375 m; VEN (holo).

Palicourea glabriflora Steyerm., Mem. New York Bot. Gard. 23: 735. 1972. *B. Maguire et al. 37490*; 4 Feb. 1954; Venezuela, T.F. Amazonas, Casiquiare, ríos Pacimoni–Yatua, Piedra Tururumeri; 110–220 m; NY (holo).

Palicourea guianensis Aublet subsp. *occidentalis* Steyerm., Mem. New York Bot. Gard. 23: 729. 1972. *De la Cruz 1638*; July 1922; Guyana, between the Demerare and Berbice rivers; NY (holo).

Palicourea guianensis Aublet subsp. *occidentalis* Steyerm. f. *glabra* Steyerm., Mem. New York Bot. Gard. 23: 730. 1972. *F. R. Fosberg 21211*; 10 Oct. 1943; Colombia; Dept. Nariño, along Río Guagui, 1–2 km S of Barbacoas; 40–50 m; NY (holo), US.

Palicourea guianensis Aublet subsp. *occidentalis* Steyerm. var. *glabrescens* Steyerm., Mem. New York Bot. Gard. 23: 730. 1972. *C. Játiva & C. Epling 682*; 8 July 1964; Ecuador, Prov. Esmeraldas, San Lorenzo; UCLA, VEN (holo).

Palicourea huberi Steyerm., Pittieria 9: 8. 1981. *G. Davidse et al. 17359*; 8 May 1979; Venezuela, T.F. Amazonas, Dept. Atabapo, Caño Yagua at Cucurital de Yagua; 120 m; MO, VEN (holo).

Palicourea insignis Steyerm., Acta Bot. Venez. 6: 176. 1971, also Mem. New York Bot. Gard. 23: 776. 1972. *T. Lasser 1221*; 22 Aug. 1944; Venezuela, Trujillo, El Páramo cerca de Escuque; VEN (holo).

Palicourea irwinii Steyerm., Mem. New York Bot. Gard. 23: 758. 1972. *H. S. Irwin et al. 47354*; 5 Aug. 1960; Brazil, Amapá, 5 km SE of Clevelandia; NY (holo).

Palicourea lasseri Steyerm., Acta Bot. Venez. 6: 171. 1971. *T. Lasser 1156*; Aug. 1944; Venezuela, Trujillo, entre Boconó y Trujillo; VEN (holo).

Palicourea meridensis Steyerm., Acta Bot. Venez. 6: 155. 1971. *J. A. Steyermark & M. Rabe 97090*; 1 Sep. 1966; Venezuela, Mérida, Río Capaz, arriba de La Azulita; 2,100–2,400 m; VEN (holo).

Palicourea nana Steyerm., Acta Bot. Venez. 6: 170. 1971. *J. A. Steyermark et al. 101055*; 16 Jan. 1968; Venezuela, Táchira, entre Las Copas y Alto de Fila de Tierra Negra; 2,879–2,880 m; VEN (holo).

Palicourea nubicola Steyerm., Acta Bot. Venez. 6: 168. 1971. *J. A. Steyermark & M. Rabe 97243*; 3–4 Sep. 1966; Venezuela, Trujillo, 30 km from Boconó; 2,300–2,500 m; VEN (holo).

Palicourea perquadrangularis Wernham var. *brevipes* Steyerm., Mem. New York Bot. Gard. 23: 774. 1972. *T. Lasser 1042*; 29 May 1944; Venezuela, Miranda, Guatire, Hacienda El Bautismo; 750–1,200 m; VEN (holo).

Palicourea perquadrangularis Wernham var. *guaya-*

nensis Steyerm., Mem. New York Bot. Gard. 23: 774. 1972. *J. A. Steyermark & J. J. Wurdack 1172*; 27 Feb. 1955; Venezuela, Bolívar, Torono-tepui, Chimantá Massif; 1,880–1,970 m; depository not designated.

Palicourea perquadrangularis Wernham var. *pubens* Steyerm., Mem. New York Bot. Gard. 23: 775. 1972. *J. A. Steyermark & L. Nevling 95934*; 24 June 1966; Venezuela, Distr. Federal, between Portachuelo and Penita (Petaquire) and Carayaca; 1,300–1,500 m; VEN (holo).

Palicourea phanerandra Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 252. 1947. *J. A. Steyermark 41952*; 26–27 Dec. 1941; Guatemala, Dept. Izabal, Cerro San Gil; 1,200 m; F (holo).

Palicourea puberulenta Steyerm., Acta Bot. Venez. 6: 154. 1971. *J. A. Steyermark 105063*; 3 Mar. 1971; Venezuela, Táchira, 3 8 km de Zumbador; 2,650–2,700 m; NY, VEN (holo).

Palicourea pustulata Steyerm., Acta Bot. Venez. 6: 156. 1971, also Mem. New York Bot. Gard. 23: 736. 1972. *J. A. Steyermark 62225*; 19 Apr. 1945; Venezuela, Monagas, Quebrada de Pajarral; 600–900 m; F, VEN (holo).

Palicourea rigida H.B.K. var. *hirtibacca* Steyerm., Mem. New York Bot. Gard. 23: 732. 1972. *Ll. Williams 12073*; 15 May 1939; Venezuela, Bolívar, Bajo Río Caura, Maripa; 80 m; VEN (holo).

Palicourea rigida H.B.K. f. *microphylla* Steyerm., Mem. New York Bot. Gard. 23: 732. 1972. *B. Maguire et al. 44713*; 20 Dec. 1959; Brazil, Minas Gerais, Serra do Cipo; 1,212 m; NY (holo).

Palicourea tachirensis Standl. & Steyerm., Fieldiana Bot. 28(3): 593. 1953. *J. A. Steyermark 57441*; 18 July 1944; Venezuela, Táchira, Alto de Lirio; 1,890–2,285 m; F (holo) = *Psychotria schlimii* Standl., 1972, 1974.

Palicourea tamaensis (Standl. & Steyerm.) Steyerm. var. *psilophylla* Steyerm., Acta Bot. Venez. 6: 153. 1971. *J. A. Steyermark et al. 100940*; 15 Jan. 1968; Venezuela, cabaceras del Río Quinimari, debajo del Cerro Las Copas; 2,500–2,700 m; VEN (holo).

Palicourea tepuicola Steyerm., Mem. New York Bot. Gard. 23: 742. 1972. *J. A. Steyermark 74630*; 25 Mar. 1953; Venezuela, Bolívar, Apacara-tepui, Chimantá Massif; 400 m; MO (2011490), NY (holo), VEN.

Palicourea venezuelensis Steyerm., Acta Bot. Venez. 6: 164. 1971. *J. A. Steyermark 99343*; 21 July 1967; Venezuela, Falcón, Sierra de San Luis; 1,300 m; VEN (holo).

Palicourea vogelii Steyerm., Mem. New York Bot. Gard. 23: 734. 1972. *S. Vogel 312*; 17 Mar. 1956; Colombia, Sierra Macarena; 400 m; M (holo).

Pentagonia grantii Steyerm., Bol. Soc. Venez. Ci. Nat. 25(107): 251. 1964. *M. L. Grant 10567*; 2 Nov. 1944; Colombia, Dept. Cundinamarca, Cordillera del Monte Cristo, 3 km NW of Mambita; 1,350 m; US (holo).

Pentagonia parvifolia Steyerm., Bol. Soc. Venez. Ci. Nat. 25(107): 232. 1964. *J. J. Wurdack 2523*; 2 Nov. 1962; Peru, Dept. Loreto, Prov. de Alto Amazonas, Cerro Campanquiz, Río Marañon; US, VEN (holo).

Pentagonia wurdackii Steyerm., Bol. Soc. Venez. Ci. Nat. 25(107): 233. 1964. *J. J. Wurdack 2435*; 26–28 Oct. 1962; Peru, Dept. Loreto, Prov. Alto Amazonas, Pongo de Manseriche, Río Marañon, 250 m; US (holo).

Perama sect. *Diperma* Kirkbr. & Steyerm., Brittonia 29: 192. 1977, sect. nov.

Perama dichotoma Poepp. & Endl. var. *hirsutula* Steyerm., Mem. New York Bot. Gard. 10(5): 236. 1963. *J. A. Steyermark & S. Nilsson 561*; 24–25 Apr. 1960; Venezuela, Bolívar, vicinity of Camp 150 at km 150 in valley of Río Uarama, NE of Luepa; 1,220 m; VEN (holo).

Perama dichotoma Poepp. & Endl. var. *monocephala* Steyerm., Ann. Missouri Bot. Gard. 74: 658. 1987. *F. Delascio 12358*; 12–14 Oct. 1984; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Huachamacari; VEN (holo), MO (3327364).

Perama galioides (H.B.K.) Poir. var. *densipilia* Steyerm., Mem. New York Bot. Gard. 10(5): 244. 1963. *F. Cardona 1630*; 18 Sep. 1946; Venezuela, Bolívar, Sabanas de Uriman; 400 m; NY, VEN (holo).

Perama galioides (H.B.K.) Poir. var. *hispida* (H.B.K.) Steyerm. f. *cinerea* Steyerm., Mem. New York Bot. Gard. 10(5): 243. 1963. *B. Maguire et al. 30886*; 14 Jan. 1951; Venezuela, T.F. Amazonas, Cerro Moriche, Río Ventuari; 800 m; NY (holo).

Perama galioides (H.B.K.) Poir. var. *intermedia* Steyerm., Mem. New York Bot. Gard. 10(5): 243. 1963. *J. A. Steyermark 59658*; 1 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,600 m; F (holo), VEN.

Perama galioides (H.B.K.) Poir. var. *galioides* f. *macrocephala* Steyerm., Mem. New York Bot. Gard. 10(5): 239. 1963. *R. S. Cowan & J. J. Wurdack 31455*; 15 Feb. 1951; Venezuela, T.F. Amazonas, Cerro Parú near Caño Asisa, Serranía Parú; 200 m; NY (holo).

Perama galioides (H.B.K.) Poir. var. *galioides* f. *quaternata* Steyerm., Mem. New York Bot. Gard. 10(5): 239. 1963. *Ll. Williams 15067*; 27 Apr. 1942; Venezuela, T.F. Amazonas, San Antonio, upper Orinoco; 121 m; F (holo), VEN.

Perama galioides (H.B.K.) Poir. var. *longiflora* Steyerm., Mem. New York Bot. Gard. 10(5): 241. 1963. *J. J. Wurdack & L. Adderley 43692*; 31 July 1959; Venezuela, T.F. Amazonas, Sabana de Mayo, Río Orinoco; 125 m; NY (holo).

Perama harleyi Kirkbr. & Steyerm., Brittonia 29: 192. 1977. *R. M. Harley et al. 16038*; 6 Feb. 1974; Brazil, Bahia, Serro do Sincora, 4 mi. S of Mucuge, on road from Cascaval by the Rio Cumbaca; 900 m; CEPEC (holo), K, NY.

Perama irwiniana Kirkbr. & Steyerm., Brittonia 29: 195. 1977. *W. R. Anderson et al. 35874*; 12 Feb. 1972; Brazil, Minas Gerais, Serra do Espinhaco, E slopes of Pico do Itambe; 1,550 m; NY, UB (holo), VEN.

Perama schultesii Steyerm., Mem. New York Bot. Gard. 23: 832. 1972. *R. E. Schultes & I. Cabrera 20061*; Apr. 1953; Colombia, Vaupés, near headwaters of Río Kuduyari; 272–300 m; US (holo).

Perama sparsiflora Standl., Steyerm. & Kirkbr., Brittonia 29: 196. 1977. *Barreto 1134*; *Brade 4739*; 15 Apr. 1935; Brazil, Minas Gerais, Serra do Cipo; F (holo).

Perama wurdackii Steyerm., Bol. Soc. Venez. Ci. Nat. 25(107): 235. 1964. *J. J. Wurdack 961*; 20 June 1962; Peru, Dept. Amazonas, Prov. Bongara, 3 km S of Pomacocha; 2,400 m; US (holo).

Pittierothamnus Steyerm., Bol. Soc. Venez. Ci. Nat. 23: 93. 1962, gen. nov. = *Amphidasya* Standl., 1972.

Pittierothamnus elineolatus Steyerm., Bol. Soc. Venez. Ci. Nat. 23: 92. 1962. *J. A. Steyermark 86323*; 19 June 1960; Venezuela, Aragua, Parque Nacional Henri Pittier; 1,300 m; VEN (holo) = *Amphidasya venezuelensis* (Standl.) Steyerm., 1972.

Platycarpum decipiens Woodson & Steyerm., Amer. J. Bot. 39: 422. 1952. *Ll. Williams 14587*; 2 Mar. 1943; Venezuela, T.F. Amazonas, San Carlos de Río Negro; 100 m; A, F (holo), MO, NY, RB, US, VEN.

Platycarpum duckei Steyerm., Amer. J. Bot. 39: 422. 1952. *A. Ducke 1005*; 25 Aug. 1942; Brazil, Amazonas, Campo Grande; INPA, K, MO (1263643), NY, R, RB, US (holo).

Platycarpum eglandulosum Steyerm., Mem. New York Bot. Gard. 10(5): 258. 1963. *B. Maguire et al. 40666*; 10 Feb. 1955; Guyana, between Chinowieng and Chi-Chi landing, Mt. Ayanganna, Pakaraima Mountains; 1,000 m; GH, NY (holo), U, US, VEN.

Platycarpum maguirei Steyerm., Mem. New York Bot. Gard. 10(5): 255. 1963. *B. Maguire et al. 42597*; 5 Jan. 1958; Venezuela, T.F. Amazonas, Cerro Neblina; 130–700 m; F, GH, K, MICH, MO (1782963), NY (holo), RB, U, US, VEN.

Platycarpum orinocense Humb. & Bonpl. var. *grandiflorum* Steyerm., Mem. New York Bot. Gard. 10(5): 254. 1963. *R. S. Cowan & J. J. Wurdack 31473*; 15 Feb. 1951; Venezuela, T.F. Amazonas, base of Cerro Parú, Serranía Parú; 200 m; NY (holo), US, VEN.

Platycarpum rhododactylum Woodson & Steyerm., Amer. J. Bot. 39: 423. 1952. *F. Cardona P. 860*; 2–15 Aug. 1943; Venezuela, Bolívar, summit of Cerro Tonoro, near Río Paragua; 700 m; F, MO (holo—1309009), NY, US, VEN.

Platycarpum rugosum Steyerm., Mem. New York Bot. Gard. 10(5): 257. 1963. *J. A. Steyermark & L. Aristeguieta 25*; 7 Mar. 1962; Venezuela, Bolívar, Uei-tepui; 1,340 m; F, NY, US, VEN (holo).

Platycarpum schultesii Steyerm. ex Schultes, Bot. Mus. Leafl. 17(3): 96. 1955. *R. E. Schultes & I. Cabrera 19929*; June 1953; Colombia, Comisara del Vaupés, Río Parana Pichuna (tributary of Río Vaupés); 200 m; F (holo), GH, US.

Pogonopus speciosus Schumann subsp. *sandwithianus* Steyerm., Acta Bot. Venez. 6: 110. 1971. *H. H. Smith 100*; 20 Aug. 1898 1899; Colombia, Dept. Magdalena, Santa Marta, near Bonda; 45 m; NY (holo).

Posoqueria williamsii Steyerm., Mem. New York Bot. Gard. 17(1): 331. 1967. *Ll. Williams 14525*; 2 Feb. 1942; Venezuela, T.F. Amazonas, San Carlos de Río Negro; VEN (holo).

Psychotria L. ser. *Altsonii* Steyerm., Mem. New York Bot. Gard. 23: 555. 1972, ser. nov.

Psychotria L. ser. *Aneurophyllae* Steyerm., Mem. New York Bot. Gard. 23: 545. 1972, ser. nov.

Psychotria L. ser. *Appunianae* Steyerm., Mem. New York Bot. Gard. 23(1): 657. 1972, ser. nov.

Psychotria L. ser. *Crocochlamys* Steyerm., Mem. New York Bot. Gard. 23(1): 593. 1972, ser. nov.

Psychotria L. sect. *Didymocarpos* Steyerm., Mem. New York Bot. Gard. 23: 516. 1972, sect. nov.

Psychotria L. sect. *Durifolia* Steyerm., Mem. New York Bot. Gard. 23: 705. 1972, sect. nov.

Psychotria L. subg. *Heteropsychotria* Steyerm., Mem. New York Bot. Gard. 23: 484. 1972, subg. nov.

Psychotria L. ser. *Mollirami* Steyerm., Mem. New York Bot. Gard. 23: 529. 1972, ser. nov.

Psychotria L. sect. *Potaroensis* Steyerm., Mem. New York Bot. Gard. 23(1): 662. 1972, sect. nov.

Psychotria L. sect. *Pseudocephaelis* Steyerm., Mem. New York Bot. Gard. 23(1): 593. 1972, sect. nov.

Psychotria adderleyi Steyerm., Mem. New York Bot. Gard. 23: 513. 1972. *B. Maguire et al. 60073*; 4 Nov. 1965; Brazil, Amazonas, Rio Cauaburi (Rio Negro) near base of Cachoeira Caranguejo; NY (holo), VEN.

Psychotria adenophora Steyerm., Mem. New York Bot. Gard. 23(1): 599. 1972. *B. Maguire et al. 29851*; 5 Dec. 1950; Venezuela, T.F. Amazonas, Río Cunucunuma, Cerro Huachamacari; 1,300–1,600 m; NY (holo).

Psychotria adpressipilis Steyerm., Mem. New York Bot. Gard. 23(1): 648. 1972. *R. Spruce 4008*; 1855–1856; Peru, Tarapoto; NY (holo).

Psychotria agostinii Steyerm., Mem. New York Bot. Gard. 23: 551. 1972. *J. A. Steyermark & G. Agostini 8*; 4 Sep. 1960; Venezuela, Aragua, Parque Nacional Henri Pittier, Pico Periquito; 1,250–1,600 m; VEN (holo).

Psychotria aguilarii Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 23. 1943. *P. C. Standley 80900*; Dec. 1940; Guatemala, Dept. Chimaltenango, between Chimaltenango and San Martín Jilotepeque; 1,500–1,700 m; F (holo).

Psychotria aligera Steyerm., Mem. New York Bot. Gard. 23: 572. 1972. *B. Maguire et al. 46872*; 20–21 Aug. 1962; Venezuela, Bolívar, Alto Río Cuyuni, Río Uiriyuk; NY (holo), VEN.

Psychotria alloantha Steyerm., Brittonia 36: 154–160. 1984; *J. J. de Granville 3127*; 16 July 1979; French Guiana, 4 km au sud du Pic Matecho (30 km ENE de Saul); CAY, P, VEN (holo).

Psychotria alticola Steyerm., Pittieria 9: 9. 1981. *H. Humbert 26739*; 6–8 Oct. 1952; Venezuela, Mérida, Sierra del Norte; 2,600–2,800 m; P (holo).

Psychotria altorum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 86. 1944. *J. A. Steyermark 34302*; Jan. 1940; Guatemala, Dept. Quezaltenango, Montaña Chicharro, SE slope Volcán Santa María; 1,400 1,500 m; F (holo).

Psychotria amplinoda Steyerm., Mem. New York Bot. Gard. 17(1): 431. 1967. *J. A. Steyermark 93230*; 2 May 1964; Venezuela, Bolívar, Auyan-tepui; 1,690 m; VEN (holo) = *P. tapajozensis* Standl., 1974.

Psychotria amplinoda Steyerm. var. *ayangannae* Steyerm., Mem. New York Bot. Gard. 17(1): 433. 1967. *S. S. Tillett et al. 45105*; 12 Aug. 1960; Guyana, Mt. Ayanganna, Thompson Camp; 1,418 m; NY (holo) = *P. tapajozensis* Standl., 1972.

Psychotria anartiothrix Steyerm., Ann. Missouri Bot. Gard. 75: 340. 1988. *G. Davidse 27651*; 22–23 July 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, lower part of Río Baria; 80 m; MO (holo 3393677), VEN.

Psychotria anceps H.B.K. var. *robustior* Steyerm., Mem. New York Bot. Gard. 23: 466. 1972. *J. A. Steyermark & M. Rabe 96039*; 7 Aug. 1966; Venezuela, Sucre, Peninsula de Paria, Quebrada Nivardo; 700–750 m; VEN (holo).

Psychotria aneurophylloides Steyerm., Mem. New York Bot. Gard. 23: 547. 1972. *J. A. Steyermark & G. S.*

Bunting 97655; 11 Mar. 1967; Venezuela, Yaracuy, Cerro La Chapa; 1,200–1,360 m; VEN (holo).

Psychotria antenniformis Steyerm., Brittonia 33: 386. 1981. *J. J. de Granville C. 159*; 12 Mar. 1971; French Guiana, Monts Atachi Bacca, Camp no. 1 et Alentours, foret sur la rive droite du Maroni au reiveau de l'ilet Assadam Tabiki; P (holo).

Psychotria apoda Steyerm., Mem. New York Bot. Gard. 23: 668. 1972, nom. nov.

Psychotria appuniana Steyerm., Mem. New York Bot. Gard. 23(1): 660. 1972, nom. nov.

Psychotria araguariensis Steyerm., Mem. New York Bot. Gard. 23: 588. 1972. *J. Murca Pires et al. 51371*; 30 Sep. 1961; Brazil, Terr. Amapá, Camp 12, Rio Araguari; depository not designated.

Psychotria araguensis Steyerm., Mem. New York Bot. Gard. 23: 551. 1972. *T. Lasser 2047*; 14 Sep. 1946; Venezuela, Aragua, Parque Nacional; VEN (holo).

Psychotria arenaria Standl. & Steyerm., Fieldiana Bot. 28(3): 594. 1953. *J. A. Steyermark 59869*; 6 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 2,410 m; F (holo) = *P. ceratantha* Standl., 1972.

Psychotria argoviensis Steyerm., Mem. New York Bot. Gard. 23: 500. 1972, nom. nov.

Psychotria aristeguietae Steyerm., Acta Bot. Venez. 6: 146. 1971. *Fairbrothers et al. 23*; 28 Jan. 1969; Venezuela, Mérida, La Carbonera; 2,300 m; NY (holo).

Psychotria aroensis Steyerm., Mem. New York Bot. Gard. 23(1): 449. 1972. *L. Aristeguieta & F. Pannier 1952*; 6–7 July 1953; Venezuela, Yaracuy, Sierra de Aroa; VEN (holo).

Psychotria aubletiana Steyerm., Mem. New York Bot. Gard. 23: 694. 1972, nom. nov.

Psychotria aubletiana Steyerm. var. *andina* Steyerm., Mem. New York Bot. Gard. 23: 695. 1972. *J. A. Steyermark et al. 98683*; 22–24 May 1967; Venezuela, Paramo de Tamá, near Quebrada Buena Vista; 2,300–2,450 m; VEN (holo).

Psychotria aubletiana Steyerm. var. *andina* Steyerm. f. *pubescens* Steyerm., Mem. New York Bot. Gard. 23: 697. 1972. *E. L. Little 15238*; 19 June 1953; Venezuela, Mérida, 15 km NE de Ejico, La Carbonera; 2,200 m; VEN (holo).

Psychotria aubletiana Steyerm. var. *cacuminis* (Steyerm.) Steyerm. f. *tomentella* Steyerm., Mem. New York Bot. Gard. 23: 697. 1972. *J. A. Steyermark 75830*; 20 June 1953; Venezuela, Bolívar, Apacaratepui; 2,000–2,150 m; F, NY, VEN (holo).

Psychotria aubletiana Steyerm. var. *centro-americana* Steyerm., Mem. New York Bot. Gard. 23: 694. 1972. *L. O. Williams & A. Molina 11237*; 30 Dec. 1962; Honduras, Dept. Morazán, La Tigra; 1,800 m; F, NY (holo).

Psychotria aubletiana Steyerm. var. *producta* Steyerm., Mem. New York Bot. Gard. 23: 698. 1972. *Ijjasz 425*; 15 May 1964; Venezuela, Mérida, entre la India y El Moro; 2,430 m; MAR (holo).

Psychotria aubletiana Steyerm. var. *vilipila* Steyerm., Ann. Missouri Bot. Gard. 71: 1176. 1984. *R. L. Liesner & A. González 10107*; 5 Apr. 1980; Venezuela, Yaracuy, Sierra de Aroa, 15–20 km NW of Cocorote on road to Aroa; MO (2777271), VEN (holo).

Psychotria avia Standl. & Steyerm., Fieldiana Bot. 28(3): 596. 1953. *J. A. Steyermark 58056*; 26 Aug. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,095–1,520 m; F (holo) = *Rudgea avia* (Standl. & Steyerm.) Steyerm., 1972.

Psychotria avilensis Steyerm., Mem. New York Bot. Gard. 23(1): 450. 1972. *B. Trujillo 1374*; 25 June 1950; Venezuela, Distr. Federal, entre Galipan y Los Venados; MAR (holo).

Psychotria ayangannesis Steyerm., Mem. New York Bot. Gard. 23(1): 594. 1972. *S. S. Tillett et al. 45059*; 12 Aug. 1960; Guyana, Thompson Camp, Mt. Ayanganna; 1,370–1,525 m; NY (holo), VEN.

Psychotria barnebyana Steyerm., Mem. New York Bot. Gard. 23: 542. 1972. *B. Maguire et al. 37483*; 4 Feb. 1954; Venezuela, T.F. Amazonas, Piedra Turumeri; depository not designated.

Psychotria bernardii Steyerm., Mem. New York Bot. Gard. 23(1): 450. 1972. *L. Bernardi 1304*; 25 June 1954; Venezuela, Mérida, Carrizal; 1,400 m; NY (holo).

Psychotria berteriana DC. subsp. *venezuelica* Steyerm., Mem. New York Bot. Gard. 23: 535. 1972. *H. Pittier 14010*; 28 May 1937; Venezuela, Aragua, Parque Nacional Henry Pittier, Rancho Grande; 1,200 m; VEN (holo).

Psychotria blakei Standl. & Steyerm., Fieldiana Bot. 28(3): 596. 1953. *E. G. Holt & E. R. Blake 743*; Apr. 1931; Venezuela, T.F. Amazonas, Cerro Yapacana; 100 m; F (holo).

Psychotria blepharophora Standl. & Steyerm. var. *pubens* Steyerm., Mem. New York Bot. Gard. 23: 693. 1972. *L. Ruíz Terán 2980*; 6 Apr. 1966; Venezuela, Mérida, Distr. Arzobispo Chacón, Mun. Libertad, Peramo de Canagua; 2,187 m; VEN (holo).

Psychotria boyanii Steyerm., Mem. New York Bot. Gard. 23(1): 659. 1972. *S. S. & C. L. Tillett 43954*; 1 July 1960; Guyana, Merume Mountains, Portang River; 1,140 m; NY (holo).

Psychotria brazoi Steyerm., Mem. New York Bot. Gard. 23(1): 610. 1972. *N. T. Silva & U. Brazao 60633*; 15 Dec. 1965; Brazil, Amazonas, above Igarape Anta, Pico de Neblina; 1,400–1,800 m; NY (holo).

Psychotria bremekampiana Steyerm., Mem. New York Bot. Gard. 23(1): 643. 1972, nom. nov.

Psychotria breweri Steyerm., Acta Bot. Venez. 14(3): 251. 1984. *J. A. Steyermark et al. 126381*; 10 Feb. 1982; Venezuela, T.F. Amazonas, Cerro Duida; 1,230 m; NY, VEN (holo).

Psychotria buntingii Steyerm., Ann. Missouri Bot. Gard. 74: 399. 1987. *G. S. Bunting et al. 10876*; 25 Feb.–3 Mar. 1982; Venezuela, Zulia, Dept. Perijá, alrededores de la Estación Hídrologica Aricuaisá-Pie de Monte; 100 250 m; JBM, MO (holo—3191936), VEN.

Psychotria calciphila Steyerm., Mem. New York Bot. Gard. 23: 471. 1972. *J. A. Steyermark 99251*; 20 July 1967; Venezuela, Falcón, Sierra de San Luis; 800–900 m; depository not designated.

Psychotria calviflora Steyerm., Mem. New York Bot. Gard. 23: 686. 1972. *Ll. Williams 12992*; 18 May 1940; Venezuela, T.F. Amazonas, S of Puerto Ayacucho; 100 m; VEN (holo).

Psychotria canaguensis Standl. & Steyerm., Fieldiana Bot. 28(3): 597. 1953. *J. A. Steyermark 56441*; 9 May 1944; Venezuela, Mérida, SW of Canagua, Quebrada de Los Salichales; 1,950–2,135 m; F (holo) = *P. amita* f. *canaguensis* (Standl. & Steyerm.) Steyerm., 1972.

Psychotria canescens Steyerm., Mem. New York Bot. Gard. 23(1): 651. 1972. *N. T. Silva & U. Brazao 60880*; 24 Jan. 1966; Brazil, Comissão de Limites Marker BR-1, Serra Pirapucú, Rio Negro, Rio Cauaburi; 1,250 m; NY (holo). Note: This specimen is also

holotype for *Pagameopsis maguirei* Steyerm. subsp. *neblinensis* Steyerm. var. *pirapucuensis* Steyerm. however, the dates and elevation differ.

Psychotria capitata Ruíz & Pavon subsp. *amplifolia* (Raeschel) Steyerm. f. *tomentosa* Steyerm., Mem. New York Bot. Gard. 23(1): 623. 1972. *A. de La Rue 13*; 15 Dec. 1948; French Guiana, Maripa, vallée de l'Oyapock; P (holo).

Psychotria capitata Ruíz & Pavon subsp. *inundata* (Benth.) Steyerm. var. *septentrionalis* Steyerm., Mem. New York Bot. Gard. 23(1): 621. 1972. *N. L. & E. G. Britton 2104*; 4 Mar. 1921; Trinidad, Valencia; NY (holo).

Psychotria capitata Ruíz & Pavon f. *trichophora* Steyerm., Mem. New York Bot. Gard. 23(1): 617. 1972. *S. Vogel 290*; 12 Mar. 1956; Colombia, Río Zanza, Sierra Macarena; M (holo).

Psychotria caquetensis Steyerm., Mem. New York Bot. Gard. 23(1): 653. 1972. *S. Vogel 81*; 12 May 1956; Colombia, Intendencia del Caqueta, near Leguizamo (Caucaya); 150 m; M (holo), NY.

Psychotria carrenoi Steyerm., Fl. Venez. 9(3): 1658. 1974. *J. A. Steyermark et al. 109428*; 24 Feb. 1974; Venezuela, Bolívar, Cerro Jaua, Meseta del Jaua; 1,800 m; VEN (holo).

Psychotria celiae Steyerm., Mem. New York Bot. Gard. 23: 700. 1972. *B. Maguire et al. 60511*; 3 Dec. 1965; Brazil, Amazonas, Serra de Neblina; 2,425 m; NY (holo).

Psychotria cerronis Steyerm., Mem. New York Bot. Gard. 23: 886. 1972. *J. A. Steyermark 97852*; 22–27 Mar. 1967; Venezuela, Bolívar, Meseta de Jaua, Cerro Jaua; 1,922–2,100 m; VEN (holo).

Psychotria chapensis Steyerm., Mem. New York Bot. Gard. 23: 552. 1972. *J. A. Steyermark et al. 100217*; 9 10 Nov. 1967; Venezuela, Yaracuy, Cerro La Chapa; 1,200–1,400 m; VEN (holo).

Psychotria clivorum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 87. 1944. *A. F. Skutch 2073*; 7 Jan. 1935; Guatemala, Dept. Suchitepéquez, Finca Moca; 1,020 m; F (holo).

Psychotria cordifolia H.B.K. subsp. *perpusilla* Steyerm., Mem. New York Bot. Gard. 23: 708. 1972. *R. Schomburgk 282*; 1841–1842; Guyana, Pirara; P (holo).

Psychotria costanensis Steyerm., Mem. New York Bot. Gard. 23(1): 658. 1972, nom. nov.

Psychotria costanensis Steyerm. subsp. *andina* Steyerm., Mem. New York Bot. Gard. 23(1): 659. 1972. *L. Bernardi 1296*; 23 June 1954; Venezuela, Barinas, El Carrizal, del Rincón; 1,450 m; NY (holo).

Psychotria costanensis Steyerm. var. *pubibractea* Steyerm., Mem. New York Bot. Gard. 23(1): 658. 1972. *J. A. & C. Steyermark 95314*; 29 Mar. 1966; Venezuela, Carabobo, S of Borburata, entre Quebrada no. 2 y Quebrada de los Verros; 750–900 m; MO (2270193), VEN (holo).

Psychotria coussareoides Standl. var. *ciliata* Steyerm., Mem. New York Bot. Gard. 23: 496. 1972. *J. A. Steyermark et al. 92929*; 10 Jan. 1964; Venezuela, Bolívar, Cerro Venamo; 950–1,000 m; NY, VEN (holo) = *P. coussareoides* Standl. var. *coussareoides*, 1974.

Psychotria crassa Benth. f. *alba* Steyerm., Ann. Missouri Bot. Gard. 71: 331. 1984. *J. A. Steyermark et al. 128062*; 26 29 Jan. 1983; Venezuela, Bolívar, Distr. Piar, Macizo de Chimantá; 2,000 m; VEN (holo).

Psychotria crassa Benth. f. *angustior* Steyerm., Ann. Missouri Bot. Gard. 71: 331. 1984. *J. A. Steyermark et al. 128992*; 7–9 Feb. 1983; Venezuela, Bolívar, Distr. Piar, Macizo de Chimantá; 2,450 m; VEN (holo).

Psychotria ctenophora Steyerm., Mem. New York Bot. Gard. 23: 690. 1972, nom. nov.

Psychotria cubitalis Standl. & Steyerm., Fieldiana Bot. 28(3): 598. 1953. *J. A. Steyermark 60380*; 20–21 Nov. 1944; Venezuela, Bolívar, Quebrada O-pau-ma; 1,065–1,220 m; F (holo) = *P. capitata* Ruíz & Pavon subsp. *inundata* (Benth.) Steyerm. var. *roraimensis* (Wernham) Steyerm., 1972.

Psychotria cypellantha Steyerm., Brittonia 36: 155. 1984. *C. Sastre 6463*; 27 Dec. 1978; French Guiana, fleuve Maroni, Pompidou-Papaichton; CAY, P, VEN (holo).

Psychotria "*davidsae*" Steyerm., Ann. Missouri Bot. Gard. 71: 1177. 1984. *J. A. Steyermark et al. 122197*; 10 May 1980; Venezuela, T.F. Amazonas, Distr. Atures, along Río Cataniapo, N side of river at dam site; MO (2899787), VEN (holo). Note: *P. davidsei* is on the label, which is spelling that conforms with 1988 ICBN.

Psychotria decurrens Steyerm., Mem. New York Bot. Gard. 23: 549. 1972. *J. A. Steyermark & G. Wessels-Boer 100391*; 13 Nov. 1967; Venezuela, Yaracuy, Sierra de Aroa, Cerro Negro; 1,100–1,250 m; VEN (holo).

Psychotria deflexa DC. subsp. *cubensis* Steyerm., Mem. New York Bot. Gard. 23: 505. 1972. *J. A. Shafer 8805*; 6–18 Feb. 1911; Cuba, Oriente, La Perla; NY (holo).

Psychotria dudleyi Steyerm., Phytologia 31(2): 227. 1975. *T. R. Dudley 13089*; 22 July 1969; Peru, Dept. Huanuco, SW slope of Río Llulla Pichas watershed, on the ascent of Cerros del Sira; 1,400 m; NA (holo).

Psychotria dunstervilleorum Steyerm., Mem. New York Bot. Gard. 23: 702. 1972. *J. A. Steyermark et al. 100762*; 12 Jan. 1968; Venezuela, Táchira, Río Quinimari, SE of Santa Ana; 2,500–2,800 m; VEN (holo).

Psychotria duricoria Standl. & Steyerm., Fieldiana Bot. 28(3): 599. 1953. *J. A. Steyermark 58048*; 25–26 Aug. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,665 m; F (holo).

Psychotria duricoria Steyerm. var. *longiloba* Steyerm., Mem. New York Bot. Gard. 23: 533. 1972. *B. & C. Maguire 35092*; 8 Feb. 1953; Venezuela, T.F. Amazonas, Serranía Yutaje, Río Manapiare, near Camp Yutaje; NY (holo).

Psychotria edaphothrix Steyerm., Ann. Missouri Bot. Gard. 75: 342. 1988. *R. L. Liesner 19595*; 5 Nov. 1985; Venezuela, Bolívar, 0–3 km W of El Polo (8 km W of El Pauji); 650–800 m; MO (holo—3393682), VEN.

Psychotria embirensis Steyerm., Mem. New York Bot. Gard. 23(1): 656. 1972. *B. A. Krukoff 4940*; 19 June 1933; Brazil, Amazonas, basin of Rio Jurua, tributary of Rio Tarauaca, near mouth of Rio Embira; NY (holo).

Psychotria everardii Wernham subsp. *neblinensis* Steyerm., Mem. New York Bot. Gard. 23: 540. 1972. *B. Maguire et al. 42266*; 1–2 Dec. 1957; Venezuela, T.F. Amazonas, Cerro de la Neblina; NY (holo).

Psychotria everardii Wernham subsp. *sipapoensis* Steyerm., Mem. New York Bot. Gard. 23: 540. 1972. *B. Maguire & L. Politi 27864*; 23 Dec. 1948; Venezuela, T.F. Amazonas, Cerro Sipapo (Paraque); 1,400 m; NY (holo).

Psychotria fernandezii Steyerm., Mem. New York Bot. Gard. 23: 554. 1972. *B. Trujillo & Fernandez 766*;

Jan. 1950; Venezuela, Yaracuy, Aroa, Pitiguao; 1,600 m; MAR (holo).

Psychotria fimbriflora Steyerm., Brittonia 33: 386. 1981. *B. S. Peña s.n.*; 14 Nov. 1975; Brazil, Amazonas, Operacao Jurua-Ponto 86-SC-18-XD; VEN (holo).

Psychotria formosissima Steyerm., Brittonia 33: 387. 1981. *O. C. Nascimento et al. 20*; 2 Apr. 1975; Brazil, Amazonas, Vaupés, Rodovia Perimetral Norte; IAN, VEN (holo).

Psychotria fosbergii Steyerm., Mem. New York Bot. Gard. 23(1): 630. 1972. *F. R. Fosberg & N. C. Fassett 21810*; 17–18 Apr. 1944; Colombia, Dept. Santander, Cordillera Oriental, Jordan; 1,100 m; US (holo).

Psychotria galbaoensis Steyerm., Brittonia 33: 387. 1981. *J. J. de Granville 2383*; 11 Mar. 1975; French Guiana, Pente nord-est des Monts Galbao, a 10 km au SE de Saul; 500–600 m; MO (2798770), VEN (holo).

Psychotria glabristipula Steyerm., Mem. New York Bot. Gard. 23: 476. 1972. *J. A. Steyermark 98939*; 16 July 1967; Venezuela, Falcón, Sierra de San Luis; 1,450 m; VEN (holo).

Psychotria glandulicalyx Steyerm., Mem. New York Bot. Gard. 23: 536. 1972. *J. A. Steyermark & J. J. Wurdack 640*; 9 Feb. 1955; Venezuela, Bolívar, Torono-tepui, Chimantá Massif; 2,165–2,180 m; F, MO (2012057), NY, VEN (holo).

Psychotria glandulicalyx Steyerm. f. *bracteifera* Steyerm., Fl. Venez. 2(3): 1364. 1984. *J. A. Steyermark 106037*; Venezuela, T.F. Amazonas, 45 km al N de las cabeceras del Río Orinoco; 1,250 m; VEN (holo).

Psychotria glandulicalyx Steyerm. subsp. *camaniensis* Steyerm., Mem. New York Bot. Gard. 23: 538. 1972. *B. Maguire et al. 31823*; 17 Feb. 1951; Venezuela, T.F. Amazonas, Cerro Camani; 1,500 m; NY (holo).

Psychotria glandulicalyx Steyerm. var. *densipubens* Steyerm., Mem. New York Bot. Gard. 23: 538. 1972. *J. A. Steyermark 98057*; 22–27 Mar. 1967; Venezuela, Bolívar, Cerro Jaua; 1,922–2,100 m; depository not designated.

Psychotria granvillei Steyerm., Brittonia 33: 389. 1981. *J. J. de Granville 2353*; 3 Mar. 1975; French Guiana, Saul, sommet des Monts la Fumee; 410 m; CAY, MO (2798769), NY, P, VEN (holo).

Psychotria guadalupensis (DC.) Howard subsp. *venezuelica* Steyerm., Mem. New York Bot. Gard. 23: 570. 1972. *G. Agostini & M. Farinas 30*; Nov. 1962; Venezuela, Aragua, Parque Nacional Henry Pittier, Rancho Grande; VEN (holo).

Psychotria guanchezii Steyerm., Ann. Missouri Bot. Gard. 74: 109. 1987. *F. Guanchez & E. Melgueiro 3644*; 15 Nov. 1984; Venezuela, T.F. Amazonas, Río Sipapo junto a la communidad indígena de la etnia Piaroa; MO (3327369), TFAV, VEN (holo).

Psychotria heterocarpa Standl. & Steyerm., Fieldiana Bot. 28(3): 600. 1953. *J. A. Steyermark 60191*; 15 Nov. 1944; Venezuela, Bolívar, Sororopan-tepui; 1,615–1,980 m; F (holo) = *P. capitata* Ruíz & Pavon subsp. *inundata* (Benth.) Steyerm. var. *roraimensis* (Wernham) Steyerm., 1972.

Psychotria heteroneura Steyerm., Mem. New York Bot. Gard. 23: 714. 1972. *N. T. Silva & U. Brazão 60607*; 14 Dec. 1965; Brazil, Amazonas, Rio Maturaca, Rio Cauaburi, Rio Negro, up to Pico de Neblina; 1,350 2,000 m; NY (holo).

Psychotria hoffmannseggiana (Willd. ex Roemer & Schultes) Muell. Arg. var. *celsa* Steyerm., Mem. New York Bot. Gard. 23(1): 608. 1972. *H. S. Irwin et al. 14771*; 13 Apr. 1966; Brazil, Bahia, Planalto do Brasil, Rio Corrente drainage, Rio Piau; depository not designated.

Psychotria hoffmannseggiana (Willd. ex Roemer & Schultes) Muell. Arg. var. f. *pubescens* Steyerm., Mem. New York Bot. Gard. 23(1): 607. 1972. *R. S. Cowan & T. Soderstrom 1897*; 18 Feb. 1962; Guyana, Potaro Gorge, Kaieteur Plateau, near Kaieteur Falls; 425 m; US, VEN (holo).

Psychotria horizontalis Sw. var. *psilophylla* Steyerm., Mem. New York Bot. Gard. 23: 472. 1972. *H. H. Smith 393*; May 1898–1899; Colombia, Dept. Magdalena, Santa Marta, near Masinga Vieja; 300–450 m; NY (holo).

Psychotria humensis Steyerm., Mem. New York Bot. Gard. 23: 548. 1972. *J. A. Steyermark 95075*; 5 Mar. 1966; Venezuela, Sucre, Peninsula de Paria, Cerro de Humo; 800–1,000 m; VEN (holo).

Psychotria hyalina Steyerm., Mem. New York Bot. Gard. 23: 670. 1972. *J. A. & C. Steyermark 95246*; 29 Mar. 1966; Venezuela, Carabobo, Río San Gian, S of Borburata; 750–900 m; MO (2223248), VEN (holo).

Psychotria iodotricha Muell. Arg. subsp. *multiflora* Steyerm., Mem. New York Bot. Gard. 23(1): 645. 1972. *J. Murca Pires 122*; 30 Nov. 1946; Brazil, Amazonas, Maues; NY (holo).

Psychotria irwinii Steyerm., Mem. New York Bot. Gard. 23: 453. 1972. *H. S. Irwin et al. 55706*; 13 Sep. 1963; Suriname, Wilhelmina Gebergte; 350 m; NY (holo), VEN.

Psychotria jauaensis Steyerm., Mem. New York Bot. Gard. 23: 889. 1972. *J. A. Steyermark 98098*; 22–27 Mar. 1967; Venezuela, Bolívar, Cerro Jaua; 1,922 2,100 m; VEN (holo).

Psychotria kukenanensis Steyerm., Fieldiana Bot. 28(3): 601. 1953. *J. A. Steyermark 59227*; 3 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,065 m; F (holo) = *P. boliviana* Standl., 1972.

Psychotria lateralis Steyerm., Brittonia 33: 391. 1981. *J. J. de Granville 2360*; 9 Mar. 1975; French Guiana, sommet des Monts Galbao, a 10 km au SE de Saul; 650 m; VEN (holo).

Psychotria leiantha Steyerm., Mem. New York Bot. Gard. 23(1): 635. 1972. *B. Maguire et al. 42449*; 18–19 Dec. 1957; Venezuela, T.F. Amazonas, Cerro de la Neblina; 1,900–2,000 m; MO (3194441), NY (holo), VEN.

Psychotria lilacina Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 252. 1947. *J. A. Steyermark 48564*; 14 July 1942; Guatemala, Dept. Huehuetenango, Cerro Huitz; 1,500–2,600 m; F (holo).

Psychotria liogieri Steyerm., Mem. New York Bot. Gard. 23: 700. 1972, nom. nov.

Psychotria lourteigiana Steyerm., Mem. New York Bot. Gard. 23: 586. 1972. *B. Maguire et al. 29786*; 29 Nov. 1950; Venezuela, T.F. Amazonas, Cerro Hauchamacari; 600 m; NY (holo).

Psychotria lupulina Benth. in Hook. subsp. *rhodoleuca* (Muell. Arg.) Steyerm. var. *maypurensis* (Humb. & Bonpl. ex Roemer & Schultes) Steyerm. f. *pubens* Steyerm., Mem. New York Bot. Gard. 23(1): 634. 1972. *J. A. Steyermark 86861*; 5 Aug. 1960; Venezuela, Bolívar, Cerro Cotorra (El Vigia); 350 m; VEN (holo).

Psychotria macrophylla Ruíz & Pavon subsp. *anomothyrsa* (Schumann & Donn. Sm.) Steyerm. f. *tomentella* Steyerm., Mem. New York Bot. Gard. 23: 564.

1972. *C. Játiva & C. Epling 735*; 12 July 1964; Ecuador, Prov. Esmeraldas, San Lorenzo; NY (holo).

Psychotria maguireorum Steyerm., Mem. New York Bot. Gard. 23(1): 625. 1972, nom. nov. Lectotype: *R. Spruce 3440*; 1853–1854; Venezuela, T.F. Amazonas, Vasiva et Pacimoni; depository not designated.

Psychotria manaraeana Steyerm., Acta Bot. Venez. 6: 143. 1971, also Mem. New York Bot. Gard. 23: 627. 1972. *J. A. Steyermark et al. 103354*; 4 Aug. 1970; Venezuela, Lara, Distr. Palavecino, La Toma, La Loma Redondo; 1,100–1,200 m; VEN (holo).

Psychotria manausensis Steyerm., Mem. New York Bot. Gard. 23: 516. 1972. *E. Ule 5386*; Jan. 1901; Brazil, Amazonas, Manaus; HBG (holo).

Psychotria maturacensis Steyerm., Mem. New York Bot. Gard. 23: 578. 1972. *N. T. Silva & U. Brazão 60842*; 15 Jan. 1966; Brazil, Amazonas, Rio Maturaca, between Missão Salesiana and Serra Pirapucu; 50–400 m; NY (holo).

Psychotria megacephala Steyerm., Mem. New York Bot. Gard. 23: 646. 1972. *B. A. Krukoff 6858*; 12 Oct.–6 Nov. 1934; Brazil, Amazonas, Rio Livramento, Mun. Humayta; NY (holo).

Psychotria meridensis Steyerm., Mem. New York Bot. Gard. 23: 531. 1972. *J. A. Steyermark 56614*; 18 May 1944; Venezuela, Mérida, above La Isla, above Tabay; 2,285–2,745 m; F, NY (holo), VEN.

Psychotria merumensis Steyerm., Mem. New York Bot. Gard. 23: 574. 1972. *S. S. Tillett 43996*; 4 July 1960; Guyana, Partang River, Merume Mt.; 1,140 m; NY (holo).

Psychotria microbracteata Steyerm., Brittonia 33: 391. 1981. *J. J. de Granville 2362*; 9 Mar. 1975; French Guiana, sommet des Monts Galbao, a 10 km au SE de Saul; CAY, MO (2798772), P, VEN (holo).

Psychotria microdon (DC.) Urban var. *meridionalis* Steyerm., Mem. New York Bot. Gard. *H. Pittier 7911*; 4 July 1916; Venezuela, Carabobo, Hacienda de Cura, near San Joquin; VEN (holo).

Psychotria minarum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 253. 1947. *J. A. Steyermark 43106*; 21 Jan. 1942; Guatemala, Dept. El Progreso, Sierra de las Minas, between Calera and summit of Volcán Siglo; 2,000–3,000 m; F (holo).

Psychotria moroidea Steyerm., Mem. New York Bot. Gard. 23: 485. 1972, nom. nov.

Psychotria multiramosa Steyerm., Mem. New York Bot. Gard. 23: 568. 1972. *S. S. Tillett et al. 45079*; 10 Aug. 1960; Guyana, Mt. Ayanganna; 1,418–1,525 m; NY (holo).

Psychotria muscosa (Jacq.) Steyerm. subsp. *breviloba* Steyerm., Mem. New York Bot. Gard. 23: 672. 1972. *W. E. Broadway 9823*; 10–26 Jan. 1922; Trinidad, heights of Aripo; NY (holo).

Psychotria nematostachya Steyerm., Mem. New York Bot. Gard. 23: 512. 1972. *J. Ewel 114*; 18 Apr. 1964; Brazil, Amazonas, cerca de la Neblina; 400 m; MAR, NY (holo).

Psychotria norae Steyerm., Mem. New York Bot. Gard. 23: 703. 1972. *J. A. Steyermark et al. 101030*; 16 Jan. 1968; Venezuela, Táchira, SE de Santa Ana, entre el Páramo de Pata de Judio y el Páramo de Cobre; 2,600–2,800 m; VEN (holo).

Psychotria occidentalis Steyerm., Mem. New York Bot. Gard. 23: 545. 1972. *H. H. Rusby & R. Squires s.n.*; May 1896; Venezuela, Terr. Delta Amacuro, lower Orinoco; NY (holo).

Psychotria officinalis (Aublet) Sandw. subsp. *wilhelminensis* Steyerm., Mem. New York Bot. Gard. 23: 615. 1972. *B. Maguire et al. 54440*; 2 Aug. 1963; Suriname, Juliana Top, Wilhelmina Gebergte; 1,200 m; NY (holo).

Psychotria oiapoquensis Steyerm., Mem. New York Bot. Gard. 23: 647. 1972. *H. S. Irwin et al. 47393*; 7 Aug. 1960; Brazil, Terr. Amapá, Rio Oiapoque; NY (holo).

Psychotria pachecoana Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(3): 205. 1940. *P. C. Standley 69922*; 30 Mar. 1939; Guatemala, Dept. Baja Verapaz, N of Santa Rosa; 1,650 m; F (holo).

Psychotria pakaraimensis Steyerm., Mem. New York Bot. Gard. 23: 509. 1972. *B. Maguire et al. 40573*; 5–6 Feb. 1955; Guyana; Pakaraima Mountains, Mt. Ayanganna; 1,000–1,500 m; NY (holo).

Psychotria pallidinervia Steyerm., Mem. New York Bot. Gard. 23: 492. 1972. *B. Maguire et al. 41996*; 7 Nov. 1957; Venezuela, T.F. Amazonas, Cerro de la Neblina; 500–700 m; NY (holo).

Psychotria pariensis Steyerm., Mem. New York Bot. Gard. 23: 513. 1972. *J. A. Steyermark 95019*; 4 Mar. 1966; Venezuela, Sucre, Cerro de Humo; 1,250–1,273 m; VEN (holo).

Psychotria parimensis Steyerm., Mem. New York Bot. Gard. 23: 691. 1972. *F. Cardona P. 1333*; 11–23 Mar. 1946; Venezuela, T.F. Amazonas, Sierra Parima; 550 m; US, VEN (holo).

Psychotria parvibractea Steyerm., Mem. New York Bot. Gard. 23: 581. 1972. *J. A. Steyermark & S. Nilsson 135*; 14 Apr. 1960; Venezuela, Bolívar, Cerro Venamo; 1,100–1,300 m; NY (holo), VEN.

Psychotria patria Standl. & Steyerm., Fieldiana Bot. 28(3): 601. 1953. *J. A. Steyermark 56411*; 9 May 1944; Venezuela, Mérida, Quebrada de Los Salichales; 1,950–2,135 m; F (holo).

Psychotria patria Standl. & Steyerm. var. *tovarensis* Steyerm., Mem. New York Bot. Gard. 23: 554. 1972. *L. Aristeguieta 7129*; 1 May 1969; Venezuela, Aragua-Distr. Federal, Colonia Tovar; NY (holo), VEN.

Psychotria paupertina Standl. & Steyerm., Fieldiana Bot. 28(3): 603. 1953. *J. A. Steyermark 57919*; 23 Aug. 1944; Venezuela, T.F. Amazonas, near Base River (Caño Negro), SE base of Cerro Duida; 215 m; F (holo).

Psychotria pectinata Steyerm., Ann. Missouri Bot. Gard. 75: 344. 1988. *R. L. Liesner 15955*; 17 July 1984; Venezuela, T.F. Amazonas; Cerro de la Neblina; 150 m; MO (holo—3393684), VEN.

Psychotria perferruginea Steyerm., Brittonia 33: 393. 1981. *J. J. de Granville B.4640*; 20 Dec. 1972; French Guiana, Montagne la Fumea, P.K.; CAY, P (holo).

Psychotria perijaënsis Steyerm., Acta Bot. Venez. 8: 250. 1973. *J. A. Steyermark et al. 105749*; 31 Mar. 1972; Venezuela, Zulia, Sierra de Perija; 1,140–1,400 m; VEN (holo).

Psychotria perpapillifera Steyerm., Mem. New York Bot. Gard. 23: 571. 1972, nom. nov. Lectotype: *Crueger s.n.*; Trinidad; Bot. Gard. Herb. n. 3127.

Psychotria peruviana Steyerm., Mem. New York Bot. Gard. 23: 667. 1972, nom. nov.

Psychotria phaneroloma Standl. & Steyerm., Fieldiana Bot. 28(3): 604. 1953. *J. A. Steyermark 58117*; 2 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,005–1,065 m; F (holo).

Psychotria phaneroloma Standl. & Steyerm. var. *angustior* Steyerm., Mem. New York Bot. Gard. 23: 591. 1972. *F. Cardona P. 2967*; Jan. 1963; Venezuela, Bolívar, Río Pauo afluente del Río Caura; 390 m; VEN (holo).

Psychotria phelpsiana Steyerm., Mem. New York Bot. Gard. 23: 889. 1972. *J. A. Steyermark 98070*; 22–27 May 1967; Venezuela, Bolívar, Cerro Jaua; 1,922–2,100 m; VEN (holo).

Psychotria piresii Steyerm., Mem. New York Bot. Gard. 23: 624. 1972. *J. Murca Pires & P. B. Cavalcante 52250*; 23 July 1962; Brazil, Terr. Amapá, Agua Azul; NY (holo).

Psychotria plowmanii Steyerm., Ann. Missouri Bot. Gard. 71: 1178. 1984. *J. A. Steyermark et al. 122132*; 9 May 1980; Venezuela, T.F. Amazonas, Dept. Atures, along Río Cataniapo, 44–45 km SE of Puerto Ayacucho; MO, VEN (holo).

Psychotria prancei Steyerm., Mem. New York Bot. Gard. 23: 656. 1972. *G. T. Prance et al. 9015*; 12 Dec. 1968; Brazil, Amazonas, Reserva Florestal Ducke, Manaus Itacoatiara road; NY (holo).

Psychotria psittacina Steyerm., Mem. New York Bot. Gard. 23: 665. 1972. *S. S. Tillett et al. 45007*; 2 Aug. 1960; Guyana, Mt. Ayanganna, upper Mazuruni River basin; 800–900 m; NY (holo).

Psychotria ptariensis Standl. & Steyerm., Fieldiana Bot. 28(3): 604. 1953. *J. A. Steyermark 59440*; 27 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 1,250–1,520 m; F (holo) = *P. imthurniana* Oliv. f. *ptariensis* (Standl. & Steyerm.) Steyerm., 1972.

Psychotria puberulenta Steyerm., Mem. New York Bot. Gard. 23: 488. 1972. *B. Maguire & D. B. Fanshawe 32618*; 16 Nov. 1951; Guyana, upper Mazaruni River, Pakaraima Mountains; 550 m; depository not designated.

Psychotria pungens Steyerm., Mem. New York Bot. Gard. 23: 677. 1972. *Leprieur 118*; French Guiana; P (holo).

Psychotria quadribracteata Steyerm., Mem. New York Bot. Gard. 23: 614. 1972. *N. T. Silva 81*; 2 Feb. 1972; Brazil, Belem, Pará, along road to Barrucão de Borracha, Inst. Agron. do Norte; NY (holo).

Psychotria ronaldii Steyerm., Ann. Missouri Bot. Gard. 74: 111. 1987. *R. L. Liesner 18214*; 4 Mar. 1985; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Huachamacari; 600 750 m; MO (holo–3327368), VEN.

Psychotria rosacea Steyerm., Mem. New York Bot. Gard. 23: 701. 1972. *J. A. Steyermark 105045*; 3 Mar. 1971; Venezuela, Táchira, entre Zumbador y Queniquea; 2,650–2,700 m; VEN (holo).

Psychotria rosea (Benth.) Muell. Arg. f. *calvescens* Steyerm., Mem. New York Bot. Gard. 23: 688. 1972. *B. Maguire et al. 36518*; 4 Dec. 1953; Venezuela, T.F. Amazonas, Río Yatua above mouth of Río Yacibo; 100–140 m; NY (holo), VEN.

Psychotria rosea (Benth.) Muell. Arg. var. *trichophora* Steyerm., Mem. New York Bot. Gard. 23: 688. 1972. *O. Haught 2190*; 30 Apr. 1937; Colombia, Dept. Sur de Santander, valley of Dorado Creek, vicinity of Puerto Berrio; 250 m; NY (holo).

Psychotria ruiz-teranii Steyerm., Mem. New York Bot. Gard. 23: 702. 1972. *L. Ruíz Terán 3199*; 21 June 1966; Venezuela, Mérida, Distr. Rangel, Las Escaleras; 2,800 m; VEN (holo).

Psychotria sanluisensis Steyerm., Mem. New York Bot. Gard. 23: 470. 1972. *J. A. Steyermark 98951*; 16 July 1967; Venezuela, Falcón, Sierra de San Luis; 1,450 m; VEN (holo).

Psychotria sanmartensis Rusby var. *costanensis* Steyerm., Mem. New York Bot. Gard. 23: 532. 1972. *J. A. Steyermark 91631*; n.d.; Venezuela, Miranda, between Petare and Guarenas, 16 km NE of Caucaquito; 1,200–1,500 m; VEN (holo).

Psychotria sastrei Steyerm., Brittonia 33: 394. 1981. *C. Sastre 2392*; 6 Oct. 1973; Colombia, Amazonas, Río Igara-Paraná, La Chorrera, Cerro Adofiki, 35 km en aval de La Chorrera; P (holo).

Psychotria saulensis Steyerm., Brittonia 33: 395. 1981. *J. J. de Granville 2361*; 9 Mar. 1975; French Guiana, sommet Monts Galbao, a 10 km au SE de Saul; 650 m; CAY, MO (2798773), VEN (holo).

Psychotria schippii Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 24. 1943. *C. L. Lundell 6193*; June–July 1936; Belize, El Cayo Distr., Valentín; F (holo).

Psychotria sciaphila S. Moore subsp. *longicalyx* Steyerm., Mem. New York Bot. Gard. 23: 641. 1972. *H. S. Irwin et al. 10161*; 10 Nov. 1965; Brazil, Goiás, Distr. Federal, Planalto do Brasil, Parque Mun. do Gama; 1,150 m; NY (holo).

Psychotria silvae Steyerm., Mem. New York Bot. Gard. 23: 581. 1972. *N. T. Silva & U. Brazão 60872*; 24 Jan. 1966; Brazil, Amazonas, Serra Pirapucí; 1,250 m; NY (holo).

Psychotria sipapoensis Steyerm., Mem. New York Bot. Gard. 23: 708. 1972. *B. Maguire & L. Politi 28778*; 2 Feb. 1949; Venezuela, T.F. Amazonas, Cerro Sipapo (Parque); 600 m; NY (holo).

Psychotria sororopanensis Standl. & Steyerm., Fieldiana Bot. 28(3): 605. 1953. *J. A. Steyermark 60175*; 15 Nov. 1944; Venezuela, Bolívar, Sororopan-tepui; 2,130–2,250 m; F (holo) = *P. sessilis* var. *angustifolia* (Muell. Arg.) Steyerm., 1972.

Psychotria spectabilis Steyerm., Mem. New York Bot. Gard. 23: 664. 1972, nom. nov.

Psychotria speluncae Standl. & Steyerm., Fieldiana Bot. 28(3): 606. 1953. *J. A. Steyermark 59521*; 29 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 1,810 m; F (holo).

Psychotria speluncae Standl. & Steyerm. subsp. *brevicalyx* Steyerm., Mem. New York Bot. Gard. 17(1): 436. 1967. *B. Maguire et al. 37148*; 10 Jan. 1954; Venezuela, T.F. Amazonas, Cerro de la Neblina; 1,700 m; NY (holo).

Psychotria speluncae Standl. & Steyerm. subsp. *exserta* Steyerm., Mem. New York Bot. Gard. 17(1): 436. 1967. *B. Maguire et al. 36921*; 27 Dec. 1953; Venezuela, T.F. Amazonas, Cerro de la Neblina, Río Yatua; 1,700 m; NY (holo).

Psychotria squamelligera Steyerm., Brittonia 36: 156. 1984. *J. J. de Granville B.5288*; 12 June 1975; French Guiana, sur la Riviere Comte, en foret sur la Montagne Soufflet; CAY, P, VEN (holo).

Psychotria standleyana Steyerm., Fieldiana Bot. 28(3): 607. 1953. *J. A. Steyermark 56681*; 19 May 1944; Venezuela, Mérida, Montaña de San Jacinto; 1,675–2,195 m; F (holo).

Psychotria steinii Steyerm., Ann. Missouri Bot. Gard. 75: 345. 1988. *B. A. Stein & A. Gentry 1553*; 15 Apr. 1984; Venezuela, T.F. Amazonas, Cerro de la Neblina, summit, Camp 2; 2,100 m; MO (holo—3393676), VEN.

Psychotria subimbricata Steyerm., Ann. Missouri Bot. Gard. 74: 400. 1987. *J. A. Steyermark & B. Manara*

125483; 31 Oct. 1981; Venezuela, Miranda, Parque Nacional Guatapo, a lo largo del Río Santa Cruz de Río Grande, al Sureste de Los Alpes; 400 m; VEN (holo).

Psychotria subpedicellata Steyerm., Mem. New York Bot. Gard. 23: 507. 1972. *G. Klug 2019*; Mar.–Apr. 1931; Peru, Dept. Loreto, Río Putumayo at mouth of Río Zubineta, Florida; 200 m; NY (holo).

Psychotria sucrensis Steyerm., Mem. New York Bot. Gard. 23: 547. 1972. *J. A. Steyermark 94956*; 3 Mar. 1966; Venezuela, Sucre, Cerro de Humo; 1,060–1,273 m; VEN (holo).

Psychotria tamaensis Standl. & Steyerm., Fieldiana Bot. 28(3): 607. 1953. *J. A. Steyermark 57309*; 15 July 1944; Venezuela, Táchira, base of Páramo de Tamá; 2,500 2,895 m; F (holo) = *Palicourea tamaensis* (Standl. & Steyerm.) Steyerm., 1971.

Psychotria tapirapecoana Steyerm., Mem. New York Bot. Gard. 23(1): 628. 1972. *F. Cardona P. 1496*; 16 24 Feb. 1946; Brazil, Amazonas, orillas del Rio Castanho; 100–140 m; US, VEN (holo).

Psychotria terepaimensis Steyerm., Mem. New York Bot. Gard. 23: 565. 1972. *B. Trujillo 1955*; 24 Jan. 1954; Venezuela, Lara, Terepaima; 1,450 m; MAR (holo).

Psychotria tetramera Steyerm., Mem. New York Bot. Gard. 23(1): 654. 1972. *Forest Dept. Rec. 7832 (field no. RB 8)*; 5 July 1957; Guyana, Chinoweg; NY (holo).

Psychotria thesceloantha Steyerm., Ann. Missouri Bot. Gard. 75: 347. 1988. *R. L. Liesner 16963*; 4 Dec. 1984; Venezuela, T.F. Amazonas, upper Caño Baria, swamp area between Río Mawarinuma and headwaters of Bío Baria; 130 m; MO (holo—3393681), VEN.

Psychotria tillettii Steyerm., Mem. New York Bot. Gard. 23: 496. 1972. *S. S. & C. L. Tillett 43946*; 12 Sep. 1960; Guyana, upper Mazaruni River basin, near Surua-gu-puh; 470 m; NY (holo).

Psychotria trichotoma Mart. & Gal. var. *trichophylla* Steyerm., Mem. New York Bot. Gard. 23: 475. 1972. *L. Bernardi 1720*; 10 Dec. 1954; Venezuela, Barinas, Mun. Pedraza, Río Curbatico; 250–350 m; NY (holo).

Psychotria trujilloi Steyerm., Mem. New York Bot. Gard. 23: 475. 1972. *B. Trujillo 1921*; 24 Jan. 1954; Venezuela, Lara, Terepaima; 1,450 m; MAR (holo).

Psychotria trujilloi Steyerm. var. *yaracuyensis* Steyerm., Ernstia 23: 37. 1984. *J. A. Steyermark & C. Espinoza 123742*; 6 Dec. 1980; Venezuela, Yaracuy, Dept. San Felipe, Cumbre Gamelotal; 1,300 m; VEN (holo).

Psychotria uberta Standl. & Steyerm., Fieldiana Bot. 28(3): 608. 1953. *J. A. Steyermark 57255*; 14 July 1944; Venezuela, Táchira, Quebrada de Palmar, foot of Páramo de Tamá; 2,500 m; F (holo).

Psychotria ulviformis Steyerm., Mem. New York Bot. Gard. 23: 638. 1972, nom. nov.

Psychotria urbaniana Steyerm., Mem. New York Bot. Gard. 23: 671. 1972, nom. nov.

Psychotria urceolata Steyerm., Brittonia 33: 395. 1981. *J. J. de Granville 2393*; 11 Mar. 1975; French Guiana, Pente NE des Monts Galbao a 10 km au SE de Saul; 500–600 m; CAY, P, VEN (holo).

Psychotria urniformis Steyerm., Mem. New York Bot. Gard. 23: 556. 1972. *S. S. Tillett et al. 45008*; 2 Aug. 1960; Guyana, upper Mazaruni River basin, Mt. Ayanganna; 800–900 m; NY (holo).

Psychotria vareschii Steyerm., Mem. New York Bot. Gard. 23: 706. 1972. *V. Vareschi 7790*; 2 Nov. 1962; Venezuela, T.F. Amazonas, Río Casiquiare, Caño Monomi; VEN (holo).

Psychotria variegata Steyerm., Mem. New York Bot. Gard. 23: 638. 1972, nom. nov.

Psychotria venezuelensis Steyerm., Mem. New York Bot. Gard. 23: 493. 1972. *B. Maguire et al. 42031*; 17 Nov. 1957; Venezuela, T.F. Amazonas, Cerro de la Neblina; 1,600–1,700 m; depository not designated.

Psychotria ventuariana Standl. & Steyerm., Fieldiana Bot. 28(3): 609. 1953. *Ll. Williams 14983*; 20 Apr. 1942; Venezuela, T.F. Amazonas, Delta del Ventuari; 124 m; F (holo).

Psychotria viridibractea Steyerm., Brittonia 36: 158. 1984. *J. J. de Granville 2793*; 1 Mar. 1977; French Guiana, Saul, sommet des Monts Galbao; 670 m; CAY, P, VEN (holo).

Psychotria wessels-boeri Steyerm., Mem. New York Bot. Gard. 23: 467. 1972. *J. G. Wessels-Boer 962*; 18 Mar. 1963; Suriname, Oelemari; U (holo).

Psychotria wilhelminensis Steyerm., Mem. New York Bot. Gard. 23: 487. 1972. *H. S. Irwin et al. 55048*; 24 Aug. 1963; Suriname, Wilhelmina Gebergte, 12 km N of Lucie River; NY (holo), VEN.

Psychotria wurdackii Steyerm., Mem. New York Bot. Gard. 23: 576. 1972. *B. Maguire et al. 42475*; 24 Dec. 1957; Venezuela, T.F. Amazonas, Río Yatua, Cerro de la Neblina; 1,100 m; depository not designated.

Psychotria yapacanensis Steyerm., Pittieria 9: 10. 1981. *O. Huber 1791*; 25 May 1978; Venezuela, Dept. Atabapo, Caño Cotua y el Cerro Yapacana; 100 m; VEN (holo).

Psychotria yaracuyensis Steyerm., Mem. New York Bot. Gard. 23: 447. 1972. *J. A. Steyermark & G. S. Bunting 97688*; 11 Mar. 1967; Venezuela, Yaracuy, N of Nirgua, Cerro La Chapa; 1,200–1,360 m; VEN (holo).

Psychotria yavitensis Steyerm., Mem. New York Bot. Gard. 23: 456. 1972. *J. A. Steyermark & G. S. Bunting 102933*; 22 Apr. 1970; Venezuela, T.F. Amazonas, 7–9 km from Yavita; 128 m; VEN (holo).

Psychotria yutajensis Steyerm., Ann. Missouri Bot. Gard. 75: 348. 1988. *R. L. Liesner & B. K. Holst 21649*; 4 Mar. 1987; Venezuela, T.F. Amazonas, Dept. Atures, summit E of unnamed peak, 8 km NW of Yutajé, W of Serranía Yutajé; 1,500–1,700 m; MO (holo—3482981), VEN.

Randia aculeata L. var. *dasyphylla* Steyerm., Mem. New York Bot. Gard. 23: 342. 1972. *J. A. Steyermark 86241*; 1 June 1960; Venezuela, Bolívar, NE of Tumeremo, between Hato Corumo and Las Chicharras; VEN (holo).

Randia aculeata L. f. *minor* Steyerm., Mem. New York Bot. Gard. 23: 341. 1972. *N. L. Britton & W. E. Hess 2702*; 5 Apr. 1913; Puerto Rico, Mayaguez, Monte Mesa; NY (holo).

Randia amazonasensis Steyerm., Mem. New York Bot. Gard. 23: 336. 1972. *B. Maguire et al. 29469*; 7 Nov. 1950; Venezuela, T.F. Amazonas, Río Orinoco, Río Cunucunuma, Playa Alta; 100 m; NY (holo).

Randia aristeguietae Steyerm., Bol. Soc. Venez. Ci. Nat. 29: 22. 1971. *L. Aristeguieta 4193*; May 1960; Venezuela, Guárico, Carretera El Rastro, Calabozo; VEN (holo), NY.

Randia brevipes Steyerm., Acta Bot. Venez. 6: 126. 1971. Pistillate: *L. Aristeguieta 5343*; Apr. 1964;

Venezuela, Bolívar, Puerto Ordaz; VEN (holo). Staminate: *N. L. Britton et al. 2684*; Trinidad, Chacachacare; NY (holo).

Randia habrophlebia Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 25. 1943. *P. C. Standley 76321*; Oct.–Nov. 1940; Guatemala, Dept. Jutiapa, vicinity of Jutiapa; 850 m; F (holo).

Randia pubiflora Steyerm., Brittonia 33: 396. 1981. *P. Cavalcante 2511*; 25 Feb. 1970; Brazil, Pará, Parque Indigena do Tumucumaque, Rio Parú de Oeste Missão Triyo; VEN (holo).

Randia venezuelensis Steyerm., Bol. Soc. Venez. Ci. Nat. 29: 23. 1971. *J. J. Wurdack & J. V. Monachino 41303*; 27 June 1956; Venezuela, Bolívar, between Río Orinoco and Piedra La Villa; NY (holo).

Ravnia longifilamentosa Steyerm., Ceiba 3: 21. 1952. *P. H. Allen 4744*; 25 July 1947; Panamá, Prov. Chiriquí, Quebrada Velo, vicinity of Finca Lerida; 1,631 m; F (holo), MO.

Ravnia panamensis Steyerm., Ceiba 3: 22. 1952. Collector and collection number not indicated; 29 June 1946; Panamá, Prov. Coclé, North Hills, El Valle de Antón; F (holo), MO.

Remijia argentea Steyerm., Mem. New York Bot. Gard. 23: 267. 1972. *B. Maguire et al. 41496*; 16 Sep. 1957; Venezuela, T.F. Amazonas, NW base of Cerro Yapacana; 125 m; NY (holo), VEN.

Remijia berryi Steyerm., Ann. Missouri Bot. Gard. 71: 332. 1984. *P. E. Berry & L. Chesney 2116*; 26 Feb.–2 Mar. 1976; Venezuela, T.F. Amazonas, Estación Experimental de Santa Barbara del Orinoco, a 1–2 km S de Trapichote; 130 m; VEN (holo).

Remijia delascioi Steyerm., Ann. Missouri Bot. Gard. 71: 332. 1984. *J. A. Steyermark et al. 130339*; 1 Mar. 1984; Venezuela, T.F. Amazonas, Cerro Vinilla; 440 m; MO (holo—3223165), VEN.

Remijia densiflora Benth. f. *glabricalyx* Steyerm., Mem. New York Bot. Gard. 23(1): 265. 1972. *B. Maguire & B. Maguire, Jr. 29079*; 22–24 Apr. 1949; Venezuela, T.F. Amazonas, Cerro Duida; 1,600 m; NY (holo).

Remijia densiflora Benth. var. *minima* Steyerm., Mem. New York Bot. Gard. 23(1): 265. 1972. *J. A. Steyermark 90269*; 27 Dec. 1961; Venezuela, Bolívar, Sierra Ichun; 625–725 m; VEN (holo).

Remijia maguirei Steyerm., Mem. New York Bot. Gard. 23(1): 256. 1972. *B. Maguire et al. 42469*; 24 Dec. 1957; Venezuela, T.F. Amazonas, Cerro de la Neblina; 1,100 m; NY (holo).

Remijia marahuacensis Steyerm., Ann. Missouri Bot. Gard. 74: 111. 1987. *J. A. Steyermark & B. K. Holst 130440*; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca, Sima Camp; 1,140 m; MO (holo—3327367), VEN.

Remijia morilloi Steyerm., Fl. Venez. 9(1): 115. 1974. *G. Morillo et al. 4192*; 29 Apr. 1974; Venezuela, T.F. Amazonas, 12–15 km NE de San Carlos de Río Negro, carretera San Carlos–Solano; VEN (holo).

Remijia pilosinervula Steyerm., Mem. New York Bot. Gard. 17(1): 232. 1967. *J. A. Steyermark & J. J. Wurdack 713*; 17 Feb. 1955; Venezuela, Bolívar, Chimantá Massif; 2,150 m; VEN (holo).

Remijia reducta Steyerm., Ann. Missouri Bot. Gard.: in press. 1989. *R. L. Liesner & G. Carnevali 22407*; 25 Oct. 1987; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro Aracamuni, summit, Proa Camp; 1,400 m; MO (holo), VEN.

Remijia roraimae (Benth.) Schumann var. *adpressa* Steyerm., Mem. New York Bot. Gard. 23(1): 262. 1972. *J. A. Steyermark 90429*; 29 Dec. 1961; Venezuela, Bolívar, Sierra Ichun; 500–625 m; VEN (holo).

Remijia roraimae (Benth.) Schumann var. *auyantepuiensis* Steyerm., Mem. New York Bot. Gard. 23(1): 263. 1972. *J. A. Steyermark 93361*; 4 May 1964; Venezuela, Bolívar, Auyan-tepui; 1,760 m; VEN (holo).

Remijia roraimae (Benth.) Schumann var. *guianensis* Steyerm., Mem. New York Bot. Gard. 23(1): 263. 1972. *B. Maguire et al. 46152-A*; 9 Sep. 1961; Guyana, Pakaraima Mountains, Chimapu Savanna; 1,210 m; depository not designated.

Remijia sessilis Steyerm., Ann. Missouri Bot. Gard. 75: 1084. 1988. *M. Nee 30967*; 20 Feb. 1985; Venezuela, T.F. Amazonas, SW side of Cerro de la Neblina; 400–500 m; MO (holo), NY, VEN.

Remijia sipapoensis Steyerm., Mem. New York Bot. Gard. 23(1): 255. 1972. *B. Maguire & L. Politi 28013*; 28 Dec. 1948; Venezuela, T.F. Amazonas, Cerro Sipapo (Paraque): NY (holo).

Remijia stenopetala Standl. & Steyerm., Fieldiana Bot. 28(3): 610. 1953. *J. A. Steyermark 60359*; 20–21 Nov. 1944; Venezuela, Bolívar, Quebrada O-paru-ma; 1,065–1,220 m; F (holo) = *R. densiflora* subsp. *stenopetala* (Standl. & Steyerm.) Steyerm., 1972.

Remijia vaupesiana Steyerm., Mem. New York Bot. Gard. 23(1): 253. 1972. *R. de Lemos Fróes 21225*; 20 Oct. 1945; Brazil, Amazonas, Rio Negro, Vaupés, Jauareté; depository not designated.

Remijia wurdackii Steyerm., Mem. New York Bot. Gard. 23(1): 259. 1972. *J. J. Wurdack & L. Adderley 42824*; 5 June 1959; Venezuela, T.F. Amazonas, Caño Cupaven; 125–150 m; NY (holo).

Retiniphyllum glabrum Steyerm., Mem. New York Bot. Gard. 12(3): 243. 1965. *R. E. Schultes & J. Murca Pires 9100*; 14–15 Nov. 1947; Brazil, Amazonas, Rio Vaupés, between Ipanore and confluence with Rio Negro; US (holo).

Retiniphyllum guianense Steyerm., Mem. New York Bot. Gard. 12(3): 242. 1965. *S. S. Tillett et al. 44824*; 5 July 1960; Guyana, upper Mazaruni River basin, Partang River, SE side of Merume Mt.; 1,140 m; NY (holo).

Retiniphyllum laxiflorum (Benth.) N. E. Brown var. *brasiliense* Steyerm., Mem. New York Bot. Gard. 12(3): 234. 1965. *B. A. Krukoff 3*; 9 Oct. 1942; Brazil, Bahia, Serra Sincora, Gorge of Zesuserra; 1,000 m; NY (holo).

Retiniphyllum laxiflorum (Benth.) N. E. Br. var. *longilobum* Steyerm., Mem. New York Bot. Gard. 12(3): 1965. *B. Maguire & L. Politi 27869*; 23 Dec. 1948; Venezuela, T.F. Amazonas, Cerro Sipapo (Paraque); 1,400 m; NY (holo).

Retiniphyllum longiflorum Steyerm., Brittonia 33: 396. 1981. *P. Cavalcante 712*; 1 Mar. 1959; Brazil, Amazonas, Rio Vaupés, Taracua; VEN (holo).

Retiniphyllum maguirei Standl. var. *reticulatum* Steyerm., Mem. New York Bot. Gard. 12(3): 239. 1965. *B. Maguire 24361*; 13 Aug. 1944; Suriname, Tafelberg, Savanna #1; 565 m; NY, VEN (holo).

Retiniphyllum parvifolium Steyerm., Brittonia 33: 397. 1981. *J. Murca Pires et al. 6063*; 12 Dec. 1956;

Brazil, Pará, Serra do Cachimbo; 425 m; NY (holo), VEN.

Retiniphyllum scabrum Benth. var. *ayangannense* Steyerm., Mem. New York Bot. Gard. 12(3): 236. 1965. *S. S. Tillett et al. 45194*; 8 Aug. 1960; Guyana, Mt. Ayanganna, above Thompson Camp; 1,370 1,525 m; NY (holo).

Retiniphyllum schomburgkii (Benth.) Muell. Arg. subsp. *occidentale* Steyerm., Mem. New York Bot. Gard. 12(3): 240. 1965. *B. Maguire & J. J. Wurdack 34531*; 17 Mar. 1953; Venezuela, T.F. Amazonas; NW base of Cerro Yapacana, Savanna #3; 150 m; NY (holo).

Retiniphyllum schomburgkii (Benth.) Muell. Arg. subsp. *occidentale* Steyerm. var. *hirticalyx* Steyerm., Mem. New York Bot. Gard. 12(3): 241. 1965. *B. Maguire et al. 41860*; 12 Oct. 1957; Colombia, 0.5–1.5 km N of Puerto Colombia (opposite Maroa); 130 m; NY (holo).

Retiniphyllum tepuiense Steyerm., Mem. New York Bot. Gard. 12(3): 237. 1965. *B. Maguire & L. Politi 28458*; 20 Jan. 1949; Venezuela, T.F. Amazonas, upper E Basin, Cerro Sipapo (Paraque); 1,600–1,800 m; NY (holo).

Retiniphyllum truncatum Muell. Arg. var. *angustifolium* Steyerm., Mem. New York Bot. Gard. 12(3): 242. 1965. *R. E. Schultes & R. Black 46-357*; 8 Nov. 1946; Colombia, Pica da Cotuhe; US (holo).

Rondeletia aristeguietae Steyerm., Mem. New York Bot. Gard. 17(1): 246. 1967. *L. Aristeguieta & C. Montoya 2149*; Feb. 1954; Venezuela, Yaracuy, Aroa; VEN (holo).

Rondeletia brachistantha Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 25. 1943. *J. A. Steyermark 36286*; Feb. 1940; Guatemala, Dept. San Marcos, Río Vega, near San Rafael and Guatemala–Mexican boundary, Volcán Tacaná; 2,500–3,000 m; F (holo).

Rondeletia chinajensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 254. 1947. *J. A. Steyermark 45637*; 1–2 Apr. 1942; Guatemala, Dept. Alta Verapaz, Cerro Chinajá; 150–700 m; F (holo).

Rondeletia cordovana Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 26. 1943. *J. A. Steyermark 29906*; Oct. 1939; Guatemala, Dept. Zacapa, Quebrada Alejandría, summit of Sierra de las Minas, vicinity of Finca Alejandría; 2,500 m; F (holo).

Rondeletia izabalensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 286. 1940. *P. C. Standley 72891*; 3 May 1939; Guatemala, Dept. Izabal, Escoba; sea level; F (holo).

Rondeletia larensis Steyerm., Mem. New York Bot. Gard. 17(1): 245. 1967. *J. Saer 727*; Jan. 1931; Venezuela, Lara, Distr. Torres, Río Sicariqua; VEN (holo).

Rondeletia macrocalyx Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 254. 1947. *J. A. Steyermark 41864*; 25 Dec. 1941; Guatemala, Dept. Izabal, Cerro San Gil; 300–900 m; F (holo).

Rondeletia myriantha Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 288. 1940. *A. F. Skutch 1569*; 31 Oct. 1934; Guatemala, Dept. Suchitepéquez, Finca Moca; 960 m; F (holo).

Rondeletia orinocensis Steyerm., Mem. New York Bot. Gard. 17(1): 247. 1967. *Ll. Williams 13329*; 15 June 1940; Venezuela, Bolívar, Cerro El Tigre, Río Cuchivero; 90 m; VEN (holo).

Rondeletia purdiei Hook. f. var. *glabrior* Steyerm., Mem. New York Bot. Gard. 17(1): 243. 1967. *H. H. Smith 320*; 17 July 1898; Colombia, Magdalena, near Masinga, Santa Marta; 78 m; NY (holo).

Rondeletia skutchii Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 289. 1940. *A. F. Skutch 2110*; 10 Jan. 1935; Guatemala, Dept. Suchitepéquez, Finca Moca; 1,260 m; F (holo).

Rondeletia venezuelensis Steyerm., Mem. New York Bot. Gard. 17(1): 243. 1967. *H. Pittier 11995*; 25 Dec. 1925; Venezuela, Cojedes, El Tinaco; NY (holo).

Rondeletia vulcanicola Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 291. 1940. *J. A. Steyermark 33220*; 31 Dec. 1939; Guatemala, Dept. Quezaltenango, Finca Pireneos, Volcán Santa María; 1,300-1,500 m; F (holo).

Rondeletia zolleriana Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 292. 1940. *J. A. Steyermark 37738*; 14 Mar 1940; Guatemala, Dept. San Marcos, between Finca El Porvenir and Loma Corona, Volcán Tajumulco; 1,300 2,000 m; F (holo).

Rudgea ayangannensis Steyerm., Mem. New York Bot. Gard. 17(1): 410. 1967. *S. S. Tillett et al. 45182*; 7 Aug. 1960; Guyana, Mt. Ayanganna, upper Mazaruni River; 900–1,100 m; NY (holo).

Rudgea berryi Steyerm. & Dwyer, Pittieria 9: 12. 1981. *P. E. Berry & C. Uhl 1558*; 24 Sep. 1975; Venezuela, T.F. Amazonas; 4 km from San Carlos de Río Negro, on road to Solano; 120 m; VEN (holo), MO.

Rudgea bolivarensis Steyerm., Mem. New York Bot. Gard. 17(1): 415. 1967. *J. A. Steyermark 59118*; 2 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,005 1,065 m; VEN (holo).

Rudgea bremekampiana Steyerm., Mem. New York Bot. Gard. 17(1): 407. 1967. *R. S. Cowan 38429*; 19 Nov. 1954; Brazil, Amapa, Rio Araguary, Serra do Navio; 70–300 m; NY (holo).

Rudgea buntingii Steyerm., Acta Bot. Venez. 6: 177. 1971. *J. A. Steyermark et al. 100252*; 9–10 Nov. 1967; Venezuela, Yaracuy, Cerro La Chapa; 1,200-1,400 m; VEN (holo), NY.

Rudgea cardonae Steyerm., Mem. New York Bot. Gard. 17(1): 403. 1967. *F. Cardona P. 1503*; 16–24 Feb. 1946; Venezuela, T.F. Amazonas, Río Castanho; 100 140 m; VEN (holo).

Rudgea carolina Standl. & Steyerm., Fieldiana Bot. 28(3): 614. 1953. *Ll. Williams 14674*; 3 July 1942; Venezuela, T.F. Amazonas, San Carlos de Río Negro; 100 m; F (holo).

Rudgea corocoroensis Steyerm., Ann. Missouri Bot. Gard. 75: 349. 1988. *R. L. Liesner & B. K. Holst 21827*; 10 Mar. 1987; Venezuela, T.F. Amazonas, 5–8 km NW of Yutajé settlement, 3 km W of Río Coro Coro; 700–1,000 m; MO (holo—3482982), VEN.

Rudgea costanensis Steyerm., Mem. New York Bot. Gard. 17(1): 420. 1967. *H. Pittier 13498*; May 1934; Venezuela, Distr. Federal, near El Limón, Valle de Puerto Cruz, El Camaticaral; 950–1,000 m; US (holo).

Rudgea enervia Steyerm., Mem. New York Bot. Gard. 17(1): 418. 1967. *S. S. Tillett et al. 45117*; 12 Aug. 1960; Guyana, Mt. Ayanganna, Thompson Camp, upper Mazaruni River; 1,418 m; NY (holo).

Rudgea hospes Standl. & Steyerm., Fieldiana Bot. 28(3): 615. 1953. *J. A. Steyermark 55509*; 12 Feb. 1944; Venezuela, Lara, between Buenos Aires to Canyon of El Callado, above Humocaro Alto; 2,285–2,740 m; F (holo).

Rudgea lucentifolia Standl. & Steyerm., Fieldiana Bot.

28(3): 616. 1953. *J. A. Steyermark 56502*; 14 May 1944; Venezuela, Mérida, Mesa del Trapiche and El Molino; 2,530 2,590 m; F (holo).

Rudgea marcano-bertii Steyerm., Pittieria 9: 12. 1981. *L. Marcano Berti & I. Pena 532-979*; Venezuela, Táchira, Mun. Lobatera, Parque Cazadero, Palo Grande-Minas de Carbon de Lobatera; 1,700 m; MER, VEN (holo).

Rudgea merumensis Steyerm., Mem. New York Bot. Gard. 17(1): 402. 1967. *S. S. Tillett et al. 44825*; 5–6 July 1960; Guyana, Merume Mt., upper Mazaruni River basin, Partang River; 1,140 m; NY (holo).

Rudgea morichensis Steyerm., Mem. New York Bot. Gard. 17(1): 424. 1967. *B. Maguire et al. 30881*; 14 Jan. 1951; Venezuela, T.F. Amazonas, Cerro Moriche, Río Ventuari; 800 m; NY (holo).

Rudgea nebulicola Steyerm., Mem. New York Bot. Gard. 17(1): 414. 1967. *J. A. Steyermark 56441*; 9 May 1944; Venezuela, Mérida, Quebrada de Los Salichales, tributary of Río Canagua; 1,950 2,135 m; VEN (holo).

Rudgea oldemanii Steyerm., Brittonia 33: 397. 1981. *R. A. A. Olderman B-627*; 31 Aug. 1966; French Guiana, Grand Matoury, Ilede Cayenne; P (holo).

Rudgea phaneroneura Steyerm., Mem. New York Bot. Gard. 17(1): 403. 1967. *J. A. Steyermark & J. J. Wurdack 330*; 2 Feb. 1955; Venezuela, Bolívar, near Summit Camp, Chimantá Massif, Central Section; 1,925 m; MO (2011378, 2011681), VEN (holo).

Rudgea prancei Steyerm., Brittonia 33: 398. 1981. *G. T. Prance et al. 14739*; 14 Sep. 1971; Brazil, Amazonas, vicinity Manaus, Reserva Ducke, vicinity of Igarapé Acara; NY, VEN (holo).

Rudgea ruiz-teranii Steyerm., Pittieria 9: 13. 1981. *L. Ruíz Terán 4703*; 12 Oct. 1967; Venezuela, Mérida, Distr. Sucre, Azulita y Lagunillas; MER, VEN (holo).

Rudgea sanarensis Steyerm., Mem. New York Bot. Gard. 17(1): 420. 1967. *L. Aristeguieta 3938*; Aug. 1959; Venezuela, Lara, Sanare; 1,500 m; VEN (holo).

Rudgea simiarum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 389. 1940. *J. A. Steyermark 38839*; 5 Apr. 1940; Guatemala, Dept. Izabal, Montaña del Mico; 50–500 m; F (holo).

Rudgea sipapoensis Steyerm., Mem. New York Bot. Gard. 17(1): 411. 1967. *B. Maguire & L. Politi 28483*; 21 Jan. 1949; Venezuela, T.F. Amazonas, Cerro Sipapo (Paraque); 125–600 m; NY (holo).

Rudgea standleyana Steyerm., Mem. New York Bot. Gard. 17(1): 409. 1967. *R. S. Cowan & J. C. Lindeman 39036*; 31 Dec. 1954; Suriname, Nassau Mountains, Marowijne River, Plateau A; 430–520 m; NY (holo).

Rudgea tillettii Steyerm., Mem. New York Bot. Gard. 17(1): 416. 1967. *S. S. Tillett et al. 43934*; 28 June 1960; Guyana, Porkknocker Camp 2 on Partang River, Merume Mountains; 625 m; NY (holo) = *P. coussareoides* Standl., 1974.

Rudgea trujilloi Steyerm., Acta Bot. Venez. 6: 178. 1971. *B. Trujillo 6555*; 18 July 1964; Venezuela, Lara, entre Quíbor y Sanare; 1,000 m; MY (holo).

Rudgea vareschii Steyerm., Acta Bot. Venez. 6: 179. 1971. *V. Vareschi 1386*; 30 May 1952; Venezuela, Mérida, Selva de Mucuy; 3,120 m; MER (holo).

Rudgea wurdackii Steyerm., Mem. New York Bot. Gard. 17(1): 413. 1967. *J. J. Wurdack & L. Adderley 42727*; 1 June 1959; Venezuela, T.F. Amazonas, Río Orinoco, above mouth of Río Atabapo; 125 m; NY (holo).

Rustia venezuelensis Standl. & Steyerm., Fieldiana Bot. 28(3): 616. 1953. *J. A. Steyermark 56333*; 6 May 1944; Venezuela, Mérida, below El Bao, between Mucuchachi and Canagua; 1,065–1,820 m; F (holo).

Sabicea aristeguietae Steyerm., Mem. New York Bot. Gard. 17(1): 309. 1967. *L. Aristeguieta 1649*; Feb. 1953. Venezuela, Barinas, Ciudad Bolivia (Pedraza); VEN (holo).

Sabicea bariensis Steyerm., Ann. Missouri Bot. Gard. 75: 350. 1988. *A. Gentry & B. Stein 47314*; 9 May 1984; Venezuela, T.F. Amazonas, upper Río Baria; 140 m; MO (holo—3393683), VEN.

Sabicea brachycalyx Steyerm., Mem. New York Bot. Gard. 17(1): 313. 1967. *J. J. Wurdack & L. Adderley 42833*; 6 June 1959; Venezuela, T.F. Amazonas, San Fernando de Atabapo; 125 m; NY (holo).

Sabicea grandifolia Steyerm., Fl. Venez. 9(1): 514. 1974. *G. Morillo et al. 4070*; 27 Apr. 1974; Venezuela, T.F. Amazonas, alrededores de San Simón de Cucuy, 2 km NE de Piedra de Cucuy; VEN (holo).

Sabicea liesneri Steyerm., Pittieria 9: 15. 1981. *J. A. Steyermark & R. L. Liesner 118876*; Venezuela, Táchira, vicinity of Las Minas, N of La Laguna, 16 km SE of Santa Ana; 1,150–1,250 m; VEN (holo), MO.

Sabicea morillorum Steyerm., Fl. Venez. 9(1): 511. 1974. *G. Morillo et al. 3903*; 24 Apr. 1974; Venezuela, T.F. Amazonas, 2 3 km NE de San Carlos de Río Negro, carretera San Carlos Solano; 100 m; VEN (holo).

Sabicea sastre Steyerm., Brittonia 33: 398. 1981. *C. Sastre 934*; 4 Mar. 1971; Colombia, Meta, Río Guatequia, 12 km en amont de Villavicencio, Quebrada de la Mendoza; P (holo).

Sabicea tillettii Steyerm., Phytologia 31(6): 484. 1975. *S. S. Tillett et al. 745-385*; 27 May–3 June 1974; Venezuela, T.F. Amazonas, Dept. Atabapo, ca. 1 km inland from mouth of Caño Chamuchina; 130 m; VEN (holo).

Sabicea velutina Benth. subsp. *chimantensis* Steyerm., Mem. New York Bot. Gard. 17(1): 315. 1967. *J. A. Steyermark & J. J. Wurdack 1340*; 10 Mar. 1955; Venezuela, Bolívar, Amuri-tepui (Chimantá Massif); 1,365 m; MO (2011341, 2012047), VEN (holo).

Sabicea velutina Benth. subsp. *duidense* Steyerm., Mem. New York Bot. Gard. 17(1): 316. 1967. *B. Maguire & B. Maguire, Jr. 29137*; 22–24 Apr. 1949; Venezuela, T.F. Amazonas, Culebra Peak, Cerro Duida; 1,600 m; NY (holo).

Sabicea venezuelensis Steyerm., Mem. New York Bot. Gard. 17(1): 309. 1967. *F. Cardona P. 707*; 21 July 1943; Venezuela, Bolívar, Raudal Aguacarita, Río Paragua; VEN (holo).

Schradera andina Steyerm., Acta Bot. Venez. 6: 122. 1971. *J. A. Steyermark et al. 103752*; 30 Sep. 1970; Venezuela, Trujillo, above Escuque, El Paramito; 1,650 m; MO (2217413), NY, VEN (holo).

Schradera bipedunculata Steyerm., Mem. New York Bot. Gard. 10(5): 263. 1963. *B. Maguire et al. 46814*; 20 Aug. 1962; Venezuela, Bolívar, Río Uiri-yuk, alto Río Cuyuni; 500–600 m; NY (holo), VEN.

Schradera brevipes Steyerm., Mem. New York Bot. Gard. 10(5): 264. 1963. *B. Maguire & L. Politi 27895*; 23 Dec. 1948; Venezuela, T.F. Amazonas, Cerro Sipapo (Paraque); 1,400 m; NY (holo).

Schradera cubensis Steyerm., Mem. New York Bot. Gard. 10(5): 267. 1963. *E. L. Ekman 9368*; 7 July 1918; Cuba, Prov. Oriente, Sierra Maestra, prope Nanacal, prope Alto de Comején; 1,100 m; NY (holo).

Schradera glabriflora Steyerm., Mem. New York Bot. Gard. 10(5): 267. 1963. *J. A. Steyermark & G. Agostini 17*; 4 Sep. 1960; Venezuela, Aragua, Parque Nacional Henri Pittier, trail above Pittier National Monument on Pico Paraiso to summit; 1,250–1,600 m; VEN (holo).

Schradera hilliifolia Steyerm., Mem. New York Bot. Gard. 10(5): 269. 1963. *J. J. Wurdack & L. S. Adderley 43316*; 4 July 1959; Venezuela, T.F. Amazonas, Maroa, Río Guainía; 130 m; NY (holo).

Schradera maguirei Steyerm., Mem. New York Bot. Gard. 10(5): 271. 1963. *B. Maguire 32974*; 4 Jan. 1952. Venezuela, T.F. Amazonas, Cerro Guaiquinima, North Valley; 1,600–1,700 m; NY (holo), VEN.

Schradera marahuacensis Steyerm., Ann. Missouri Bot. Gard. 74: 114. 1987. *J. A. Steyermark & B. K. Holst 130721*; 21–22 Feb. 1985; Venezuela, T.F. Amazonas, Dept. Atabapo, Cerro Marahuaca, Sima Camp; 1,140 m; MO (holo –3327359), VEN.

Schradera nilssonii Steyerm., Bol. Soc. Venez. Ci. Nat. 23: 83. 1962. *J. A. Steyermark & S. Nilsson 196*; 15 Apr. 1960; Venezuela, Bolívar, Fila de La Danta; 1,200 m; NY, VEN (holo).

Schradera puberula Steyerm., Mem. New York Bot. Gard. 10(5): 273. 1963. *J. Cuatrecasas 15182*; 19–28 Aug. 1943; Colombia, Dept. El Valle, Cordillera Occidental, bosques Hoya del Río Digua, Piedra de Moler; 900–1,180 m; F (holo).

Schradera pulverulenta Steyerm., Acta Bot. Venez. 4(1): 113. 1964. *J. Cuatrecasas 21086*; 18–22 May 1946; Colombia, Dept. del Valle, Río Calima (region del Chocó); 30–50 m; US (holo), VEN.

Schradera subsessilis Steyerm., Mem. New York Bot. Gard. 10(5): 275. 1963. *R. A. Howard 12302*; 2 Aug. 1950; Dominican Republic, Prov. Barahona, Monteada Nueva to Loma Alta; 1,500 m; NY (holo).

Schradera ternata Steyerm., Mem. New York Bot. Gard. 10(5): 275. 1963. *S. S. Tillett et al. 44992*; 2 Aug. 1960; Guyana, NE side of Mt. Ayanganna; 884–915 m; NY (holo).

Schradera vahlii Steyerm., Mem. New York Bot. Gard. 10(5): 277. 1963, nom. nov.

Schradera vahlii Steyerm. var. *acutifolia* Steyerm., Mem. New York Bot. Gard. 10(5): 277. 1963. *A. C. Smith 10289*; 26 Mar. 1956; Dominica, vicinity of Fresh Water Lake, near Laudat; 450–600 m; NY (holo), US.

Schradera yutajensis Steyerm., Mem. New York Bot. Gard. 10(5): 276. 1963. *B. & C. K. Maguire 35356*; 21 Feb. 1953; Venezuela, T.F. Amazonas, Caño Yutaje, Cerro Yutaje; 1,500 m; NY (holo).

Sickingia aristeguietae Steyerm., Bol. Soc. Venez. Ci. Nat. 15(81): 3. 1954. *L. Aristeguieta & F. Pannier 1824*; 1 July 1953; Venezuela, Yaracuy, Selva de Aroa; VEN (holo) = *Simira aristeguietae* (Steyerm.) Steyerm., 1974.

Simira erythroxylon (Willd.) Bremek. var. *meridensis* Steyerm., Acta Bot. Venez. 6: 113. 1971. *E. E. Little 15354*; 21 July 1953; Venezuela, Mérida, San Juan Bautista; 1,000 m; NY (holo).

Simira erythroxylon (Willd.) Bremek. var. *saxicola* Steyerm., Acta Bot. Venez. 6: 112. 1971. *J. J. Wurdack & J. V. Monachino 39858*; 13 Dec. 1955; Venezuela, Bolívar, Orinoco River, Isla Sta. Elba; 80–90 m; NY (holo), VEN.

Simira ignicola Steyerm., Ann. Missouri Bot. Gard. 75: 1086. 1988. *J. A. Steyermark et al. 131659*; 9 Sep. 1985; Venezuela, Bolívar, Distr. Cedeño, 1 km S of Quebrada La Flore, affluent of Río Ore, affluent of Río Paraguaza; 85 m; MO (holo – 3295642), VEN.

Simira lezamae Steyerm., Acta Bot. Venez. 8: 248. 1973. *A. Torres Lezamae 203*; 15 Apr. 1972; Venezuela, Barinas, Distr. Obispos, Mun. Cruz Paredes; 360 m; VEN (holo).

Simira wurdackii Steyerm., Mem. New York Bot. Gard. 23(1): 304. 1972. *J. J. Wurdack 2461*; 26–28 Oct. 1962; Perú, Dept. Loreto, Prov. Alto Amazonas, Río Marañon, Pongo de Manseriche; 250 m; US (holo), VEN.

Sipanea Aublet subsect. *Cryptotricha* Steyerm., Mem. New York Bot. Gard. 17(1): 264. 1967, subsect. nov.

Sipanea Aublet subsect. *Luteovillosae* Steyerm., Mem. New York Bot. Gard. 17(1): 270. 1967, subsect. nov.

Sipanea Aublet subsect. *Nudae* Steyerm., Mem. New York Bot. Gard. 17(1): 268. 1967, subsect. nov.

Sipanea Aublet subsect. *Phanerotricha* Steyerm., Mem. New York Bot. Gard. 17(1): 266. 1967, subsect. nov.

Sipanea ayangannensis Steyerm., Mem. New York Bot. Gard. 17(1): 269. 1967. *S. S. Tillett et al. 45114*; 12 Aug. 1960; Guyana, upper Mazaruni River, Mt. Ayanganna; 1,418 m; NY (holo).

Sipanea carrenoi Steyerm., Ann. Missouri Bot. Gard. 71: 333. 1984. *J. A. Steyermark et al. 115598*; 22 Feb. 1978; Venezuela, Bolívar, Gran Sabana; 1,130 m; MO (3223163), VEN (holo).

Sipanea cowanii Steyerm., Mem. New York Bot. Gard. 17(1): 265. 1967. *R. S. Cowan & T. R. Soderstrom 1863*; 18 Feb. 1962; Guyana, Kaieteur Plateau, near Johnson's View, Kaieteur Falls, Potaro Gorge; 425 m; US (holo).

Sipanea gleasonii Steyerm., Mem. New York Bot. Gard. 17(1): 265. 1967. *H. A. Gleason 431*; 18 June–8 July 1921; Guyana, Tumatumari; NY (holo).

Sipanea glomerata H.B.K. var. *paucinervia* Steyerm., Mem. New York Bot. Gard. 17(1): 282. 1967. *B. Maguire et al. 30458*; 28 Dec. 1950; Venezuela, T.F. Amazonas, 30 km above Playa Alta; 200 m; NY (holo).

Sipanea ovalifolia Bremek. var. *villosissima* Steyerm., Brittonia 36: 159. 1984. *G. Cremers 6460*; 26 Apr. 1980; French Guiana, 4 km SE de Saul; 600–700 m; CAY (holo), VEN.

Sipanea prancei Steyerm., Brittonia 33: 400. 1981. *G. T. Prance et al. 10528*; 14 Feb. 1971; Brazil, Roraima, Indian trail from Surucucu, near Maita Indian village; NY (holo), VEN.

Sipanea pratensis Aublet var. *dichotoma* (H.B.K.) Steyerm. f. *brachycarpa* Steyerm., Mem. New York Bot. Gard. 17(1): 276. 1967. *B. Maguire & L. Politi 27324*; 19 Nov. 1948; Venezuela, T.F. Amazonas, Danta (Tapir) Falls, Río Cuao, Río Orinoco; 125 m; VEN (holo).

Sipanea pratensis Aublet var. *dichotoma* (H.B.K.) Steyerm. f. *breviflora* Steyerm., Mem. New York Bot. Gard. 17(1): 277. 1967. *J. A. Steyermark 89276*; 1–11 Feb. 1961; Venezuela, Bolívar, cerro between Las Nieves and base of slopes SE of Cerro Picacho Altiplanicie de Nuria; 100–300 m; VEN (holo).

Sipanea pratensis Aublet var. *dichotoma* (H.B.K.) Steyerm. f. *glabriloba* Steyerm., Mem. New York Bot. Gard. 17(1): 276. 1967. *J. J. Wurdack & L. Adderley 42916*; n.d.; Venezuela, T.F. Amazonas, Yavita–Pimichin trail near Yavita, Río Atabapo; 125–140 m; NY (holo).

Sipanea pratensis Aublet var. *dichotoma* (H.B.K.) Steyerm. f. *glabrior* Steyerm., Mem. New York Bot. Gard.

17(1): 2777. 1967. *J. J. Wurdack & J. V. Monachino 39823*; 12 Dec. 1955; Venezuela, Bolívar, Cerro San Borja; 100–300 m; NY (holo).

Sipanea pubinoda Steyerm., Mem. New York Bot. Gard. 17(1): 278. 1967. *L. Williams 15656*; 29 May 1942; Venezuela, T.F. Amazonas, Capihuara, Alto Casiquiare; 120 m; VEN (holo).

Sipanea setacea Steyerm., Ann. Missouri Bot. Gard. 74: 114. 1987. *O. Huber et al. 8246*; 31 Aug. 1983; Venezuela, Bolívar, Distr. Piar, Cerro El Venado, 20 km E of Canaima; 1,300 m; NY (holo).

Sipaneopsis Steyerm., Mem. New York Bot. Gard. 17(1): 284. 1967, gen. nov.

Sipaneopsis foldatsii Steyerm., Mem. New York Bot. Gard. 17(1): 288. 1967. *E. Foldats 3678*; 4 Sep. 1960; Venezuela, T.F. Amazonas, Santa Cruz, Río Atabapo, Río Atacavi; VEN (holo).

Sipaneopsis huberi Steyerm., Ernstia 23: 37. 1984. *O. Huber & E. Medina 5786*; 6 Feb. 1981; Venezuela, T.F. Amazonas, Dept. Río Negro; 350 m; MO (3235600), VEN (holo).

Sipaneopsis maguirei Steyerm., Mem. New York Bot. Gard. 17(1): 287. 1967. *B. Maguire et al. 41438*; 13 Sep. 1957; Colombia, Cacagual Savanna, Río Atabapo, between San Fernando de Atabapo and Caño Temi; 135 m; NY (holo).

Sipaneopsis morichensis Steyerm., Mem. New York Bot. Gard. 17(1): 286. 1967. *B. Maguire et al. 30878*; 14 Jan. 1951; Venezuela, T.F. Amazonas, Cerro Moriche, Río Ventuari; 800 m; NY (holo).

Sipaneopsis pacimoniensis Steyerm., Mem. New York Bot. Gard. 17(1): 289. 1967. *B. Maguire et al. 37570*; 7 Feb. 1954; Venezuela, T.F. Amazonas, Río Pacimoni; 100–140 m; NY (holo).

Sipaneopsis wurdackii Steyerm., Mem. New York Bot. Gard. 17(1): 288. 1967. *B. Maguire et al. 37639*; 9 Feb. 1954; Venezuela, T.F. Amazonas, Caño Hechimoni; 100–130 m; NY (holo).

Spermacoce perijaënsis Steyerm., Acta Bot. Venez. 8: 252. 1973. *J. A. Steyermark et al. 105747*; 31 Mar. 1972; Venezuela, Zulia, Sierra de Perija; 1,140 m; VEN (holo).

Sphinctanthus insignis Steyerm., Brittonia 33: 400. 1981. *R. P. Belem & R. S. Pinheiro 2738*; 8 Oct. 1966; Brazil, Bahia, Guaratinga; VEN (holo), NY.

Stachyarrhena acutiloba Steyerm., Mem. New York Bot. Gard. 12(3): 220. 1965. *A. Ducke 1844*; 24 Nov. 1945; Brazil, Amazonas, Tabatinga; NY (holo).

Stachyarrhena reticulata Steyerm., Mem. New York Bot. Gard. 12(3): 220. 1965. *B. Maguire et al. 36259*; 18 Nov. 1953; Venezuela, T.F. Amazonas, river margin between San Fernando de Atabapo and Cacagual; 130 m; NY (holo).

Tocoyena brevifolia Steyerm., Mem. New York Bot. Gard. 12(3): 196. 1965. *Ll. Williams 16039*; 7 May 1943; Venezuela, T.F. Amazonas, baja Sanariapo, laja Carestia; 120 m; VEN (holo), F.

Tocoyena costanensis Steyerm., Bol. Soc. Venez. Ci. Nat. 25(106): 73. 1963. *E. Delgado 160*; 22 May 1938; Venezuela, Distr. Federal, Avila; VEN (holo).

Tocoyena costanensis Steyerm. subsp. *andina* Steyerm., Acta Bot. Venez. 6: 125. 1971. *L. Ruíz Terán* 1433; n.d.; Venezuela, Mérida, La Cuchilla; VEN (holo).

Tocoyena cuatrecasasii Steyerm., Acta Bot. Venez. 4(1): 113. 1964. *J. Cuatrecasas 9198*; 6 Apr. 1940; Colombia, Comisaria del Caqueta, Cordillera Oriental, Sucre, Quebrada de la Calana; 1,000–1,100 m; US (holo).

Tocoyena guianensis K. Schum. var. *communis* Steyerm., Mem. New York Bot. Gard. 12(3): 194. 1965. *H. S. Irwin et al. 47620*; 18 Aug. 1960; Brazil, Terr. Amapa, Río Oiapoque opposite Pedro Alice; NY (holo).

Tocoyena guianensis K. Schum. var. *glabriuscula* Steyerm., Mem. New York Bot. Gard. 12(3): 195. 1965. *B. Maguire & J. J. Wurdack 34923*; Venezuela, T.F. Amazonas, Piedra Cucuy, Río Negro; 100–200 m; depository not designated.

Tocoyena orinocensis Standl. & Steyerm., Fieldiana Bot. 28(3): 617. 1953. *J. A. Steyermark 58442*; 8 Sep. 1944; Venezuela, T.F. Amazonas, below mouth of Río Sanariapo, along Orinoco River; 100 m; F (holo).

Tresanthera thyrsiflora Steyerm., Bol. Soc. Venez. Ci. Nat. 25(107): 248. 1964. *A. L. Bernardi 5829A*; 23 Nov. 1956; Venezuela, Miranda, selvas pluviales del Guatopo; 400–600 m; NY (holo).

Yutajea Steyerm., Ann. Missouri Bot. Gard. 74: 676. 1987, gen. nov.

Yutajea liesneri Steyerm., Ann. Missouri Bot. Gard. 74: 676. 1987. *R. L. Liesner & B. K. Holst 21826*; 10 Mar. 1987; Venezuela, T.F. Amazonas, Dept. Atures, 5–8 km NW of Yutaje settlement, 3 km W of Río Coro Coro, W of Serranía de Yutaje; MO (holo), VEN.

RUTACEAE

Amyris ignea Steyerm., Fieldiana Bot. 28(2): 272. 1952, nom. nov.

Casimiroa emarginata Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 165. 1944. *J. A. Steyermark 36931*; 28 Feb. 1940; Guatemala, Dept. San. Marcos, Tajumulco, Volcán Tajumulco; 2,300–2,800 m; F (holo).

Diomma fruticosa Steyerm., Fieldiana Bot. 28(2): 272. 1952. *J. A. Steyermark 60820*; 20 Nov. 1944; Venezuela, Bolívar, Río Karuai, between La Laja and Santa Teresita de Kavanayen; 1,220 m; F (holo).

Esenbeckia echinoidea Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 164. 1944. *P. C. Standley 74456*; 15 Oct. 1940; Guatemala, Dept. Chiquimula, between Ramírez and Cumbre de Chiquimula; 400–600 m; F (holo).

Galipea guatemalensis Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 165. 1944. *J. A. Steyermark 39448*; 14 Apr. 1940; Guatemala, Dept. Izabal, Río Dulce; F (holo).

Lubaria szczerbanii Steyerm., Brittonia 32: 17. 1980. *J. A. Steyermark et al. 117221*; 23 24 May 1978; Venezuela, Bolívar, Cerro Guaiquinima, a lo largo del afluente de Río Carapo, río arriba del Salto Szcerbanari; 730–750 m; US, VEN (holo).

Rauia subtruncata Steyerm., Ann. Missouri Bot. Gard. 75: 315. 1988. *R. L. Liesner & A. González 5991*; 1 3 Aug. 1978; Venezuela, Bolívar, 20–25 km SW of Manteco, on road to San Pedro de las Dos Bocas; 200 m; MO (holo—3396481), VEN.

Ravenia ruellioides Oliver var. *ptariana* Steyerm., Fieldiana Bot. 28(2): 273. 1952. *J. A. Steyermark 59511*; 29 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 1,810 m; F (holo).

Raveniopsis aracaënsis Kallunki & Steyerm., Brittonia 39: 409. 1987. *G. T. Prance et al. 29016*; 12 Feb. 1984; Brazil, Amazonas, Serra Aracá, plateau of N Massif, S extreme of N part of Aracá; F, INPA (holo), K, MO, NY, US.

Raveniopsis breweri Steyerm., Brittonia 32: 48. 1980.

J. A. Steyermark et al. 116166; 28 Feb. 1978; Venezuela, Bolívar, Auyan-tepui, N de la Misión de Camarata; 1,950 m; VEN (holo).

Raveniopsis cowaniana Steyerm. & Luteyn, Ann. Missouri Bot. Gard. 71: 316. 1984. *J. Luteyn 9413*; 7–8 Feb. 1984; Venezuela, Río Negro, Cerro de la Neblina; 1,880 m; VEN (holo).

Raveniopsis jauaensis Steyerm., Bol. Soc. Venez. Ci. Nat. 32(132/133): 338. 1976. *J. A. Steyermark et al. 108876*; 10 Feb. 1974; Venezuela, Bolívar, Meseta del Jaua; 1,410 m; VEN (holo).

Raveniopsis liesneri Steyerm., Ann. Missouri Bot. Gard. 75: 317. 1988. *R. L. Liesner 16605*; 15 18 Nov. 1984; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro de la Neblina, Camp 4; 780 m; MO (holo—3405796), VEN.

Rutaneblina Steyerm. & Luteyn, Ann. Missouri Bot. Gard. 71: 314. 1984, gen. nov.

Rutaneblina pusilla Steyerm. & Luteyn, Ann. Missouri Bot. Gard. 71: 314. 1984. *J. A. Steyermark 129798*; 8 Feb. 1984; Venezuela, T.F. Amazonas, Cerro de Neblina; 1,880 m; MO (3223149), VEN (holo).

Zanthoxylum aguilarii Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(3): 146. 1940. *P. C. Standley 63209*; 21 Jan. 1939; Guatemala, Dept. Sacatepéquez, above Dueñas; 1,600–1,800 m; F (holo).

Zanthoxylum nubium Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 243. 1940. *J. A. Steyermark 31430*; 8 Nov. 1939; Guatemala, Dept. Chiquimula, Volcán de Quezaltepeque, 3–4 mi. NE of Quezaltepeque; 1,500 2,000 m; F (holo).

Zanthoxylum pallidum Steyerm., Fieldiana Bot. 28(2): 273. 1952. *J. A. Steyermark 56580*; 18 May 1944; Venezuela, Mérida, above Tabay, 2,285–2,745 m; F (holo).

Zanthoxylum tachirense Steyerm., Fieldiana Bot. 28(2): 274. 1952. *J. A. Steyermark 57111*; 7 July 1944; Venezuela, Táchira, above La Grita, below Páramo de la Negra; 2,430–2,510 m; F (holo).

SABIACEAE

Meliosma dives Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 60. 1944. *J. A. Steyermark 46773*; May 1942; Guatemala, Dept. Suchitepéquez, Volcán de Santa Clara, above Chicacao; 1,250 m; F (holo).

Meliosma maxima Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 61. 1944. *J. A. Steyermark 38170*; Mar. 1940; Guatemala, Dept. Izabal, between Bananera and La Presa, Montaña del Mico; 300 m; F (holo).

Meliosma nubicola Steyerm. & Lasser, Bol. Soc. Venez. Ci. Nat. 26: 463. 1966. *J. A. Steyermark & M. Farinas 90967*; 21 Oct. 1962; Venezuela, Distr. Federal, Altos de No León; 2,400 m; VEN (holo).

Meliosma pittieriana Steyerm., Fieldiana Bot. 28(2): 354. 1952. *J. A. Steyermark 61524*; 18 Mar. 1945; Venezuela, Anzoátegui, Quebrada Seca; 1,000–1,100 m; F (holo).

Meliosma tepuiensis Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 448. 1967. *J. A. Steyermark 75701*; 19 June 1953; Venezuela, Bolívar, Apacara-tepui, Chimantá Massif; 1,900–1,950 m; NY (holo).

SALICACEAE

Salix cordata Muehlenb. f. *mollis* Palmer & Steyerm., Ann. Missouri Bot. Gard. 25: 770. 1938. *J. A. Steyermark 12491*; 4 Aug. 1936; U.S.A., Missouri, Dent Co.; MO (holo—1174271).

Salix cordata Muehlenb. f. *subintegra* Palmer & Steyerm., Ann. Missouri Bot. Gard. 25: 770. 1938. *J. A. Steyermark 20910*; 28 Nov. 1936; U.S.A., Missouri, Phelps Co., shore of lake at Yaney Mills Spring; MO (holo) = *S. rigida* Muehlenb. f. *subintegra* (Palmer & Steyerm.) Steyerm., 1960.

Salix sericea Marsh f. *glabra* Palmer & Steyerm., Ann. Missouri Bot. Gard. 25: 769. 1938. *J. A. Steyermark 12548*; 4 Aug. 1936; U.S.A., Missouri, Dent Co.; MO (holo—1130660). Note: The original description erroneously cites two different collections with the number 12918 as both the holotype and paratype.

SANTALACEAE

Thesium tepuiense Steyerm., Fieldiana Bot. 28(1): 225. 1951. *J. A. Steyermark 60237*; 15–17 Nov. 1944; Venezuela, Bolívar, between Ptari-tepui and Sororopan-tepui; 1,615 m; F (holo), MO (1621266).

SAPINDACEAE

Allophylus parimensis Steyerm., Ann. Missouri Bot. Gard. 75: 333. 1988. *J. A. Steyermark 107033*; 18 Apr.–23 May 1973; Venezuela, T.F. Amazonas, Sierra Parima, vecinidades de Simarawochi, Río Matacuni; 795 830 m; MO (holo—2669225), VEN.

Cupania andina Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 463. 1966. *J. A. Steyermark 56301*; 4 May 1944; Venezuela, Mérida, between Mucuty and Mucuchachi; 1,065–2,430 m; VEN (holo).

Cupania kavanayena Steyerm., Fieldiana Bot. 28(2): 343. 1952. *J. A. Steyermark 60912*; 11 Dec. 1944; Venezuela, Bolívar, Quebrada de Kavanayen; 1,200–1,220 m; F (holo) = *Matayba kavanayena* (Steyerm.) Steyerm., 1966.

Cupania kukenanica Steyerm., Fieldiana Bot. 28(2): 344. 1952. *J. A. Steyermark 59182*; 2 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,065 m; F (holo).

Cupania roraimae Steyerm., Fieldiana Bot. 28(2): 346. 1952. *J. A. Steyermark 59107*; 1 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,065–1,220 m; F (holo).

Cupania tepuiensis Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 446. 1967. *J. A. Steyermark & J. J. Wurdack 1133*; 26 Feb. 1955; Venezuela, Bolívar, Agparaman-tepui, Chimantá Massif; 1,880–1,955 m; MO (3021963), NY (holo).

Dipterodendron venezuelense Steyerm., Fieldiana Bot. 28(2): 346. 1952. *J. A. Steyermark 56569*; 15 May 1944; Venezuela, Mérida, between San Isidro Alto and Santa Cruz de Mora; 760–1,800 m; F (holo) = *Dilodendron elegans* (Radlk.) Gentry & Steyerm., 1987.

Llagunoa venezuelana Steyerm., Fieldiana Bot. 28(2): 347. 1952. *J. A. Steyermark 56507*; 14 May 1944; Venezuela, Mérida, above El Molino; 2,010–2,135 m; F (holo).

Matayba affinis Steyerm., Ann. Missouri Bot. Gard. 75: 1067. 1988. *G. Davidse et al. 17011*; 30 Apr.–1 May 1979; Venezuela, T.F. Amazonas, Dept. Atabapo, Cucurital de Caname, S bank of the middle part of Caño Caname; 100 m; MO (holo 2744469), VEN.

Matayba chimantensis Steyerm., Mem. New York Bot. Gard. 17(1): 447. 1967. *J. A. Steyermark 74656*; 25 Mar. 1953; Venezuela, Bolívar, Río Apacara, Apacara-tepui, Chimantá Massif; 400 m; MO (2011418), VEN (holo).

Maytayba jauaensis Steyerm., Bol. Soc. Venez. Ci. Nat. 32(132/133): 347. 1976. *J. A. Steyermark et al. 109673*; 28 Feb.–1–2, 5 Mar. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Jaua; 1,810–1,880 m; VEN (holo) = *M. oligandra* Sandw., 1988.

Matayba longipes Radlk. subsp. *tepuiensis* Steyerm., Ann. Missouri Bot. Gard. 75: 1069. 1988. *R. S. Cowan & J. J. Wurdack 31450*; 13 Feb. 1951; Venezuela, T.F. Amazonas, Serranía Parú, Caño Asisi, Top Camp to Caño Camp; 1,400 m; MO (holo—2997923), NY.

Matayba oligandra Sandw. var. *occidentalis* Steyerm., Ann. Missouri Bot. Gard. 75: 1069. 1988. *B. Maguire & L. Politi 28399*; 17 July 1949; Venezuela, T.F. Amazonas, Caño Grande, Río Cuao, Río Orinoco; 125 m; MO (holo—2934861), NY.

Matayba ptariana Steyerm., Fieldiana Bot. 28(2): 350. 1952. *J. A. Steyermark 60203*; 15 Nov. 1944; Venezuela, Bolívar, Salto de Iwaracaru-meru; 1,015 m; F (holo).

Matayba ptariana Steyerm. subsp. *guaiquinimae* Steyerm., Ann. Missouri Bot. Gard. 74: 635. 1987. *O. Huber 10388*; 27 Mar. 1985; Venezuela, Bolívar, Dept. Heres, Meseta de Guaiquinima; 1,400 m; MO (holo—3382924), NY, VEN.

Matayba reducta Steyerm., Fieldiana Bot. 28(2): 351. 1952. *J. A. Steyermark 60365*; 20–21 Nov. 1944; Venezuela, Bolívar, Quebrada O-paru-ma; 1,065–1,220 m; F (holo).

Matayba yutajensis Steyerm., Ann. Missouri Bot. Gard. 75: 1070. 1988. *B. & C. K. Maguire 35143*; 11 Feb. 1953; Venezuela, T.F. Amazonas, Serranía Yutaje, NW Ridge; 1,400 m; MO (holo—2934874), NY, VEN.

Matayba sororopaniana Steyerm., Fieldiana Bot. 28(2): 352. 1952. *J. A. Steyermark 60201*; 15 Nov. 1944; Venezuela, Bolívar, Sororopan-tepui; 1,656–1,980 m; F (holo).

Matayba venezuelana Steyerm., Fieldiana Bot. 28(2): 353. 1952. *J. A. Steyermark 60663*; 28 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,220 m; F (holo).

Paullinia manarae Steyerm., Acta Bot. Venez. 3: 202. 1968. *B. J. Manara s.n.*; 4 Oct. 1965; Venezuela, Distr. Federal, Naiguatá, Lomas de Las Delicias, Quebrada de Basenilla y Quebrada Guayoyo; 1,390–1,500 m; VEN (holo).

Paullinia mexiae Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(3): 155. 1940. *Y. Mexia 8855*; 19 Nov. 1937; Mexico, Guerrero, Distr. Adama, Temisco, Barranco de la Guacamaya, Sierra Madre del Sur, N of Río Balsas; F (holo), MO (1181481).

Paullinia mollicoma Steyerm., Fieldiana Bot. 28(2): 353. 1952. *J. A. Steyermark 60579*; 25 Nov. 1944; Venezuela, Bolívar, Quebrada O-paru-ma; 915–1,065 m; F (holo).

Paullinia naiguatensis Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 457. 1966. *J. A. Steyermark 91874*; 2 Nov. 1963; Venezuela, Distr. Federal, Cerro Naiguatá; VEN (holo).

Paullinia nuriensis Steyerm., Acta Bot. Venez. 3: 179. 1968. *J. A. Steyermark 89005*; 3 Feb. 1961; Venezuela, Bolívar, Cerro El Picacho, Altiplanicie de Nuria; 620 m; NY (holo).

Paullinia toxicodendroides Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 460. 1966. *J. A. Steyermark 92079*; 15–19 Nov. 1963; Venezuela, Distr. Federal, Cerro Naiguatá; 1,000–1,300 m; VEN (holo).

Serjania hispida Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 171. 1944. *J. A. Steyermark 43926*; 19 Feb. 1942; Guatemala, Dept. Alta Verapaz, along road between San Cristóbal and Chixoy; 1,200–1,300 m; F (holo).

Serjania lobulata Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 14. 1943. *P. C. Standley 73715*; Oct. 1940; Guatemala, Dept. Chiquimula, near the divide on road from Zacapa to Chiquimula; 660 m; F (holo).

Serjania macrocarpa Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 15. 1943. *W. A. Kellerman 7532*; 23 Feb. 1908; Guatemala, Dept. Izabal, Los Amates; F (holo).

Serjania phaseoloides Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 171. 1944. *J. A. Steyermark 50908*; 18 Aug. 1942; Guatemala, Dept. Huehuetenango, along Río Cuilco between Cuilo and San Juan; 1,200–1,300 m; F (holo).

Talisia caudata Steyerm., Ann. Missouri Bot. Gard. 75: 1072. 1988. *B. Maguire & L. Politi 28615*; 25 Jan. 1949; Venezuela, T.F. Amazonas, Cerro Sipapo, trail from Base Camp; 125 m; MO (holo—3304133, 3304132), NY.

Talisia glandulifera Steyerm., Ann. Missouri Bot. Gard. 75: 1072. 1988. *S. Mori et al. 15027*; 1 Oct. 1982; French Guiana, Saul, Monte La Fumée; 200–400 m; MO (holo—3427739), NY.

Talisia heterodoxa Steyerm., Ann. Missouri Bot. Gard. 75: 1073. 1988. *R. L. Liesner & A. González 11151*; n.d.; Venezuela, Bolívar, Represa Guri islands, 6–18 km S of dam; 220–240 m; MO (holo—2926530), VEN.

Talisia maruayana Steyerm., Ann. Missouri Bot. Gard. 75: 1070. 1988. *R. L. Liesner & B. K. Holst 20394*; 26 Apr. 1986; Venezuela, Bolívar, Amaruay-tepui; 550–810 m; MO (holo—3446405, 3446406, 3446407, 3446408), VEN. (mss. name = *T. amaruayensis*).

Talisia morilloi Steyerm., Acta Bot. Venez. 10: 237. 1975. *G. Morillo et al. 3339*; 16 July 1973; Venezuela, Topo Tacamahaco (Tamanaco), Quebrada Río Grande; 900–1,000 m; VEN (holo).

Talisia pentantha Steyerm., Ann. Missouri Bot. Gard. 75: 1075. 1988. *F. Ehrendorfer 74104-23*; 4 Oct. 1974; Venezuela, Bolívar, Canaima, W of Avensa Camp; 500 m; VEN (holo).

Talisia sancarlosiana Steyerm., Ann. Missouri Bot. Gard. 75: 1075. 1988. *L. Marcano Berti & P. Alcedo 119-979*; 11–17 Mar. 1970; Venezuela, T.F. Amazonas, between San Carlos and Solano; MER (holo).

Talisia tiricensis Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 448. 1967. *J. A. Steyermark & J. J. Wurdack 116*; 16 Jan. 1955; Venezuela, Bolívar, Río Tirica (Río Aparuren), above Techine-mero; 470 m; NY (holo).

Toulicia anomala Steyerm., Ann. Missouri Bot. Gard. 75: 1076. 1988. *J. J. Wurdack & J. V. Monachino 41253*; 17 Jan. 1956; Venezuela, Bolívar, Río Suapure, middle Orinoco; 110–120 m; MO (holo—3310903), NY.

SAPOTACEAE

Chrysophyllum ficoides Steyerm., Acta Bot. Venez. 2: 279. 1967. *J. A. Steyermark 93431*; 5 May 1964; Venezuela, Bolívar, Auyan-tepui; VEN (holo).

Chrysophyllum monachinoanum Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 432. 1966. *J. A. Steyermark et al. 92333*; 29–30 Dec. 1963; Venezuela, Bolívar, Cerro Venamo; 950–1,150 m; VEN (holo).

Pouteria auyantepuiensis Steyerm., Acta Bot. Venez. 2:

278. 1967. *J. A. Steyermark 93917*; Venezuela, Bolívar, Auyan-tepui, 1,850 m; depository not designated.
Pouteria spectabilis Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 436. 1966. *J. A. Steyermark & S. Nilsson 768*; 24–25 Apr. 1960; Venezuela, Bolívar, near headwaters of Río Aponguao, NE of Luepa; 1,200 m; VEN (holo).
Pouteria venamoënsis Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 434. 1966. *J. A. Steyermark et al. 92414*; 29–30 Dec. 1963; Venezuela, Bolívar, Cerro Venamo; 950–1,150 m; VEN (holo).

SARRACENIACEAE

Heliamphora heterodoxa Steyerm., Fieldiana Bot. 28(1): 239. 1951. *J. A. Steyermark 59766*; 2 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 2,000–2,200 m; F (holo).
Heliamphora heterodoxa Steyerm. var. *exappendiculata* Maguire & Steyerm., Mem. New York Bot. Gard. 29: 54. 1978. *J. J. Wurdack 34262*; 29 Jan. 1953; Venezuela, Bolívar, Chimantá-tepui, NW slope of Churi-tepui; 2,050 m; NY (holo).
Heliamphora heterodoxa Steyerm. var. *exappendiculata* f. *glabella* Steyerm., Ann. Missouri Bot. Gard. 71: 311. 1984. *J. A. Steyermark 93712*; 11 May 1964; Venezuela, Bolívar, Auyan-tepui; 1,600–1,800 m; VEN (holo).
Heliamphora minor Gleason f. *laevis* Steyerm., Ann. Missouri Bot. Gard. 71: 311. 1984. *F. Cardona 2661*; Jan. 1949; Venezuela, Bolívar, Cerro Auyan; 2,100 m; VEN (holo).

SAXIFRAGACEAE

Heuchera puberula Mack. & Bush f. *glabrata* Steyerm., Rhodora 51: 117. 1949. *J. A. Steyermark 66615*; 2 Oct. 1948; U.S.A., Missouri, Shannon Co., Jam Up Bluff along Jack's Fork of Current River, 4 mi. N of Teresita, 6 mi. NW of Monteer; F (holo).

SCROPHULARIACEAE

Calceolaria yuparum Steyerm., Acta Bot. Venez. 10: 243. 1975. *J. A. Steyermark et al. 105721*; 22–23, 28 Mar. 1972; Venezuela, Zulia, Sierra de Perija; 1,440–1,460 m; US, VEN (holo) = *C. mexicana* Benth. subsp. *prostrata* (Kränzlin) Molau, 1988.
Castilleja altorum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 85. 1944. *J. A. Steyermark 49908*; Aug. 1942; Guatemala, Dept. Huehuetenango, Cerro Chemalito, Sierra de los Cuchumatanes; 3,100–3,150 m; F (holo).
Pedicularis canadensis L. f. *albescens* Steyerm., Rhodora 54: 258. 1952. *J. A. Steyermark 67499*; 1 May 1949; U.S.A., Missouri, Wright Co., along route 5, 2.5 mi. S of Mansfield; F (holo).
Penstemon digitalis (Sweet) Nutt. f. *baueri* Steyerm., Rhodora 43: 663. 1941. *J. A. Steyermark 27665*; 1 July 1939; U.S.A., Missouri, Osage Co., 3 mi. NE of Westphalia, along Maries River; F (holo).
Russelia laciniata Standl. & Steyerm., Field Mus. Bot. Ser. 22(5): 379. 1940. *J. A. Steyermark 37982*; 16 Mar. 1940; Guatemala, Dept. San Marcos, above Finca El Porvenir, along Río Cabús near Cueva de las Palomas, Volcán Tajumulco; 1,300–1,500 m; F (holo).

SELAGINELLACEAE

Selaginella gigantea Steyerm. & A. R. Smith, Ann. Missouri Bot. Gard. 73: 209. 1986. *J. A. & C. Steyermark 95418*; 1 Apr. 1966; Venezuela, Carabobo, entre Los Tanques y La Toma, Río San Jían; 750 m; US (holo), VEN.

SIMAROUBACEAE

Picramnia caracasana Engler f. *tomentella* Steyerm., Fieldiana Bot. 28(2): 274. 1952. *J. A. Steyermark 57019*; 25 June 1944; Venezuela, Distr. Federal, E of El Junquito; 1,980–2,130 m; F (holo).
Picramnia nuriensis Steyerm., Acta Bot. Venez. 3: 177. 1968. *J. A. Steyermark 88591*; 19–23 Jan. 1961; Venezuela, Bolívar, Cerro El Picacho; Altiplanicie de Nuria; 450–620 m; NY (holo).
Picramnia tristamina Steyerm., Fieldiana Bot. 28(2): 275. 1952. *Ll. Williams 13918*; 23 Jan. 1942; Venezuela, T.F. Amazonas, camino de Yavita; 128 m; F (holo).

SMILACACEAE

Smilax auraimensis Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 472. 1966. *J. A. Steyermark 90823*; 16 Jan. 1962; Venezuela, Bolívar, Sierra Auraima; 400 m; VEN (holo).
Smilax chimantensis Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 440. 1967. *J. A. Steyermark 74652*; 25 Mar. 1953; Venezuela, Bolívar, Río Apacara, Apacara-tepui, Chimantá Massif; 400 m; NY (holo).
Smilax duidae Steyerm., Fieldiana Bot. 28(1): 154. 1951. *J. A. Steyermark 58057*; 26 Aug. 1944; Venezuela, T.F. Amazonas, Cerro Duida, Caño Negro; 260–610 m; F (holo).
Smilax jauaensis Steyerm. & Maguire, Mem. New York Bot. Gard. 23: 854. 1972. *J. A. Steyermark 98073*; 22 27 Mar. 1967; Venezuela, Bolívar, Cerro Jaua; 1,922–2,100 m; VEN (holo).
Smilax lasseriana Steyerm., Fieldiana Bot. 28(1): 154. 1951. *J. A. Steyermark 60121*; Venezuela, Bolívar, Sororopan-tepui; 2,255 m; F (holo).
Smilax pittieriana Steyerm., Fieldiana Bot. 28(1): 155. 1951. *J. A. Steyermark 60251*; 15–17 Nov. 1944; Venezuela, Bolívar, on mesa between Ptari-tepui and Sororopan-tepui; 1,615 m; F (holo).
Smilax staminea Griseb. f. *obtusata* Steyerm., Fieldiana Bot. 28(1): 156. 1951. *J. A. Steyermark 59695*; 1 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,700–1,800 m; F (holo).

SOLANACEAE

Athenaea locuples Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 375. 1940. *J. A. Steyermark 37953*; 16 Mar. 1940; Guatemala, Dept. San Marcos, above Finca El Porvenir, along Río Cabus, near Cueva de las Palomas, Volcán Tajumulco; 1,300–1,500 m; F (holo) = *Witheringia stramonifolia* H.B.K., 1974.
Athenaea macrocardia Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 375. 1940. *J. A. Steyermark 30004*; 14 Oct. 1939; Guatemala, Dept. Zacapa, Río Lima, Sierra de Las Minas, below Finca Alejandría; 2,000 m; F (holo) = *A. viscosa* (Schrader) Fern., 1974.
Cestrum aristeguietae Steyerm., Acta Bot. Venez. 6: 86. 1971. *J. A. & C. Steyermark 95463*; 2 Apr. 1966; Venezuela, Carabobo, Río San Gean, S of Borburata; 350 m; US VEN (holo).
Cestrum pariense Steyerm., Acta Bot. Venez. 1(2): 62. 1966. *J. A. Steyermark & G. Agostini 91026*; 18

July 1962; Venezuela, Sucre, Cerro Patao; 850 m; VEN (holo).

Cyphomandra bolivarensis Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 441. 1966. *J. A. Steyermark 60094*; 13 Nov. 1944; Venezuela, Bolívar, Sororopan-tepui; 2,225 2,255 m; VEN (holo).

Cyphomandra rojasiana Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 376. 1940. *J. A. Steyermark 33743*; 8 Jan. 1940; Guatemala, Dept. Quezaltenango, Volcán Santa María; 1,300–1,500 m; F (holo).

Cyphomandra villosa Steyerm., Phytologia 9(6): 348. 1964. *M. Acosta Solis 7743*; 12 Apr. 1944; Ecuador, Prov. Loja, region central, Las Chinchas; 2,250 m; F (holo).

Lycianthes barbatula Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 228. 1947. *J. A. Steyermark 46653*; 23 May 1942; Guatemala, Dept. Suchitepéquez, Volcán de Santa Clara; 1,250–2,650 m; F (holo).

Lycianthes chiapensis (Brandegee) Standl. var. *sparsistellata* Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 274. 1940. *J. A. Steyermark 31555*; 10 Nov. 1939; Guatemala, Dept. Chiquimula, Cerro Tixixí; 500–1,500 m; F (holo) = *L. chiapensis* (Brandegee) Standl. var. *chiapensis*, 1976.

Lycianthes orogenes Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 229. 1947. *J. A. Steyermark 52104*; 20 Sep. 1942; Guatemala, Dept. Chimaltenango, SW slope Volcán Fuego; 1,200–1,600 m; F (holo).

Markea costanensis Steyerm., Acta Bot. Venez. 3: 211. 1968. *J. A. Steyermark 94382*; 12 Oct. 1965; Venezuela, Distr. Federal, between Colonia Tovar–Junquito road and Hacienda El Limón; 1,300–1,500 m; VEN (holo).

Markea grandiflora Steyerm., Phytologia 9(6): 349. 1964. *M. Acosta Solis 7009*; 18 Jan. 1944; Ecuador, Prov. Pichincha, bajada de Loche a Condor Mackay, Cordillera Occidental; 2,700–3,100 m; F (holo).

Markea reticulata Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 461. 1967. *J. A. Steyermark 75157*; 19 Apr. 1953; Venezuela, Bolívar, Abacapa-tepui, Chimantá Massif; 1,200 1,600 m; VEN (holo).

Vierembergia espinosae Steyerm., Phytologia 9(6): 349. 1964. *R. Espinosa 1076*; 24 Nov. 1946; Ecuador, Prov. Loja, Namanda; 1,500 m; F (holo).

Physalis amica Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 231. 1947. *J. A. Steyermark 36175*; 20 Feb. 1940; Guatemala, Dept. San Marcos, between La Vega ridge and NE slopes Volcán Tacaná, along Río Vega; 2,500–3,000 m; F (holo).

Physalis calidaria Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 231. 1947. *P. C. Standley 67488*; 4 Mar. 1939; Guatemala, Dept. Quezaltenango, Fuentes Georginas, W Volcán Zunil; 2,850 m; F (holo).

Physalis campanula Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 18. 1943. *J. A. Steyermark 36067*; Feb. 1940; Guatemala, Dept. San Marcos, Quebrada Canjula, between Sibinal and Canjula, Volcán Tacaná; 2,200–2,500 m; F (holo).

Physalis carnosa Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 19. 1943. *J. A. Steyermark 37766*; Mar. 1940; Guatemala, Dept. San Marcos, Ocos; F (holo).

Physalis chimalteca Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(25): 232. 1947. *P. C. Standley 61803*; 3 Jan. 1939; Guatemala, Dept. Chimaltenango, Volcán de Acatenango, above Las Calderas; 2,400–2,700 m; F (holo) = *P. calidaria* Standl. & Steyerm., 1974.

Physalis lassa Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 19. 1943. *J. A. Steyermark 32868*; Dec. 1939; Guatemala, Dept. Jalapa, between Jalapa and Montaña Miramundo; 1,500–2,000 m; F (holo).

Solanum alpicum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 232. 1947. *J. A. Steyermark 50303*; 8 Aug. 1942; Guatemala, Dept. Huehuetenango, Cerro Chemal, Sierra de los Cuchumatanes; 3,700–3,800 m; F (holo) = *S. demissum* Lindl., 1974.

Solanum decurtatum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(1): 20. 1943. *C. L. Lundell 2012*; Mar. 1933; Guatemala, Petén, Lago de Yaxha; F (holo) = *S. blodgetii* Chapman, 1974.

Solanum fontium Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 234. 1947. *P. C. Standley 67473*; 4 Mar. 1939; Guatemala, Dept. Quezaltenango, Fuentes Georginas, W Volcán Zunil; 2,850 m; F (holo).

Solanum huehuetecum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 234. 1947. *J. A. Steyermark 51039*; 23 Aug. 1942; Guatemala, Dept. Huehuetenango, above Democracia on trail to Jutal; 1,000 m; F (holo).

Solanum muenscheri Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 275. 1940. *W. C. Muenscher 12360*; 14 Apr. 1937; Guatemala, Dept. Sololá, near Santa María; 3,150 m; F (holo).

Solanum puberuloba Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 444. 1966. *J. A. Steyermark & S. Nilsson 185*; 15–17 Apr. 1960; Venezuela, Bolívar, Fila de La Danta; 1,200 m; VEN (holo).

Solanum rufistellatum Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 445. 1966. *J. A. Steyermark & S. Nilsson 178*; 15–17 Apr. 1960; Venezuela, Bolívar, Fila de La Danta; 1,200 m; VEN (holo).

Solanum verapazense Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 276. 1940. *P. C. Standley 69756*; 30 Mar. 1939; Guatemala, Dept. Baja Verapaz, N of Santa Rosa; F (holo) = *S. torvum* Swartz, 1974.

STAPHYLEACEAE

Turpinia multijuga Steyerm., Fieldiana Bot. 28(2): 341. 1952. *J. A. Steyermark 56455*; 10 May 1944; Venezuela, Mérida, road to El Molino, Cuesta de Rincón and Cuesta del Barro; 1,925–2,175 m; F (holo).

STERCULIACEAE

"*Buettneria*" *venezuelensis* Steyerm., Acta Bot. Venez. 3: 183. 1968. *J. A. Steyermark 87782*; 26 Nov. 1960; Venezuela, Terr. Delta Amacuro, between La Margarita and Puerto Miranda, Río Acure; 80–100 m; NY (holo). Note: *Byttneria* is the correct spelling.

Melochia humboldtiana Steyerm., Fieldiana Bot. 28(2): 365. 1952. *J. A. Steyermark 62436*; 1 May 1945; Venezuela, Sucre, between Cocollar and Guamal; 1,200 m; F (holo).

STYRACACEAE

Styrax andinus Steyerm., Pittieria 4: 12. 1972. *J.-P. Veillon 14*; 1971; Venezuela, Mérida, San Eusebio, La Carbonera; 2,600 m; VEN (holo).

Styrax costanus Steyerm., Fieldiana Bot. 28(3): 490.

1953. *J. A. Steyermark 61575*; 20 Mar. 1945; Venezuela, Anzoátegui, Bergantín, Cerro Peonia (Cerro Los Pajaritos); 1,600–1,800 m; F (holo).

Styrax duidae Steyerm., Fieldiana Bot. 28(3): 491. 1953. *J. A. Steyermark 58242*; 2 Sep. 1944; Venezuela, T.F. Amazonas, Cerro Duida; 1,025 1,200 m; F (holo).

Styrax jauaensis Steyerm., Bol. Soc. Venez. Ci. Nat. 32: 390. 1976. *J. A. Steyermark et al. 109574*; 27 Feb. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Jaua; 2,228–2,250 m; VEN (holo).

Styrax longipedicellatus Steyerm., Acta Bot. Venez. 10: 242. 1975. *V. Barnes 43*; Apr.–June 1950; Venezuela, T.F. Amazonas, region del Duida y Marahuaca; VEN (holo).

Styrax tepuiense Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 456. 1967. *J. A. Steyermark & J. J. Wurdack 1028*; 21 Feb. 1955; Venezuela, Bolívar, Torono-tepui, Chimantá Massif; 2,030–2,150 m; NY (holo).

Styrax tepuiensis Steyerm. & Maguire subsp. *guaiquinimae* Maguire & Steyerm., Mem. New York Bot. Gard. 29(1): 218. 1978. *B. Maguire 32758*; 25 Dec. 1951; Venezuela, Bolívar, Río Paragua, Cerro Guaiquinima; NY (holo).

Styrax tepuiensis Steyerm. & Maguire subsp. *huachamacarii* Maguire & Steyerm., Mem. New York Bot. Gard. 29(1): 218. 1978. *B. Maguire et al. 30001*; 6 Dec. 1950; Venezuela, Terr. Amazonas, Cerro Huachamacari; NY (holo).

Styrax vulcanicola Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 264. 1940. *J. A. Steyermark 36801*; 27 Feb. 1940; Guatemala, Dept. San Marcos, between town of Tajumulco and Tecutla, NW slopes of Volcán Tajumulco; 1,800 2,500 m; F (holo).

Styrax wurdackiorum Steyerm., Acta Bot. Venez. 10: 241. 1975. *J. A. Steyermark et al. 106573*; 7 10 Dec. 1972; Venezuela, Bolívar, carretera El Dorado hacia Santa Elena de Uairen; 1,200–1,400 m; VEN (holo).

SYMPLOCACEAE

Symplocos abietorum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 221. 1947. *J. A. Steyermark 48482*; 9 July 1942; Guatemala, Dept. Huehuetenango, Rancho de Teja, Sierra de los Cuchumatanes; 3,330 m; F (holo).

Symplocos acananensis Steyerm., Ann. Missouri Bot. Gard. 74: 656. 1987. *J. A. Steyermark et al. 131868*; 1 3, 20 May 1986; Venezuela, Bolívar, vicinity of Guadequen, Río Acanán, affluent of Río Carrao, W of Cerro Los Hermanos; 470 m; MO (3514025), VEN (holo).

Symplocos chimantensis Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 459. 1967. *J. A. Steyermark & J. J. Wurdack 1100*; 23 Feb. 1955; Venezuela, Bolívar, Torono-tepui, Chimantá Massif; 1,955 2,090 m; NY (holo).

Symplocos culminicola Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 222. 1947. *J. A. Steyermark 31489*; 8 Nov. 1939; Guatemala, Dept. Chiquimula, Volcán de Quezaltepeque; 2,000 m; F (holo).

Symplocos jauaensis Steyerm. & Maguire, Mem. New York Bot. Gard. 23: 876. 1972. *J. A. Steyermark 98072*; 22–27 Mar. 1967; Venezuela, Bolívar, Cerro Jaua; 1,922–2,100 m; VEN (holo), NY.

Symplocos lasseri Steyerm., Fieldiana Bot. 28(3): 492. 1953. *T. Lasser & J. A. Steyermark 55103*; 30 Dec. 1943; Venezuela, Distr. Federal, Cordillera del Avila, above Caracas; 1,585–1,820 m; F (holo).

Symplocos neblinae Maguire & Steyerm., Mem. New York Bot. Gard. 29(1): 229. 1978. *B. Maguire et al. 42378*; 13 Dec. 1957; Venezuela, Terr. Amazonas, Cerro de la Neblina; 2,200 m; NY (holo).

Symplocos pittieriana Steyerm., Fieldiana Bot. 28(3): 492. 1953. *J. A. Steyermark 57335*; 15 July 1944; Venezuela, Táchira, base of Páramo de Tamá; 2,500–2,895 m; F (holo).

Symplocos roraimensis Steyerm., Fieldiana Bot. 28(3): 494. 1953. *J. A. Steyermark 58761*; 27 Sep. 1944; Venezuela, Bolívar, Mt. Roraima; 2,255–2,620 m; F (holo) = *S. pycnophylla* Sleumer, 1978.

Symplocos tamana Steyerm., Fieldiana Bot. 28(3): 495. 1953. *J. A. Steyermark 57340*; 15 July 1944; Venezuela, Táchira, base of Páramo de Tamá; 2,500–2,895 m; F (holo).

Symplocos vatteri Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 222. 1947. *J. A. Steyermark 48463*; 9 July 1942; Guatemala, Dept. Huehuetenango, Rancho de Teja, Sierra de los Cuchuamatanes; 3,330 m; F (holo).

Symplocos yapacanensis Steyerm., Acta Bot. Venez. 10: 242. 1975. *J. A. Steyermark & G. S. Bunting 103185*; 5 7 Mar 1970; Venezuela, T.F. Amazonas, Cerro Yapacana; 1,000–1,200 m; VEN (holo).

TAXODIACEAE

Taxodium distichum Rich. f. *confusum* Palmer & Steyerm., Ann. Missouri Bot. Gard. 25: 769. 1938. *J. A. Steyermark 11261*; 28 June 1936; U.S.A., Missouri, Wayne Co., Markham Springs, 3 mi. W of Williamsville; MO (holo).

TEPUIANTHACEAE

Tepuianthaceae Maguire & Steyerm., Mem. New York Bot. Gard. 29(2): 8. 1981, fam. nov.

Tepuianthus Maguire & Steyerm., Mem. New York Bot. Gard. 29(2): 9. 1981, gen. nov.

Tepuianthus aracensis Steyerm. & Maguire, Acta Amazonica 16/17: 219. 1986/1987. *J. Pipoly et al. 6838*; 18 Mar. 1984; Brazil, Amazonas, Serra Acacá, summit of southern massif; 1,200 m; INPA (holo), MO (3327363), NY.

Tepuianthus auyantepuiensis Maguire & Steyerm., Mem. New York Bot. Gard. 29(2): 10. 1981. *J. A. Steyermark et al. 116093*; 27 Feb. 1978. Venezuela, Bolívar, Auyan-tepui; 1,940 m; NY, VEN (holo).

Tepuianthus colombianus Maguire & Steyerm., Mem. New York Bot. Gard. 32: 16. 1981. *R. E. Schultes & I. Cabrera 15056*; 22–25 Jan. 1952; Colombia, Vaupés, near summit of Cerro Isibukuri; GH (holo).

Tepuianthus sarisarinamensis Maguire & Steyerm., Mem. New York Bot. Gard. 32: 16. 1981. *J. A. Steyermark et al. 109237*; 19–20 Feb. 1974; Venezuela, Meseta del Jaua, Cerro Sarisariñama; 1,350 m; NY, VEN (holo).

Tepuianthus sarisarinamensis Maguire & Steyerm. subsp. *duidensis* Maguire & Steyerm., Mem. New York Bot. Gard. 32: 18. 1981. *B. Maguire et al. 29543*; 19 Nov. 1950; Venezuela, T.F. Amazonas, Cerro Duida; 1,500 m; NY (holo).

Tepuianthus savannensis Maguire & Steyerm., Mem. New York Bot. Gard. 29(2): 14. 1981. *O. Huber et*

al. 3759; 7 May 1979; Venezuela, T.F. Amazonas, Dept. Atabapo, Caño Yagua; 120 m; VEN (holo); NY.

Tepuianthus yapacanensis Maguire & Steyerm., Mem. New York Bot. Gard. 29(2): 12. 1981. *B. Maguire et al. 30683*; 3 Jan. 1951; Venezuela, T.F. Amazonas, Cerro Yapacana; 120 m; NY (holo).

THEACEAE

Acopanea Steyerm., Ann. Missouri Bot. Gard. 71: 323. 1984, gen. nov.

Acopanea ahogadoi Steyerm., Ann. Missouri Bot. Gard. 71: 1984. *J. A. Steyermark et al. 129924*; 14–16 Feb. 1984; Venezuela, Bolívar, Piar, Macizo del Chimantá; 1,920 m; MO (3234986), NY, VEN (holo).

Bonnetia bolivarensis Steyerm., Ann. Missouri Bot. Gard. 74: 102. 1987. *O. Huber 9818*; 19 Nov. 1984; Venezuela, Bolívar, Ptari-tepui; 2,400 m; MO, VEN (holo).

Bonnetia chimantensis Steyerm., Ann. Missouri Bot. Gard. 71: 326. 1984. *J. A. Steyermark & J. J. Wurdack 680*; 9 Feb. 1955; Venezuela, Bolívar, Chimantá Massif, Torono-tepui; 2,090 m; F, NY, VEN (holo).

Bonnetia duidae Kobuski & Steyerm., J. Arnold Arbor. 29: 411. 1948. *J. A. Steyermark 58186*; 1 Sep. 1944; Venezuela, T.F. Amazonas, Cerro Duida, summit, Brocchinia Hills; 1,700–1,980 m; F (holo), NY = *Neogleasonia duidae* (Kobuski & Steyerm.) Maguire, 1972.

Bonnetia euryanthera Steyerm., Ann. Missouri Bot. Gard. 74: 647. 1987. *J. A. Steyermark et al. 124311*; 14 Feb. 1981; Venezuela, Bolívar, Meseta de Jaua; 2,020 m; MO, NY (holo), VEN.

Bonnetia guaiquinimae Steyerm., Ann. Missouri Bot. Gard. 74: 102. 1987. *J. A. Steyermark 117421*; 26 May 1978; Venezuela, Bolívar, Cerro Guaiquinima; 1,250 m; MO, VEN (holo).

Bonnetia huberiana Steyerm., Ann. Missouri Bot. Gard. 71: 326. 1984. *J. A. Steyermark & J. J. Wurdack 633*; 9 Feb. 1955; Venezuela, Bolívar, Chimantá Massif, Torono-tepui; 2,165–2,180 m; F, NY, US, VEN (holo).

Bonnetia liesneri Steyerm., Ann. Missouri Bot. Gard.: in press, 1989. *R. L. Liesner & F. Delascio 22105*; 18 Oct. 1987; Venezuela, T.F. Amazonas, Dept. Río Negro, Cerro Aracamuni, Popa Camp; 1,550 m; MO (holo), VEN.

Bonnetia maguireorum Steyerm., Ann. Missouri Bot. Gard. 71: 330. 1984, nom. nov.

Bonnetia neblinensis Steyerm., Ann. Missouri Bot. Gard. 71: 330. 1984, nom. nov.

Bonnetia ptariensis Steyerm., Ann. Missouri Bot. Gard. 74: 102. 1987. *J. A. Steyermark et al. 115645*; 23 Feb. 1978; Venezuela, Bolívar, Ptari-tepui; MO, VEN (holo).

Bonnetia tepuiensis Kobuski & Steyerm., J. Arnold Arbor. 29: 399. 1948. *J. A. Steyermark 60871*; 5–6 Dec. 1944; Venezuela, Bolívar, Carrao-tepuí (Ptari-tepui); 1,675–1,980 m; F (holo), NY.

Bonnetia tepuiensis Kobuski & Steyerm. subsp. *minor* Steyerm., Ann. Missouri Bot. Gard. 71: 326. 1984. *J. A. Steyermark & J. J. Wurdack 990*; 20 Feb. 1955; Venezuela, Chimantá Massif; 1,975 m; F, NY, US, VEN (holo).

Bonnetia toronoensis Steyerm., Ann. Missouri Bot. Gard. 71: 327. 1984. *J. A. Steyermark & J. J. Wurdack 1047*; 21 Feb. 1955; Venezuela, Bolívar, Chimantá Massif, Torono-tepui; 2,030–2,150 m; F, NY, US, VEN (holo).

Bonnetia tristyla Gleason subsp. *nervosa* Steyerm., Ann. Missouri Bot. Gard. 74: 103. 1987. *J. A. Steyermark & G. S. Bunting 103153*; 5 May 1970; Venezuela, T.F. Amazonas, Cerro Yapacana, below summit; 825 m; VEN (holo). Note: Superfluous publication in: Ann. Missouri Bot. Gard. 74: 649. 1987. *B. Maguire et al. 30632*; 2 Jan. 1951; Venezuela, T.F. Amazonas, Cerro Yapacana; NY, VEN (holo).

Laplacea fruticosa (Schrader) Kobuski var. *chimantae* Steyerm., Ann. Missouri Bot. Gard. 74: 650. 1987. *J. A. Steyermark & J. J. Wurdack 879*; 17 Feb. 1955; Venezuela, Bolívar, Chimantá Massif, central section, along W branch headwaters of Río Tirica above upper falls; 2,090 m; F, NY, VEN (holo).

Laplacea pubescens Planchon & Linden ex Triana & Planchon var. *minor* Steyerm., Ann. Missouri Bot. Gard. 74: 652. 1987. *B. Maguire et al. 30285*; 17 Dec. 1959; Venezuela, T.F. Amazonas, Cerro Huachamacari, between Summit Camp amd SW escarpment; 1,850 m; NY (holo).

Ternstroemia acrodantha Kobuski & Steyerm., Fieldiana Bot. 28(2): 381. 1952. *J. A. Steyermark 56582*; 18 May 1944; Venezuela, Mérida, above Tabay; 2,285–2,745 m; F (holo), GH.

Ternstroemia camelliifolia Linden & Planch. var. *minor* Kobuski & Steyerm., Field. Bot. 28(2): 383. 1952. *J. A. Steyermark 56979*; 19 June 1944; Venezuela, Distr. Federal, El Junquito, Cordillera de la Costa; 1,830 2,130 m; F (holo).

Ternstroemia unilocularis Kobuski & Steyerm., Fieldiana Bot. 28(2): 383. 1952. *J. A. Steyermark 61626*; 20 Mar. 1945; Venezuela, Anzoátegui, Cerro Paeonía (Cerro Los Pajaritos); 1,800–2,000 m; F (holo), GH.

THYMELAEACEAE

Daphnopsis dircoides Steyerm., Fieldiana Bot. 28(2): 420. 1952. *J. A. Steyermark 60136*; 14 Nov. 1944; Venezuela, Bolívar, Sororopan-tepui; 2,255 m; F (holo).

Daphnopsis ficina Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 254. 1940. *J. Garcia Salas 1442*; Jan. 1932; Guatemala, Dept. Guatemala, La Cienaguilla, San José Pinula; 1,600 m; F (holo).

Daphnopsis guaiquinimae Steyerm., Ann. Missouri Bot. Gard. 74: 652. 1987. *J. A. Steyermark et al. 117977*; 9 Apr. 1979; Venezuela, Bolívar, Cerro Guaiquinima; 1,650 m; MO, VEN (holo).

Daphnopsis malacophylla Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 68. 1944. *J. A. Steyermark 49104*; 18 July 1942; Guatemala, Dept. Huehuetenango, Cerro Cananá, Sierra de los Cuchumatanes; 2,500–2,800 m; F (holo).

Daphnopsis nevlingiana Steyerm., Ann. Missouri Bot. Gard. 74: 653. 1987. *J. A. Steyermark et al. 109199*; 16 18 Feb. 1974; Venezuela, Bolívar, Cerro Sarisariñama, Meseta de Jáua, summit; MO, VEN (holo).

Daphnopsis retifera Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 254. 1940. *J. A. Steyermark 31758*; 13 Nov. 1939; Guatemala, Dept. Jutiapa, between railroad station of Mita and Asunción Mita; 650 m; F (holo) = *D. monocephala* Donn. Sm., 1962.

Schoenobiblus amazonicus Steyerm., Ann. Missouri Bot. Gard. 74: 654. 1987. *G. Wessels-Boer 1953*; 5 Aug. 1967; Venezuela, T. F. Amazonas, 2.5 km S of Puerto Ayacucho; MER (holo), MY.

TILIACEAE

Mortoniodendron Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(2): 157. 1940, gen. nov.

Mortoniodendron guatemalense Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(3): 157. 1940. *W. R. Hatch & C. L. Wilson 54*; 21 July 1936; Guatemala, Dept. Isabal, Río Dulce; F (holo).

Mortoniodendron membranaceum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(3): 158. 1940. *T. G. Yuncker et al. 8519*; 19 July 1938; Honduras, Dept. Atlántida, above Puente Alto stop on S.F. Co. RR, E of La Ceiba; 240 m; F (holo).

TRIGONIACEAE

Trigonia costanensis Steyerm. & Badillo, Acta Bot. Venez. 6: 77. 1971. *A. Madriz 37*; 8 Oct. 1967; Venezuela, Yaracuy, Norte de Nirgua; 1,200 m; MY (holo).

Trigonia rasa Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 59. 1944. *P. C. Standley 78584*; 28 Nov. 1940; Guatemala, Dept. Santa Rosa, Río Panal, Volcán Tecuamburro; F (holo) = *T. eriosperma* (Lamarck) Fromm & Sons subsp. *membranacea* (A. C. Smith) Lleras, 1978.

TURNERACEAE

Erblichia standleyi Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 356. 1940. *T. G. Yuncker et al. 8323*; July 1938; Honduras, Dept. Atlantida, Salado Riva, above Salado, vicinity of La Ceiba; F (holo) = *E. odorata* Seeman, 1979.

Erblichia xylocarpa var. *mollis* Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 355. 1940. *J. A. Steyermark 33448*; Jan. 1940; Guatemala, Dept. Quezaltenango, Quebrada San Gerónimo, Finca Pireneos, Volcán de Santa María; 1,300–2,000 m; F (holo) = *E. odorata* Seeman var. *mollis* (Standl. & Steyerm.) L. O. Williams, 1979.

URTICACEAE

Boehmeria ramiflora Jacq. var. *vinacea* Steyerm., Acta Bot. Venez. 3: 197. 1968. *J. A. & C. Steyermark 95187*; 27–28 Mar. 1966; Venezuela, Carabobo, Río San Gian, Borburato, Planta Electrica, Los Teques, and La Toma; 750 m; VEN (holo).

Pilea killipiana Standl. & Steyerm., Fieldiana Bot. 24(3): 415. 1952. *J. A. Steyermark 44757*; n.d.; Guatemala, Alta Verapaz, along Río Icvolay, N and NW of Finca Cubilquitz to Quebrada Diablo; 250–350 m; F (holo).

Pilea mimema Standl. & Steyerm., Fieldiana Bot. 24(3): 417. 1952. *W. R. Hatch & C. L. Wilson 162*; n.d.; Guatemala, Alta Verapaz, Senahú, Cerro Sillab; F (holo).

Urera killipiana Standl. & Steyerm., Fieldiana Bot. 24(3): 427. 1952. *A. F. Skutch 892*; n.d.; Guatemala, Quezaltenango, Volcán Zunil; F (holo).

VALERIANACEAE

Valeriana delicata Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 255. 1947. *J. A. Steyermark 50936*; 19 Aug. 1942; Guatemala, Dept. Huehuetenango, Cumbre Papal; 1,400–3,000 m; F (holo) = *V. robertianifolia* Briq., 1976.

Valeriana texana Steyerm., Ann. Missouri Bot. Gard. 19: 393. 1932. *J. A. Moore & J. A. Steyermark 3528*; 21 July 1931; U.S.A., Texas, Culberson Co., Guadalupe Mountains, upper McKittrick Canyon; 2,000 m; GH (holo), MO (1011707).

VELLOZIACEAE

Vellozia duidae Steyerm., Fieldiana Bot. 28(1): 157. 1951. *J. A. Steyermark 58270*; 2 Sep. 1944; Venezuela, T.F. Amazonas; Cerro Duida; 1,025–1,200 m; F (holo) = *V. tubiflora* (A. Rich.) H.B.K., 1969.

VERBENACEAE

Aegiphila hoffmannioides Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 227. 1947. *J. A. Steyermark 48843*; 15–16 July 1942; Guatemala, Dept. Huehuetenango, near Maxbal, Sierra de los Cuchumantes; 1,500 m; F (holo) = *Hoffmannia nicotanifolia* (Mart. & Gal.) L. Williams, 1975 in the Rubiaceae not Verbenaceae.

Clerodendron mimicum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(5): 227. 1947. *J. A. Steyermark 48631*; 14 July 1942; Guatemala, Dept. Huehuetenango, Cerro Huitz, Sierra de los Cuchumatanes; 1,500–2,600 m; F (holo) = *Gibsoniothamnus mimicus* (Standl. & Steyerm.) L. Williams, 1974 in the Scrophulariaceae not Verbenaceae.

Clerodendron pithecobium Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(5): 373. 1940. *P. C. Standley 67887*; 8 Mar. 1939; Guatemala, Dept. Quezaltenango, La Shuya, SW of San Martín Chile Verde; 1,620 m; F (holo).

Lantana ruiz-teranii López-Palacios & Steyerm., Ernstia 36: 10. 1986. *L. E. Ruíz Terán & S. López Palacios 10907*; Venezuela, Bolívar, Distr. Roscio, Gran Sabana, Santa Elena de Uairén; 900 m; MER (holo); VEN.

VIOLACEAE

Hybanthus sylvicola Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(4): 176. 1944. *C. L. Wilson 329*; 20 Mar. 1939; Guatemala, Dept. Alta Verapaz, Pilapec, Finca Los Alpes; 270 m; F (holo).

Orthion Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 22(4): 249. 1940, gen. nov.

Rinorea oraria Steyerm. & Fernandez, Brittonia 30: 43. 1978. *G. Morillo et al. 3355*; 17 July 1973; Venezuela, Distr. Federal, Cordillera Costanera, S of Camuri Grande; 700–800 m; COL (holo), VEN.

Viola triloba Schwein f. *albida* Steyerm., Rhodora 54: 256. 1952. *J. A. Steyermark 67440*; 29 Apr. 1949; U.S.A., Missouri, Stone Co., along Route 13, 0.5 mi. NE of Lampe; F (holo).

Viola venezuelensis Steyerm., Fieldiana Bot. 28(2): 403. 1952. *J. A. Steyermark 57077*; 7 July 1944; Venezuela, Mérida, Páramo de la Negra; 2,745–3,045 m; F (holo).

Viola viarum Pollard f. *pilifera* Palmer & Steyerm., Brittonia 10: 116. 1958. *J. A. Steyermark 78500*; 28 Apr. 1955; U.S.A., Missouri, Gentry Co. along branch tributary to ravines on N and E side of Grand River, 1.5–2 mi. S of McFall; F (holo).

VISCACEAE

Phoradendron aguilarii Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 40. 1944. *J. A. Steyermark 31889*; 18 Nov. 1939; Guatemala, Dept. Jutiapa, Vol-

cán Suchitán, NW of Asunción Mita; 1,000–2,050 m; F (holo).

Phoradendron aphyllum Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 412. 1966. *J. A. Steyermark & S. Nilsson 473*; 20 22 Apr. 1960; Venezuela, Bolívar, Cerro Uei; 1,100 m; VEN (holo).

Phoradendron huehuetecum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 41. 1944. *P. C. Standley 82597*; Jan. 1941; Guatemala, Dept. Huehuetenango, near Tachique, E of Huehuetenango; 1,900 m; F (holo).

Phoradendron insigne Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 415. 1966. *J. A. Steyermark & L. Aristeguieta 59*; 9 Mar. 1962; Venezuela, Bolívar, Río Uarama valley below Uarama-tepui; 1,200 m; VEN (holo) = *P. semivenosum* Rizz., 1982.

Phoradendron karuaianum Steyerm., Fieldiana Bot. 28(1): 222. 1951. *J. A. Steyermark 60659*; 27 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,220 m; F (holo).

Phoradendron ptarianum Steyerm., Fieldiana Bot. 28(1): 222. 1951. *J. A. Steyermark 59483*; 29 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 1,810 m; F (holo).

Phoradendron tenuiflorum Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 442. 1967. *J. A. Steyermark 75426*; Venezuela, Bolívar, Chimantá-tepui (Toronto-tepui), Chimantá Massif; VEN (holo).

Phoradendron tepuianum Steyerm., Fieldiana Bot. 28(1): 223. 1951. *J. A. Steyermark 59688*; 1 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,600 m; F (holo).

Phoradendron treleaseanum Standl. & Steyerm., Field Mus. Nat. Hist., Bot. Ser. 23(2): 41. 1944. *W. A. Kellerman 7630*; Jan. 1908; Guatemala, Dept. Baja Verapaz, Sierra de las Minas, opposite El Rancho (El Progreso); 700 m; F (holo).

Phoradendron uleanum Steyerm., Fieldiana Bot. 28(1): 223. 1951, nom. nov. = *P. undulatum* (Pohl) Eichl., 1982.

VITACEAE

Cissus venezuelensis Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 427. 1966. *J. A. Steyermark et al. 92987*; 11 Feb. 1964; Venezuela, Bolívar, km 119 and 123 S of El Dorado; 1,030–1,100 m; depository not designated.

VOCHYSIACEAE

Euphronia acuminatissima Steyerm., Ann. Missouri Bot. Gard. 74: 91. 1987. *J. J. Wurdack & L. S. Adderley 43762*; 5 Aug. 1959; Venezuela, T.F. Amazonas, Río Orinoco, Sabana Cumare on right bank of Caño Cumare, Río Atabapo; 125 150 m; MO (holo—2427924); NY.

Qualea apodocarpa Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 473. 1966. *J. A. Steyermark 90467*; 30 Dec. 1961; Venezuela, Bolívar, Río Ichun, debajo del Salto María Espuma; 500 m; VEN (holo) = *Ruizterania apodocarpa* (Steyerm.) Marcano Berti, 1969.

Qualea ferruginea Steyerm., Fieldiana Bot. 28(2): 295. 1952. *J. A. Steyermark 60914*; 11 Dec. 1944; Venezuela, Bolívar, Quebrada de Kavanayen; 1,200–1,220 m; F (holo) = *Ruizterania ferruginea* (Steyerm.) Marcano Berti, 1969.

Qualea rubiginosa Stafleu var. *angustior* Steyerm., Acta Bot. Venez. 2: 239. 1967. *J. A. Steyermark 94203*; 18 May 1964; Venezuela, Bolívar, Auyan-tepui; 1,000 m; VEN (holo) = *Ruizterania rubiginosa* (Stafleu) Marcano Berti var. *angustior* (Steyerm.) Marcano Berti, 1969.

Vochysia pauciflora Steyerm., Bol. Soc. Venez. Ci. Nat. 26: 424. 1966. *J. A. Steyermark et al. 92902*; 9 Jan. 1954; Venezuela, Bolívar, Cerro Venamo; 900 m; VEN (holo).

WINTERACEAE

Drimys brasiliense Miers var. *ptaritepuiensis* Steyerm., Fieldiana Bot. 28(1): 235. 1951. *J. A. Steyermark 59537*; 30 Oct. 1944; Venezuela, Bolívar, Ptari-tepui; 2,100–2,285 m; F (holo).

XYRIDACEAE

Albolboda gleasoniana Steyerm., Fieldiana Bot. 28(4): 820. 1957, nom. nov.

Albolboda macrostachya Spruce var. *robustior* Steyerm., Fieldiana Bot. 28(1): 104. 1951. *J. A. Steyermark 59349*; 26 Oct. 1944; Venezuela, Bolívar, NW to Río Karuai, Gran Sabana; 1,220 m; F (holo).

Albolboda ptaritepuiana Steyerm., Fieldiana Bot. 28(1): 104. 1951. *J. A. Steyermark 59760*; 2 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 2,000 2,200 m; F (holo) = *Orectanthe ptaritepuiana* (Steyerm.) Maguire, 1958.

Aratitiyopea Steyerm. & Berry, Ann. Missouri Bot. Gard. 71: 297. 1984, gen. nov.

Xyris albescens Steyerm., Fieldiana Bot. 28(1): 105. 1951. *J. A. Steyermark 59734*; 2 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 2,000 2,200 m; F (holo).

Xyris capillaris Steyerm., Fieldiana Bot. 28(1): 107. 1951. *J. A. Steyermark 57835*; 22 Aug. 1944; Venezuela, T.F. Amazonas, between Esmeralda Savanna and SE base of Cerro Duida; 200 m; F (holo).

Xyris culmenicola Steyerm., Fieldiana Bot. 28(1): 108. 1951. *J. A. Steyermark 58233*; 2 Sep. 1944; Venezuela, T.F. Amazonas, Cerro Duida, Brocchinia Hills; 1,700–1,980 m; F (holo).

Xyris esmeraldae Steyerm., Fieldiana Bot. 28(1): 109. 1951. *J. A. Steyermark 57821*; 22 Aug. 1944; Venezuela, T. F. Amazonas, between Esmeralda Savanna and SE base of Cerro Duida; 200 m; F (holo).

Xyris jauana L. B. Smith & Steyerm., Bol. Soc. Venez. Ci. Nat. 32: 277. 1976. *J. A. Steyermark et al. 109390*; 22–28 Feb. 1974; Venezuela, Bolívar, Meseta del Jaua, Cerro Jaua; 1,750–1,800 m; depository not designated.

Xyris lanulobractea Steyerm., Fieldiana Bot. 28(1): 109. 1951. *J. A. Steyermark 59336*; 26 Oct. 1944; Venezuela, Bolívar, Gran Sabana; 1,220 m; F (holo).

Xyris ptariana Steyerm., Fieldiana Bot. 28(1): 110. 1951. *J. A. Steyermark 59919*; 7 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 2,410–2,450 m; F (holo).

Xyris scabridula Steyerm., Fieldiana Bot. 28(1): 111. 1951. *J. A. Steyermark 58168*; 1 Sep. 1944; Venezuela, T.F. Amazonas, Cerro Duida, Brocchinia Hills; 1,700–1,980 m; F (holo).

Xyris schneeana Smith & Steyerm., Acta Bot. Venez. 2: 149. 1967. *L. Schnee 1577*; 19 Apr. 1956; Venezuela, Bolívar, Auyan-tepui; MY (holo).

Xyris setigera Oliver var. *elongata* Steyerm., Fieldiana Bot. 28(1): 112. 1951. *J. A. Steyermark 59660*; 1 Nov. 1944; Venezuela, Bolívar, Ptari-tepui; 1,600 m; F (holo).

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Appendix I

Eponymy. Plants named in honor of Julian Steyermark. These are all the names found while examining the literature cited in the bibliography. It is not a complete list. Additions or corrections would be most welcome.

TRIBES		
Steyermarkochloeae Davidse & Ellis		Poaceae
GENERA		
Aristeyera H. Moore = *Asterogyne* H. Wendle		Arecaceae
Jasarum Bunting		Araceae
Steyerbromelia L. B. Smith		Bromeliaceae
Steyermarkia Standl.		Rubiaceae
Steyermarkiella H. Robinson		Musci
Steyermarkina R. M. King & H. Robinson		Asteraceae
Steyermarkochloa Davidse & Ellis		Poaceae
SPECIES	TYPE	
Abuta steyermarkii (Standl.) Standl.		Menispermaceae
Achnopogon steyermarkii Aristeg.	*Steyermark 93512*	Asteraceae
Aegiphila steyermarkii Mold.	*Steyermark 59960*	Verbenaceae
Amanoa steyermarkii Jabl.	*Steyermark 93238*	Euphorbiaceae
Anomospermum steyermarkii Krukoff & Barneby	*Frões 21466*	Menispermaceae
Anthurium julianii Bunting	*Steyermark 97325*	Araceae
Anthurium steyermarkii Bunting	*Steyermark 74850*	Araceae
Aphanocarpus steyermarkii (Standl.) Steyerm.		Rubiaceae
Aristolochia steyermarkii Standl. = *Aristolochia arborea* J. Linden, 1966	*Steyermark 33455*	Aristolochiaceae
Arthrostylidium steyermarkii McClure	*Steyermark 59926*	Poaceae
Asketanthera steyermarkii Markgraf	*Steyermark 99348*	Apocynaceae
Aspidosperma steyermarkii Woodson	*Steyermark 59858*	Apocynaceae
Axonopus steyermarkii Swallen	*Steyermark 58001*	Poaceae
Azorella julianii Math. & Const.	*Steyermark 55894*	Apiaceae
Befaria steyermarkii A. C. Smith	*Steyermark 62711*	Ericaceae
Begonia steyermarkii L. B. Smith & B. G. Schubert	*Steyermark 75502*	Begoniaceae
Beloperone steyermarkii Leonard	*Steyermark 56869*	Acanthaceae
Besleria steyermarkiorum Wiehler	*Steyermark 111182*	Gesneriaceae
Bidens steyermarkii Sherff	*Steyermark 50998*	Asteraceae
Blepharodon julianii Morillo	*Steyermark 111304*	Asclepiadaceae
Blepharodon steyermarkii R. Holm	*Steyermark 60813*	Asclepiadaceae
Bonnetia steyermarkii Kobuski	*Steyermark 59570*	Theaceae
Bouvardia steyermarkii Standl.	*Steyermark 29671*	Rubiaceae
Brachionidium julianii Carnevali & Ramirez	*Steyermark 129512*	Orchidaceae
Brachionidium steyermarkii Foldats	*Steyermark 98592*	Orchidaceae
Brocchinia steyermarkii L. B. Smith	*Steyermark 60347*	Bromeliaceae
Bulbophyllum steyermarkii Foldats	*Steyermark 100818*	Orchidaceae
Bursera steyermarkii Standl.	*Steyermark 30068*	Burseraceae
Byrsonima steyermarkii Anderson	*Steyermark 97979*	Malpighiaceae
Caladium steyermarkii Bunting	*Steyermark 102035*	Araceae
Calceolaria steyermarkii Pennell = *Calceolaria fusca* Pennell, 1988	*Steyermark 54475*	Scrophulariaceae
Campylocentrum steyermarkii Foldats	*Steyermark 96715*	Orchidaceae
Capparis steyermarkii Standl.	*Steyermark 39387*	Capparidaceae
Carex steyermarkii Standl.	*Steyermark 48542*	Cyperaceae
Castilleja steyermarkii Pennell	*Steyermark 57137*	Scrophulariaceae
Cecropia steyermarkii Cuatr.	*Steyermark 109842*	Cecropiaceae
Cephalocarpus steyermarkii Gilly	*Steyermark 56940*	Cyperaceae
Chiococca steyermarkii Standl.	*Steyermark 36237*	Rubiaceae
Chrysophyllum steyermarkii Monachino	*Steyermark 57717*	Sapotaceae
Citharexylum steyermarkii Mold.	*Steyermark 31433*	Verbenaceae
Cladium steyermarkii T. Koyama = *Rhynchocladium steyermarkii* (T. Koyama) T. Koyama, 1972	*Steyermark & Wurdack 1225*	Cyperaceae
Clidemia steyermarkii Wurd.	*Steyermark 96653*	Melastomataceae
Clitoria steyermarkii Fantz	ined.	Fabaceae
Clusia steyermarkii Maguire	*Steyermark 75977*	Clusiaceae
Cobaea steyermarkii Standl.	*Steyermark 37759*	Polemoniaceae
Coccoloba steyermarkii Standl.	*Steyermark 39533*	Polygonaceae
Columnea steyermarkii Morton	*Steyermark & Nilsson 41*	Gesneriaceae

Connarus steyermarkii Prance	*Steyermark 91995*	Connaraceae
Conomorpha steyermarkiana Agost. = *Cybianthus steyermarkianus* (Agost.) Agost., 1988	*Cardona Puig 2723*	Myrsinaceae
Cosmos steyermarkii Sherff	*Steyermark 31341*	Asteraceae
Cottendorfia steyermarkii (L. B. Smith) L. B. Smith		Bromeliaceae
Couepia steyermarkii Maguire	*Steyermark 60025*	Chrysobalanaceae
Coussapoa steyermarkii Cuatr.	*Steyermark 60002a*	Urticaceae
Crumenaria steyermarkii Standl.	*Steyermark 30448*	Rhamnaceae
Cuchumatanea steyermarkii Seidensch. & Beaman	*Beaman 3962*	Asteraceae
Cyathea steyermarkii Tryon	*Steyermark 105194*	Cyatheaceae
Cybianthus steyermarkianus (Agost.) Agost.		Myrsinaceae
Cyclanthera steyermarkii Standl.	*Steyermark 34047*	Cucurbitaceae
Cynanchum julianii Morillo	*Morillo 10102*	Asclepiadaceae
Dacryodes steyermarkii Sandw.	*Steyermark 92354*	Burseraceae
Dahlia coccinea var. *steyermarkii* Sherff	*Steyermark 50341*	Asteraceae
Daphnopsis steyermarkii Nevling	*Steyermark & Wurdack 781*	Thymelaeaceae
Davilla steyermarkii Kubitzki	*Steyermark 117841*	Dilleniaceae
Dendrophthora steyermarkii Rizz. = *Dendrophthora squamigera* (Benth.) O. Kuntze, 1982	*Steyermark 98573*	Loranthaceae
Diacidium steyermarkii (Maguire) Anderson		Malpighiaceae
Dicella julianii (Macbr.) Anderson		Malpighiaceae
Dichapetalum steyermarkii Prance	*Steyermark 89875*	Dichapetalaceae
Dicranoloma steyermarkii Bartr.	*Steyermark 74980b*	Musci
Dioclea steyermarkii R. H. Maxwell	ined.	Fabaceae
Distictis steyermarkii Gentry	*Steyermark 105274*	Bignoniaceae
Duranta steyermarkii Mold.	*Steyermark 62102*	Verbenaceae
Echeveria steyermarkii Standl.	*Steyermark 43145*	Crassulaceae
Elaphoglossum steyermarkii Mickel	*Steyermark 128500*	Aspleniaceae
Elleanthus steyermarkii Barringer	*Steyermark 54873*	Orchidaceae
Elvasia steyermarkii Maguire	*Steyermark 96342*	Ochnaceae
Epidendrum steyermarkii A. D. Hawkes	*Moritz 1065*	Orchidaceae
Epiphyllum steyermarkii Croizat	*Steyermark 108741*	Cactaceae
Eriocaulon steyermarkii Mold.	*Steyermark 58868*	Eriocaulaceae
Eriosorus paucifolius var. *steyermarkii* A. F. Tryon	*Steyermark 59913*	Adiantaceae
Erythroxylum steyermarkii Plowman	*Steyermark 107840*	Erythroxylaceae
Espeletia steyermarkii Cuatr. = *E. brassicoidea* var. *contracta* Cuatr., 1964	*Steyermark 57217*	Asteraceae
Eugenia steyermarkii Standl.	*Steyermark 36210*	Myrtaceae
Eupatorium steyermarkianum Badillo	*Steyermark 56795*	Asteraceae
Euphorbia steyermarkii Standl.	*Standley 74673*	Euphorbiaceae
Everardia steyermarkii Gilly	*Steyermark 59781*	Cyperaceae
Exochogyne steyermarkii Gilly	*Steyermark 57820*	Cyperaceae
Fissidens steyermarkii Bartr.	*Steyermark 36576*	Musci
Freziera steyermarkii Kobuski	*Steyermark 61443*	Theaceae
Gomphicus steyermarkii Foldats	*Steyermark 100883*	Orchidaceae
Gonolobus steyermarkii Woodson	*Steyermark 37661*	Asclepiadaceae
Graffenrieda steyermarkii Wurd.	*Steyermark 74883*	Melastomataceae
Greigia steyermarkii L. B. Smith	*Steyermark 42553*	Bromeliaceae
Guettarda steyermarkii Standl.	*Steyermark 56601*	Rubiaceae
Guzmania steyermarkii L. B. Smith	*Steyermark & Nilsson 428*	Bromeliaceae
Helianthostylis steyermarkii C. C. Berg	*Steyermark 102860*	Moraceae
Heliconia julianii Barreiros	*Steyermark 102678*	Heliconiaceae
Henriettella steyermarkii Wurd.	*Steyermark 90647*	Melastomataceae
Heteropsis steyermarkii Bunting	*Steyermark 102607*	Araceae
Heteropterys steyermarkii Anderson	*Steyermark 105009*	Malpighiaceae
Hexapterella steyermarkii Maas & Maas	*Liesner 22622*	Burmanniaceae
Hidalgoa steyermarkii Sherff	*Steyermark 48814*	Asteraceae
Hoffmannia steyermarkii Steyerm. = *H. rotata* J. D. Smith, 1975	*Steyermark 36426*	Rubiaceae
Hookeriopsis steyermarkii Bartr.	*Steyermark 59942*	Musci
Hydrangea steyermarkii Standl.	*Steyermark 36044*	Saxifragaceae
Hydrocotyle steyermarkii Math. & Const.	*Steyermark 54566*	Apiaceae
Hymenophyllopsis steyermarkii Vareshi	*Steyermark 75644*	Hymenophyllopsidaceae
Hyperbaena steyermarkii Standl. = *Abuta steyermarkii* (Standl.) Standl., 1944	*Steyermark 39454*	Menispermaceae
Hypericum steyermarkii Standl.	*Steyermark 34760*	Clusiaceae
Ilex julianii Edwin	*Steyermark 91538*	Aquifoliaceae
Ilex steyermarkii Edwin	*Steyermark 75501*	Aquifoliaceae

Jasarum steyermarkii Bunting	*Steyermark 105500*	Araceae
Juglans steyermarkii Manning	*Steyermark 51140*	Juglandaceae
Justicia steyermarkii Standl. & Steyerm.	*Steyermark 48934*	Acanthaceae
Lagenocarpus steyermarkii Gilly	*Steyermark 59363*	Cyperaceae
Leandra steyermarkii Wurd.	*Steyermark 102757*	Melastomataceae
Ledothamnus steyermarkii A. C. Smith	*Steyermark 59484*	Ericaceae
Leothrix steyermarkii Mold.	*Steyermark 59779*	Eriocaulaceae
Lepanthes steyermarkii Foldats	*Steyermark 98381*	Orchidaceae
Lepanthopsis steyermarkii Foldats	*Steyermark 99218*	Orchidaceae
Lepidopilum steyermarkii Bartr.	*Steyermark 56138*	Musci
Licania steyermarkii Maguire	*Steyermark 60768*	Chrysobalanaceae
Lindmania steyermarkii L. B. Smith	*Steyermark & Wurdack 827*	Bromeliaceae
Lycopodium steyermarkii Ollgaard, ined.	*Steyermark 97895*	Lycopodiaceae
Lysimachia steyermarkii Standl.	*Steyermark 34772*	Primulaceae
Macrocentrum steyermarkii Wurd.	*Maguire et al. 53864*	Melastomataceae
Macrolobium steyermarkii Cowan	*Steyermark 90939*	Fabaceae
Malaxis steyermarkii Correll	*Steyermark 51672*	Orchidaceae
Mandevilla steyermarkii Woodson	*Steyermark 58504*	Apocynaceae
Mapania steyermarkii T. Koyama	*Koyama 7506*	Cyperaceae
Marcgravia steyermarkii de Roon	*Steyermark 108921*	Marcgraviaceae
Marsdenia steyermarkii Woodson	*Steyermark 36019*	Asclepiadaceae
Matelea steyermarkii Woodson	*Steyermark 35810*	Asclepiadaceae
Maxillaria steyermarkii Foldats	*Steyermark 98384*	Orchidaceae
Meriania steyermarkii Gleason	*Steyermark 56513*	Melastomataceae
Miconia steyermarkii Gleason	*Steyermark 58262*	Melastomataceae
Microlicia steyermarkii Gleason = *Microlicia benthamiana* Triana ex Cogn., 1973	*Steyermark 59331*	Melastomataceae
Micropholis steyermarkii Monachino	*Steyermark 60650*	Sapotaceae
Monstera steyermarkii Bunting	*Bunting 4805*	Araceae
Mouriri steyermarkii Standl.	*Steyermark 39446*	Melastomataceae
Myrcia exploratoris McVaugh; dedicated to Dr. Julian Steyermark	*Steyermark 60879*	Myrtaceae
Myriocladus steyermarkii Swallen	*Steyermark & Wurdack 819*	Poaceae
Navia steyermarkii L. B. Smith	*Steyermark 58012*	Bromeliaceae
Nothochlaena steyermarkii Vareschi	*Steyermark 75534*	Polypodiaceae
Ocotea julianii van der Werff	*Steyermark & Wurdack 921*	Lauraceae
Ocotea steyermarkiana C. K. Allen	*Steyermark 93476*	Lauraceae
Octomeria steyermarkii Garay & Dunsterville	*Dunsterville 833*	Orchidaceae
Odontocarya steyermarkii Barneby	*Steyermark 101939*	Menispermaceae
Odontonema steyermarkii Leonard	*Steyermark 35020*	Orchidaceae
Oncidium steyermarkii Foldats	*Steyermark 96993*	Orchidaceae
Ophellantha steyermarkii Standl.	*Steyermark 51398*	Euphorbiaceae
Oreopanax steyermarkii A. C. Smith	*Steyermark 42649*	Araliaceae
Ormosia steyermarkii Rudd	*Steyermark 60503*	Fabaceae
Ouratea steyermarkii Sastre	*Steyermark 112797*	Ochnaceae
Oxythece steyermarkiana Monachino	*Steyermark 603321*	Sapotaceae
Oyedaea steyermarkii Blake	*Steyermark 45686*	Asteraceae
Pachyphyllum steyermarkii Foldats	*Steyermark 98345*	Orchidaceae
Paepalanthus perplexans var. *steyermarkii* Mold.	*Steyermark 115640*	Eriocaulaceae
Paepalanthus steyermarkii Mold.	*Steyermark 59369*	Eriocaulaceae
Pagamea steyermarkii Standl. = *Aphanocarpus steyermarkii* (Standl.) Steyerm., 1965, 1967	*Steyermark 59744*	Rubiaceae
Panicum steyermarkii Swallen	*Steyermark & Wurdack 954*	Poaceae
Parabignonia steyermarkii Sandw.	*Steyermark 93003*	Bignoniaceae
Peperomia steyermarkii Yuncker	*Steyermark 61874*	Piperaceae
Perissocarpa steyermarkii (Maguire) Steyerm. & Maguire		Ochnaceae
Persea steyermarkii C. K. Allen	*Steyermark 37061*	Lauraceae
Phainantha steyermarkii Wurdack	*Steyermark 108984*	Melastomataceae
Philacra steyermarkii Maguire	*Steyermark 93844*	Ochnaceae
Philodendron steyermarkii Bunting	*Steyermark 102603*	Araceae
Phoebe steyermarkiana C. K. Allen = *Ocotea julianii* van der Werff	*Steyermark & Wurdack 921*	Lauraceae
Phoradendron steyermarkii Rizz.	*Steyermark 115564*	Viscaceae
Phthirusa steyermarkiana Rizz.	*Steyermark 112735*	Loranthaceae
Piper steyermarkii Yuncker	*Steyermark 59996*	Piperaceae
Piptocarpha steyermarkii Aristeg.	*Steyermark 91450*	Asteraceae

Pitcairnia steyermarkii L. B. Smith	*Steyermark 126510*	Bromeliaceae
Pleurothallis steyermarkii C. Schwein.	*Steyermark 57246*	Orchidaceae
Podocarpus steyermarkii Buchh. & Gray	*Steyermark 60876*	Podocarpaceae
Psittacanthus julianthus Rizz.	*Steyermark 103267*	Loranthaceae
Psychotria steyermarkii Standl.	*Steyermark 33700*	Rubiaceae
Pourouma steyermarkii Standl. & Cuatr.	*Steyermark 60665*	Cecropiaceae
Pterozonium steyermarkii Vareschi	*Steyermark & Wurdack 1059*	Adiantaceae
Quararibea steyermarkii Cuatr.	*Steyermark 61959*	Bombacaceae
Rapatea steyermarkii Maguire	*Steyermark 60868*	Rapateaceae
Rauwolfia steyermarkii Woodson	*Steyermark 57428*	Apocynaceae
Remijia steyermarkii Standl.	*Steyermark 58392*	Rubiaceae
Rhodospatha steyermarkii Bunting	*Steyermark 96161*	Araceae
Rhychocladium steyermarkii (Koyama) Koyama		Cyperaceae
Rhynchospora steyermarkii Koyama	*Steyermark 87853*	Cyperaceae
Roupala steyermarkii Sleumer	*Steyermark 33447*	Proteaceae
Russelia steyermarkii Carlson	*Steyermark 42980*	Scrophulariaceae
Schistocarpha steyermarkii H. Robinson	*Kellerman 7223*	Asteraceae
Selaginella steyermarkii Alston	*Steyermark 50501*	Selaginellaceae
Selenipedium steyermarkii Foldats	*Steyermark & Nilsson 237*	Orchidaceae
Sematophyllum steyermarkii Bartr.	*Steyermark 39923*	Musci
Senecio steyermarkiana Robinson	*Kellerman 7223*	Asteraceae
Senecio steyermarkii Greenman	*Steyermark 49556*	Asteraceae
Senecio steyermarkii Cuatr. = *Senecio meridianus* Cuatr.	*Steyermark 56268*	Asteraceae
Sideroxylon steyermarkii Standl.	*Steyermark 33858*	Sapotaceae
Simsia steyermarkii H. Robinson & Brettell	*Steyermark 42931*	Asteraceae
Sipapoa steyermarkii Maguire = *Diacidium steyermarkii* (Maguire) Anderson, 1981	*Steyermark 98016*	Malpighiaceae
Sloanea steyermarkii C. E. Smith	*Steyermark 93571*	Elaeocarpaceae
Stegolepis steyermarkii Maguire	*Steyermark & Aristegueita 17*	Rapateaceae
Stelis steyermarkii Foldats	*Steyermark 98661*	Orchidaceae
Stenopadus steyermarkii Aristeg.	*Steyermark 93808*	Asteraceae
Stenospermation steyermarkii Bunting	*Steyermark 87511*	Araceae
Stomatochaeta steyermarkii Aristeg.	*Steyermark 97917*	Asteraceae
Swartzia steyermarkii Cowan	*Steyermark 89491*	Fabaceae
Tapura julianii Macbr.	*Klug 2010*	Dichapetalaceae
Taralea steyermarkii Schery = *T. reticulata* (Benth.) Ducke	*Steyermark 60822*	Fabaceae
Tauschia steyermarkii Math. & Const.	*Steyermark 50280*	Apiaceae
Telipogon steyermarkii Foldats	*Steyermark 98568*	Orchidaceae
Ternstroemia steyermarkii Kobuski	*Steyermark 61665*	Theaceae
Tetrapterys julianii Macbr. = *Dicella julianii* (Macbr.) Anderson, 1981	*Klug 347*	Malpighiaceae
Thalictrum steyermarkii Standl.	*Steyermark 36575*	Ranunculaceae
Tibouchina steyermarkii Wurd.	*Steyermark 97854*	Melastomataceae
Tillandsia steyermarkii L. B. Smith	*Steyermark 106763*	Bromeliaceae
Topobea steyermarkii Wurd.	*Steyermark 91084*	Melastomataceae
Trichipteris steyermarkii Tryon = *Cyathea venezuelensis* A. R. Smith, 1981	*Steyermark 94923*	Cyatheaceae
Turnera steyermarkii Arbo	ined.	Turneraceae
Utricularia steyermarkii P. Taylor	*Steyermark 93837*	Lentibulariaceae
Vaccinium steyermarkii Luteyn	*Steyermark 128976a*	Ericaceae
Verbesina steyermarkii Standl.	*Steyermark 30698*	Asteraceae
Virola steyermarkii Rodrigues, ined.	*Steyermark 109187*	Myristicaceae
Vochysia steyermarkii Marcano Berti	*Ll. Williams 14162*	Vochysiaceae
Weinmannia steyermarkii Cuatr. = *W. velutina* f. *steyermarkii* (Cuatr.) Bernardi	*Steyermark 59759*	Cunoniaceae
Weinmannia velutina f. *steyermarkii* (Cuatr.) Bernardi		Cunoniaceae
Xylobium steyermarkii Foldats	*Steyermark 62185a*	Orchidaceae
Note: this collection number is incorrectly cited in the literature.		
Xyris steyermarkii Maguire & L. B. Smith	*Steyermark & Wurdack 1096*	Xyridaceae

NAMES NOT VERIFIED

Dolio steyermarkii	
Ecclinusa steyermarkii Aubr., ined.?	Sapotaceae

Lindsaea steyermarkiana	Pennstaedtiaceae
Lueheopsis julianii Macbr.	Tiliaceae
Phragmipedium steyermarkii	Orchidaceae
Plagiochila steyermarkii H. Robinson	Musci
Serjania steyermarkii	Sapindaceae

Appendix II

Collectors Index. This cross-reference is arranged alphabetically by the collectors' last names; these are followed by initials and full name in parentheses. Then appear sequential listing of collection numbers with taxa and author. Taxa listed in Appendix I are included. Collector eponymy is shown with italics. A few duplicate numbers, resulting from manuscript names or possible errors, are also italicized. Most co-collectors have been omitted except when they collected under separate number series.

COLLECTORS NOT GIVEN

s.n. Orthrosanthus chimboracensis var. intermedius Steyerm.
s.n. Ravnia panamensis Steyerm.

ABRAMS, L. R. (LeRoy)

3957 Grindelia hallii Steyerm.

ACOSTA SOLIS, M.

5054 Clethra rugosa Steyerm.
7008 Siparuna rugosa Steyerm.
7009 Markea grandiflora Steyerm.
7743 Cyphomandra villosa Steyerm.
8233 Siparuna verrucosa Steyerm.

ADAMS, W. (Wayne)

s.n. Trillium recurvatum Beck f. foliosum Steyerm.
s.n. Trillium recurvatum Beck f. petaloideum Steyerm.

AGOSTINI, G. (Getulio)

30 Psychotria guadalupensis subsp. venezuelica Steyerm.
84 Maytenus *agostinii* Steyerm.
1120 Piper *agostiniorum* Steyerm.

AGUILAR, J. I. (José Ignacio)

810 Calyptranthes *aguilarii* Standl. & Steyerm.
1757 Eugenia rheedioides Standl. & Steyerm.

ALLART, A.

225 Gonzalagunia dicocca subsp. venezuelenesis Steverm.

ALLEN, P. H. (Paul Hamilton)

2153 Stegolepis *allenii* Steyerm.
2240 Voyria *allenii* Steyerm.
3560 Chimarrhis decurrens Steverm.
4576 Coussarea darienensis Steyerm.
4744 Ravnia longifilamentosa Steyerm.

ALSTON, A. H. G. (Arthur Hugh Garfit)

6167 Piper arieianum var. yaracuyense f. nubicolum Steyerm.
6533 Galium canescens f. *alstonii* Steyerm.

ANDERSON, W. R. (William)

35874 Perama irwiniana Kirkbr. & Steyerm.

ARISTEGUIETA, L. (Léandro)

555 Emmeorrhiza umbellata subsp. septentrionalis var. pubens Steyerm.
1649 Sabicea *aristeguietae* Steyerm.
1824 Sickingia *aristeguietae* Steyerm.
1924 Peperomia aroensis Steyerm.
1948 Peperomia pseudoglabella Steyerm.
1952 Psychotria aroensis Steyerm.
1989 Elaegia magniflora Steyerm.
2149 Rondeletia *aristeguietae* Steyerm.
2295 Ilex glaucophylla Steverm.
3036 Dacryodes costanensis Steyerm.
3938 Rudgea sanarensis Steyerm.
4193 Randia *aristeguietae* Steyerm.
4250 Borreria capitata f. glabra Steyerm.
5264 Alibertia acuminata var. obtusiuscula Steyerm.
5343 Randia brevipes Steyerm. (pistillate)
6466 Borojoa universitatis Steyerm.
7129 Psychotria patria var tovarensis Steyerm.

AYMARD, G. (Gerardo)

4631 Zinowiewia *aymardii* Steyerm.

BADILLO, V. M. (Victor)

3126 Manettia *badilloi* Steyerm.
4866 Gunnera pittieriana Badillo & Steyerm.

BALDWIN, J. T., JR.

4077 Utricularia *baldwinii* Steyerm.

BARNES, V.

43 Styrax longipedicellatus Steyerm.

BARRETO

1134 Perama sparsiflora Standl., Steyerm. & Kirkbr.

BARTEL, K. E.

s.n. Liatris cylindracea f. *bartelli* Steyerm.
1 Dipsacus sylvestris Huds. f. albidus Steyerm.

BARTLETT, H. H. (Harley Harris)

8300 Diodia hyssopifolia var. linearis f. glabriuscula Steyerm.

BAUER, B.

s.n. Ruellia pedunculata f. *baueri* Steyerm.

BAUTISTA, J. A. (John Louis)

5037 Peperomia glabella var. obtusa Steyerm.

BEAMAN

3962 Cuchumatanea steyermarkii Seidensch. & Beaman

BELEM, R. P.

2738 Sphinctanthus insignis Steyerm.

BERLANDIER, J. L. (John Louis)

766 (2186) Grindelia tenella Steyerm.

BERNARDI, A. L.

3180 Hoffmannia *bernardii* Steyerm.
5829a Tresanthera thyrsiflora Steyerm.

BERNARDI, L. (Luciano)

611 Manettia *bernardii* Steyerm.
985 Arachnothrix reflexa var. meridensis Steyerm.
1248 Manettia paramorum Steyerm.
1296 Psychotria costanensis subsp. andina Steyerm.
1304 Psychotria *bernardii* Steyerm.
1690 Pagamea plicata var. multinervia Steyerm.
1720 Psychotria trichotoma var. trichophylla Steyerm.
2011 Guettarda *bernardii* Steyerm.
2325 Coussarea *bernardii* Steyerm.
6746 Neea *bernardii* Steyerm.
7437 Palicourea buntingii var. glabrior Steyerm.

BERRY, P. E. (Paul)

694 Piper otto-huberi var. eciliatum Steyerm.
1558 Rudgea *berryi* Steyerm. & Dwyer
2096 Faramea *berryi* Steyerm.
2116 Remija *berryi* Steyerm.
2152 Ouratea macurucoensis Maguire & Steyerm.
3670 Eugenia mcvaughii Steyerm. & Lasser
3825 Piper *berryi* Steyerm.
3923 Pereromia *berryi* Steyerm.

BLANCO, C. (Carlos)

1158 Guapira sipapoana Steyerm.

BLANKINSHIP, J. W. (Joseph William)

s.n. Grindelia nana var. altissima f. puberula Steyerm.

BLYDENSTEIN, J.

250 Diodia teres subsp. prostrata f. latifolia Steyerm.

BOLANDER, H. N. (Harry Nicholas)

389 Grindelia hirsutula f. cacumena Steyerm.

BONO, J. (José)

3797 Hillia *bonoi* Steyerm.

BOOM, B. (Brian)

5274 Ferdinandusa *boomii* Steyerm.
5278 Faramea *boomii* Steyerm.
6417 Peperomia *boomii* Steyerm.

BORDENER, V. (Valerie)

s.n. Podophyllum peltatum f. biltmoreanum Steyerm.

BRADE

4739 Perama sparsiflora Standl., Steyerm. & Kirkbr.

BRANDEGEE, K. (Katherine, or Mary Katherine Curran nee Layne)

s.n. Grindelia rubricaulis var. latifolia f. pubescens Steyerm.

BRAUN, E. L. (Lucy)

s.n. Silphium terebinthinaceum var. *lucy-brauniae* Steyerm.

BRETELER, F.

3463 Hoffmannia pauciflora subsp. venezuelensis Steyerm.
4082 Piper veraguense var. venezuelense Steyerm.
4089 Manettia *breteleri* Steyerm.
4095 Diodia radula subsp. venezuelensis Steyerm.
4204 Diodia teres subsp. prostrata f. leiocarpa Steyerm.
4832 Ouratea inconformis Maguire & Steyerm.

BREWER, C., JR.

248 Navia *breweri* L. B. Smith & Steyerm.

BRINKLEY

250 Echinacea purpurea var. arkansana Steyerm.
268 Clematis versicolor f. pubescens Steyerm.

BRITTON, N. L. (Nathaniel Lord)

2104 Psychotria capitata subsp. inundata var. septentrionalis Steyerm.
2684 Randia brevipes Steyerm. (staminate)
2702 Randia aculeata f. minor Steyerm.

BROADWAY, W. E.

9823 Psychotria muscosa subsp. breviloba Steyerm.

BUCHTIEN, O. (Otto)

1719 Faramea anisocalyx var. schwackei f. dentata Steyerm.

BUNTING, G. S. (George)

2332 Piper deliciasanum Steyerm.
4461 Peperomia choroniana var. heterodoxa Steyerm.
4509 Ladenbergia *buntingii* Steyerm.
4805 Monstera steyermarkii Bunting
10876 Pyschotria *buntingii* Steyerm.

BUSH, B. F. (Benjamin)

7041 Diospyros virginiana f. pumila Palmer & Steyerm.
10332 Corylus americana f. indehiscens Palmer & Steyerm.

CÁRDENAS DE GUAVARA, L. (Lourdes)

805 Arachnothris rugulosa var. tachirensis Steyerm.

CARDONA P., F. (or F. Cardona Puig) (Felix)

309b Pagameopsis maguirei subsp. pusillus var. glabrus Steyerm.

707 Sabicea venezuelensis Steyerm.
819 Duroia bolivarensis Steyerm.
860 Platycarpum rhododactylum Woodson & Steyerm.
1051 Sloanea merevariensis Pittier ex Steyerm.
1115 Faramea *cardonae* Standl. & Steyerm.
1117 Malanea guaiquinimensis Steyerm.
1333 Psychotria parimensis Steyerm.
1383 Palicourea *cardonae* Steyerm.
1480 Ilex *cardonae* Steyerm.
1496 Psychotria tapirapecoana Steyerm.
1503 Rudgea *cardonae* Steyerm.
1610 Gleasonia duidana var. oblanceolata Steyerm.
1630 Perama glalioides var. densipila Steyerm.
2190 Stenopadus taloumifolius var. magnifolius Steyerm.
2204 Ouratea ramosissima Maguire & Steyerm.
2288 Quelchia *cardonae* Steyerm.
2661 Heliamphora minor f. laevis Steyerm.
2723 Conomorpha steyermarkiana Agost.
2943 Ilex magnifructa var. minor Steyerm.
2967 Psychotria phaneroloma var. angustior Steyerm.

CARLSON, M. C.

1744 Ardisia *carlsonae* Steyerm.

CARNEVALI, G. (Germán)

640 Peperomia *carnevalii* Steyerm.

CASTELLANOS, E.

46 Borreria aristeguietaeana Steyerm.

CAVALCANTE, P.

712 Retiniphyllum longiflorum Steyerm.
2511 Randia pubiflora Steyerm.

CHARDÓN PALACIOS, C. E. (Carlos Eugenio)

179 Arachnothrix venezuelensis Steyerm.

CLARK, H. L. (Howard)

6742 Catostemma pubistylum Steyerm.
6980 Neea *clarkii* Steyerm.
7794 Guapira sancarlosiana Steyerm.
8111 Schoepfia *clarkii* Steyerm.
8117 Catostemma sancarlosiana Steyerm.
8126 Catostemma *clarkii* Steyerm.

CONGDON, J. W.

s.n. Grindelia aggregata Steyerm.

CONICIT, E.

2663 Piper bredemeyeri f. escabridum Steyerm.

COOPER, G. P.

586 Bertiera aequaliramosa Steyerm.

CORE

1367 Joosia umbellifera var. caucana Steyerm.

COWAN, R. S. (Richard Sumner)

1863 Sipanea *cowanii* Steyerm.
1897 Psychotria hoffmannseggiana f. pubescens Steyerm.
31061 Orthaea paruensis Maguire, Steyerm. & Luteyn
31104 Ouratea paruensis Maguire & Steyerm.
31130 Chondrococcus laevis Steyerm.
31241 Pagamea diceras Steyerm.
31378 Roupala paruensis Steyerm.
31388 Rhamnus longipes Steyerm.
31405 Schefflera guanayensis subsp. paruensis Maguire, Steyerm. & Frodin
31447 Duroia paruensis Steyerm.
31450 Matayba longipes subsp. tepuiensis Steyerm.
31455 Perama galioides f. macrocephala Steyerm.
31462 Ouratea brevicalyx Maguire & Steyerm.
31473 Platycarpum orinocense var. grandiflorum Steyerm.
38429 Rudgea bremekampiana Steyerm.
39036 Rudgea standleyana Steyerm.

CREMERS, G.

6460 Sipanea ovalifolia var. villosissima Steyerm.

CROAT, T. B. (Thomas)

6647 Geophila *croatii* Steyerm.
54112 Coccocypselum *croatii* Steyerm.
54158a Ilex gransabanensis Steyerm.
59478 Ilex abscondita Steyerm.

CROIZAT, L. (Léon Camille Marius)

624 Ouratea *croizatii* Maguire & Steyerm.

CRUEGER

s.n. Psychotria perpapillifera Steyerm.

CUATRECASAS, J. (José)

9198 Tocoyena *cuatrecasasii* Steyerm.
11515 Elaeagia multinervia Steyerm.
13694 Cuatrecasasiodendron colombianum Steyerm.
14827 Joosia umbellifera var. occidentalis Steyerm.
15182 Schradera puberula Steyerm.
15192 Dioicodendron *cuatrecasasii* Steyerm.
17165 Cuatrecasasiodendron spectabile Steyerm.
21086 Schradera pulverulenta Steyerm.
21682 Elaeagia *cuatrecasasii* Steyerm.
23870 Elaeagia alterniramosa Steyerm.
24332 Arachnothrix reflexa var. calycina Steyerm.

CURRAN, H.

s.n. Faramea occidentalis var. brachycalyx Steyerm.

CUTLER, H. C. (Hugh Carson)

8363 Utricularia *cutleri* Steyerm.
8365 Utricularia cearana Steyerm.

DAVIDSE, G. (Gerrit)

12910 Alibertia *davidsei* Steyerm.
15825 Coccocypselum apurense Steyerm.
16382 Guapira *davidsei* Steyerm.
16558 Neea *davidsei* Steyerm.
17011 Matayba affinis Steyerm.
17359 Palicourea huberi Steyerm.

17427 Botryarrhena venezuelensis Steyerm.
22679 Ilex polita Steyerm.
22719 Ilex *davidsei* Steyerm.
27327 Morinda longipedunculata Steyerm.
27651 Psychotria anartiothrix Steyerm.
27719 Ilex *davidsei* Steyerm.
27733 Sloanea *davidsei* Steyerm.

DAVIDSON, A. (Anstruther)

736 (96) Grindelia arizonica var. microphylla Steyerm.

DAVIDSON, M. E.

892 Croton standleyi Steyerm.

DAWSON, E. Y. (Yale)

14163a Declieuxia dasyphylla f. ciliata Steyerm.
14594 Euphorbia machrisiae Steyerm.
14672 Diodia angustata Steyerm.
14685 Croton inaequilobus Steyerm.
14770 Utricularia *dawsonii* Steyerm.
14776 Phyllanthus *dawsonii* Steyerm.
14918 Phyllanthus websterianus Steyerm.
14973 Croton douradensis Steyerm.

DE GRANVILLE, J. J. (Jacques)

C.159 Psychotria antenniformis Steyerm.
2353 Psychotria *granvillei* Steyerm.
2360 Psychotria lateralis Steyerm.
2361 Psychotria saulensis Steyerm.
2362 Psychotria microbracteata Steyerm.
2383 Psychotria galbaoensis Steyerm.
2393 Psychotria urceolata Steyerm.
2793 Psychotria viridibractea Steyerm.
3127 Psychotria alloantha Steyerm.
B.4640 Psychotria perferruginea Steyerm.
B.5288 Psychotria squamelligera Steyerm.

DE LA CRUZ, J. S.

1638 Palicourea guianensis subsp. occidentalis Steyerm.
2164 Malanea *cruzii* Steyerm.

DE LA RUE, A.

13 Psychotria capitata subsp. amplifolia f. tomentosa Steyerm.

DE LEMOS FRÓES, R. (Ricardo) see Fróes, R. L.

DEAM, C. C. (Charles Clemon)

40 Mikania guatemalensis Standl. & Steyerm.

DELASCIO CHITTY, F. (Francisco)

8471 Chomelia *delascioi* Steyerm.
12358 Perama dichotoma var. monocephala Steyerm.
13161 Peperomia *delascioi* Steyerm.

DELGADO, E.

160 Tocoyena costanensis Steyerm.
233 Linociera avilensis Steyerm.

DUCKE, A. (Adolpho)

81 Henriquezia verticillata var. apiculata Steyerm.
522 Burdachia *duckei* Steyerm.
683 Pagamea coriacea var. pubescens Steyerm.
799 Duroia nitida Steyerm.
1005 Platycarpum *duckei* Steyerm.
1141 Borojoa *duckei* Steyerm.
1167 Ferdinandusa *duckei* Steyerm.
1332 Duroia eriopila var. brevidentata Steyerm.
1557 Kotchubaea *duckei* Steyerm.
1844 Stachyarrhena acutiloba Steyerm.
1943 Malanea subtruncata Steyerm.
8462 Pagamea puberula Steyerm. (RB 22951)

DUDLEY, T. R.

13089 Psychotria *dudleyi* Steyerm.
13543 Pagamea *dudleyi* Steyerm.

DUNSTERVILLE, G. C. K. (Geoffrey)

833 Octomeria steyermarkii Garay & Dunsterville

DUQUE, J. M.

1559 Elaeagia barbata Steyerm.

EASTWOOD, A. (Alice)

s.n. Grindelia hirsutula var. brevisquama f. pedunculoides Steyerm.
794 Grindelia rubricaulis var. latifolia f. minor Steyerm.

EGLER, W. A.

46683 Hillia irwinii Steyerm.
47729 Malanea *egleri* Steyerm.

EHRENDORFER, F. (Friedrich)

74104-23 Talisia pentantha Steyerm.

EKMAN, E. L. (Erik Leonard)

9368 Schradera cubensis Steyerm.

ESPINOSA, R.

1076 Nierembergia *espinosae* Steyerm.

EVINGER, E. L.

513 Mitracarpus frigidus var. peruvianus Steyerm.

EWEL, J.

114 Psychotria nematostachya Steyerm.
135 Pochota *ewelii* Steyerm.
209 Brunellia neblinensis Steyerm. & Cuatr.

FAIRBROTHERS

23 Psychotria aristeguietae Steyerm.

FANSHAWE, D. B.

877 Faramea brevipes Steyerm.
1147 Ixora potaroensis Steyerm.
1255 Guettarda *fanshawei* Steyerm.

FARIÑAS, M.

433 Phyllanthus tepuicola Steyerm.

FERRIS, R. (Roxanne)

3391 Grindelia squarrosa var. nuda f. angustior Steyerm.

FLORSCHUTZ, J.

1180 Faramea costata Steyerm.

FOLDATS, E. (Ernesto)

2784 Ouratea subamplexicaulis Maguire & Steyerm.

3670 Palicourea *foldatsii* Steyerm.
3678 Sipaneopsis *foldatsii* Steyerm.
3758 Kotchubaea micrantha Steyerm.
7100 Chimantaea cinerea f. glabra Steyerm.
7192 Hillia *foldatsii* Steyerm.

FOREST DEPT. (Field No.)

CAP 41 Appunia sparsiflora Steyerm.
WB 388 Isertia parviflora var. hirta Steyerm.
WB 500 Appunia tenuiflora var. leiophylla Steyerm.
G 569 Faramea irwinii Steyerm.
F 877 Faramea brevipes Steyerm.

FOREST DEPT. (Record No.)

7227 Ouratea fasciculata Maguire & Steyerm.
7832 Psychotria tetramera Steyerm. (Field No. R.B. 8)

FOSBERG, F. R. (Francis Raymond)

21211 Palicourea guianensis subsp. occidentalis f. glabra Steyerm.
21418 Arachnothrix reflexa var. breviloba Steyerm.
21810 Psychotria *fosbergii* Steyerm.
21825 Amphidasya intermedia Steyerm.
22964 Arachnothrix *fosbergii* Steyerm.
23141 Arachnothrix lojensis Steyerm.

FRÓES, R. L. (Ricardo)

21225 Remijia vaupesiana Steyerm.
21466 Anomospermum steyermarkii Krukoff & Barneby
22885 Henriquezia nitida var. subcuneata Steyerm.

FUNCK & SCHLIM

1500 Palicourea bostrychostachya Steyerm.

GARCIA, F.

55 Palicourea *garciae* Steyerm.

GARCIA, J.

80 Faramea *garciae* Steyerm.
128 Borojoa venezuelensis Steyerm.

GARCIA, T.

147 Chimarrhis microcarpa var. speciosa Steyerm.

GARCIA SALAS, J.

1442 Daphnopsis ficina Standl. & Steyerm.

GATTINGER

s.n. Arenaria patula f. media Steyerm.

GENTLE, P. H. (Percy)

116 Psittacanthus mayanus Standl. & Steyerm.
871 Ipomoea heterodoxa Standl. & Steyerm.
2264 Piper vaccinum Standl. & Steyerm.
2619 Phyllanthus longipes Steyerm.

GENTRY, A. (Alwyn)

46694 Schefflera simplex Steyerm. & Holst
46887 Piper *gentryi* Steyerm.
47314 Sabicea bariensis Steyerm.

GENTRY, H. S. (Howard Scott)

2525 Tinantia erecta f. puberula Standl. & Steyerm.

GHIESBREGHT

871 Arenaria chiapensis Standl. & Steyerm.

GLEASON, H. A. (Henry Allan)

431 Sipanea *gleasonii* Steyerm.

GONZÁLEZ, T. (Tomás)

s.n. Colubrina venezuelensis Steyerm.

GRANT, J. M.

s.n. Grindelia stricta var. aestuarina Steyerm.

GRANT, M. L.

10567 Pentagonia *grantii* Steyerm.

GREENE, E. L. (Edward Lee)

s.n. Grindelia humilis f. reflexa Steyerm.

GREGG, J.

44 Menodora helianthemoides var. engelmannii Steyerm.

GUANCHEZ, F. (Francisco)

3644 Psychotria *guanchezii* Steyerm.

HALL, E. (Elihu)

266 Grindelia integrifolia var. virgata f. villosa Steyerm.

HALLE, F.

1018 Coussarea *hallei* Steyerm.

HARLEY, R. M.

15006 Geophila *harleyi* Steyerm.
16038 Perama *harleyi* Kirkbr. & Steyerm.
17069 Pagamea *harleyi* Steyerm.

HATCH, W. R.

54 Mortoniodendron guatemalense Standl. & Steyerm.
162 Pilea mimema Standl. & Steyerm.

HAUGHT, O.

2190 Psychotria rosea var. trichophora Steyerm.
3068 Faramea occidentalis subsp. lonchocalyx Steyerm.
5400 Hippotis grandiflora Steyerm.

HELLER, A. A. (Amos Arthur)

12579 Grindelia nana var. turbinella Steyerm.

HENDERSON, A. (Andrew)

501 Prestoea humilis Henderson & Steyerm.

HENDERSON, L. F.

2791 Grindelia howellii Steyerm.

HERNÁNDEZ, I. (Lionel)

348 Ochthocosmus micranthus Steyerm.

HEYDE & LUX

6392 Tinantia longipedunculata Standl. & Steyerm.

HOFFMANN

s.n. Grindelia camporum var. abbreviata Steyerm.

HOLST, B. (Bruce Kendall)

3426 Schefflera yutajensis Steyerm. & Holst
3523 Paepalanthus *holstii* Steyerm.
3539 Lindmania *holstii* Steyerm. & L. B. Smith
3617 Ilex summa Steyerm.

HOLT, E. G.

743 Psychotria blakei Standl. & Steyerm.

HOWARD, R. A.

12302 Schradera subsessilis Steyerm.

HOWELL, J. T. (John Thomas)

4352 Grindelia rubricaulis var. permixta Steyerm.
5201 Grindelia camporum var. interioris f. foliacea Steyerm.
5221 Grindelia hirsutula var. brevisquama f. glabrata Steyerm.
5338 Grindelia hirsutula var. brevisquama Steyerm.
5473 Grindelia arenicola Steyerm.
5496 Grindelia camporum var. parviflora Steyerm.
6574 Grindelia rubricaulis var. elata Steyerm.
7545 Grindelia stricta var. aestuarina f. elongata Steyerm.
8106 Grindelia arenicola var. pachyphylla Steyerm.
10805 Grindelia humilis f. pubescens Steyerm.
11414 Grindelia hirsutula var. subintegra Steyerm.
11658 Grindelia maritima f. anomala Steyerm.

HOYOS, J. (Jesús)

46 Kotchubaea morilloi Steyerm.
90 Ouratea asisae Maguire & Steyerm.

HUBER, O. (Otto)

441 Maytenus *huberi* Steyerm.
543 Croton *huberi* Steyerm.
1229 Maytenus insculpta Steyerm.
1447 Ouratea ayacuchae Maguire & Steyerm.
1456 Neea ignicola Steyerm.
1693 Neea robusta Steyerm.
1791 Psychotria yapacanensis Steyerm.
1848 Piper *otto-huberi* Steyerm.
1904 Ouratea *huberi* Maguire & Steyerm.
2504 Ouratea deminuta Maguire & Steyerm.
3759 Tepuianthus savannensis Maguire & Steyerm.
4437 Ilex paruensis Steyerm.
5058 Navia *huberiana* L. B. Smith, Steyerm. & H. Robinson
5481 Ouratea pumila Maguire & Steyerm.
5536 Ouratea pumila var. heterodoxa Maguire & Steyerm.
5763 Ouratea longistyla Maguire & Steyerm.
5786 Sipaneopsis *huberi* Steyerm.
6136 Panopsis parimensis Steyerm.
6184 Navia culcitaria L. B. Smith, Steyerm. & H. Robinson
6945 Aphanocarpus steyermarkii f. elongatus Steyerm.
8246 Sipanea setacea Steyerm.
9123 Coccocypselum *huberi* Steyerm.
9467 Stegolepis *huberi* Steyerm.
9818 Bonnetia bolivarensis Steyerm.
10388 Matayba ptariana subsp. guaiquinimae Steyerm.
11849 Symbolanthus yaviensis Steyerm.

HUMBERT, H. (Henrí)

26739 Psychotria alticola Steyerm.

HUTCHINSON, P. C.

6799 Hillia wurdackii Steyerm.

IJJASZ

425 Psychotria aubletiana var. producta Steverm.

IRWIN, H. S. (Howard)

10161 Psychotria sciaphila subsp. longicalyx Steyerm.
14771 Psychotria hoffmannseggiana var. celsa Steyerm.
18688 Manettia *irwinii* Steyerm.
23537 Hindsia *irwinii* Steyerm.
27120 Mitracarpus pusillus Steyerm.
47354 Palicourea *irwinii* Steyerm.
47393 Psychotria oiapoquensis Steyerm.
47620 Tocoyena guianensis var. communis Steyerm.
54949 Isertia wilhelminensis Steyerm.
55048 Psychotria wilhelminensis Steyerm.
55299 Bertiera diversiramea Steyerm.
55706 Psychotria *irwinii* Steyerm.

JANGOUX, J. (Jacques)

10157 Borreria *jangouxii* Steyerm.
10193 Piper perijaense Steyerm.

JÁTIVA, C. (Carlos)

682 Palicourea guianensis subsp. occidentalis var. glabrescens Steyerm.
735 Psychotria macrophylla subsp. anomothyrsa f. tomentella Steyerm.

JENSEN, L. P.

s.n. Cassia fasciculata f. *jensenii* Palmer & Steyerm.

JOHNSON, H.

523 Poikilacanthus setiferus Standl. & Steyerm.

JOHNSTON, J. R.

1026 Verbesina agricolarum Standl. & Steyerm.
1255 Clethra *johnstonii* Standl. & Steyerm.
1480 Eugenia jutiapensis Standl. & Steyerm.
1525 Berberis *johnstonii* Standl. & Steyerm.
1643 Thalictrum *johnstonii* Standl. & Steyerm.
1812 Hypericum arbuscula Standl. & Steyerm.

1887 Struthanthus *johnstonii* Standl. & Steyerm.

JOLY, C.

5630 Piper arieianum var. yaracuyense f. barbulaense Steyerm.

JOOR

s.n. Grindelia littoralis Steyerm.

JÖRGENSEN, P.

2643 Menodora pinnatisecta Steyerm.
3694 Genipa americana var. caruto f. *jorgensenii* Steyerm.

KELLERMAN, W. A. (William Ashbrook)

5175 Euphorbia pantomalaca Standl. & Steyerm.
7223 Schistocarpha steyermarkii H. Robinson
7223 Senecio steyermarkiana H. Robinson
7532 Serjania macrocarpa Standl. & Steyerm.
7630 Phoradendron treleaseanum Standl. & Steyerm.

KILLIP, E. P. (Ellsworth Paine)

16585 Polygala santanderensis Killip & Steyerm.
26780 Geophila cordifolia var. peruviana Steyerm.

KIRKWOOD, J. E. (Joseph Edward)

20 Menodora coulteri var. minima Steyerm.

KLUG, C.

347 Tetrapterys julianii Macbr.
1969 Mabea *klugii* Steyerm.
2010 Tapura julianii Macbr.
2019 Psychotria subpedicellata Steyerm.
2064 Mabea standleyi Steyerm.
2164 Bertiera guianensis subsp. pubiflora Steyerm.
2362 Coussarea *klugii* Steyerm.
3084 Hippotis subelongata Steyerm.
3206 Mabea elata Steyerm.
3452 Kotchubaea montana Steyerm.

KOYAMA, T. (Tetsuo)

7506 Mapania steyermarkii T. Koyama

KRUKOFF, B. A. (Boris Alexander)

3 Retiniphyllum laxiflorum var. brasiliense Steyerm.
1983 Mabea pirioides Steyerm.
4940 Psychotria embirensis Steyerm.
6210 Drypetes amazonica Steyerm.
6297 Omphalea elaeophoroides Steyerm.
6455 Pseudoconnarus *krukovii* Steyerm.
6858 Psychotria megacephala Steyerm.
8396 Conceveiba *krukoffii* Steyerm.
8513 Richeria submembranacea Steyerm.
8556 Rourea *krukovii* Steyerm.
8616 Conceveiba simulata Steyerm.
8698 Conceveiba magnifica Steyerm.
10650 Elaeagia microcarpa Steyerm.

KUNTZE, O. (Carl Ernst Otto)

1643 Mitracarpus frigidus var. andinus Steyerm.

KUYLEN, H.

151 Clethra bimatris Standl. & Steyerm.

LANJOUW, J. (Joseph)

802 Palicourea crocea var. riparia f. heterodoxa Steyerm.

LASSER, T. (Tobias)

1042 Palicourea perquadrangularis var. brevipes Steyerm.
1156 Palicourea *lasseri* Steyerm.
1221 Palicourea insignis Steyerm.
1417 Coccocypselum guianense var. patens Steyerm.
1682 Coussarea *lasseri* Steyerm.
2047 Psychotria araguensis Steyerm.

LASSER, T. & J. A. STEYERMARK

55103 Symplocos *lasseri* Steyerm. (possibly a Steyermark number)

LEPRIEUR, F. R. M.

118 Psychotria pungens Steyerm.

LESUER, H. (Harde)

1016 Grindelia confusa Steyerm.

LIESNER, R. L. (Ronald)

4096 Neea mapourioides Steyerm.
5991 Rauia subtruncata Steyerm.
6222 Piper pseudoacreanum Steyerm.
6405 Piper *liesneri* Steyerm.
7729 Peperomia falconensis Steyerm.
8176 Piper cerronianum Steyerm.
8211 Piper wingfieldii Steyerm.
8959 Neea sebastianii Steyerm.
9699 Piper sierra-aroense Steyerm.
9767 Piper cordiforme Steyerm.
10022 Piper linguliforme Steyerm.
10107 Psychotria aubletiana var. villipila Steyerm.
10494 Piper arieianum var. yaracuyense f. puberulum Steyerm.
10555 Peperomia fundacionensis Steyerm.
10891 Piper longiappendiculatum Steyerm.
11151 Talisia heterodoxa Steyerm.
11277 Neea bracteosa Steyerm.
11479 Sloanea bolivarensis Steyerm.
11647 Piper fundacionense Steyerm.
11873 Piper *ronaldii* Steyerm.
15866 Navia *liesneri* L. B. Smith, Steyerm. & H. Robinson
15955 Psychotria pectinata Steyerm.
16013 Pagameopsis maguirei subsp. pusillus Steyerm.
16025 Navia filifera L. B. Smith, Steyerm. & H. Robinson
16026 Navia crassicaulis L. B. Smith, Steyerm. & H. Robinson
16355 Pochota mawarinumae Steyerm.
16502 Neea *liesneri* Steyerm.
16605 Raveniopsis *liesneri* Steyerm.
16688 Ilex glabella Steyerm.
16720 Maytenus pustulata Steyerm.
16809 Sauvagesia marahuacensis subsp. neblinensis Steyerm.
16901 Peperomia gentryi Steyerm.
16960 Faramea paludicola Steyerm.
16963 Psychotria thesceloantha Steyerm.

17493 Coussarea evoluta Steyerm.
17599 Ilex spathulata Steyerm.
17677a Sauvagesia marahuacensis Steyerm.
18214 Psychotria *ronaldii* Steyerm.
18403 Neea huachamacarae Steyerm.
18428 Neea marahuacae Steyerm.
18452 Pochota fuscolepidota Steyerm.
18455 Sloanea longiaristata Steyerm.
18469 Ilex *liesneri* Steyerm.
18595 Ilex acutidenticulata Steyerm.
18637 Pochota *liesneri* Steyerm.
18796 Ilex paujiensis Steyerm.
19479 Ilex ciliolata Steyerm.
19595 Psychotria edaphothrix Steyerm.
19878 Ilex longipilosa Steyerm.
20394 Talisia maruayana Steyerm.
20394 Talisia amaruayiensis Steyerm., ined. mss.
20514 Neea amaruayensis Steyerm.
20800 Guapira bolivarensis Steyerm.
21248 Pochota redmondii Steyerm.
21640 Faramea yutajensis Steyerm.
21649 Psychotria yutajensis Steyerm.
21826 Yutajea *liesneri* Steyerm.
21827 Rudgea corocoroensis Steyerm.
21904 Aechmea siapensis L. B. Smith & Steyerm.
21968 Piper mosaicum Steyerm.
21998 Navia terramarae L. B. Smith & Steyerm.
22041 Navia patria L. B. Smith & Steyerm.
22062 Navia platyphylla L. B. Smith & Steyerm.
22064 Cephalodendron aracamuniensis Steyerm.
22075 Sauvagesia guianensis subsp. aracamuniensis Steyerm.
22079 Symbolanthus aracamuniensis Steyerm.
22105 Bonnetia *liesneri* Steyerm.
22153 Neblinathamnus aracamunianus Steyerm.
22197 **Rapatea aracamuniana Steyerm.**
22203 Navia iosothrix L. B. Smith & Steyerm.
22262 Coussarea *liesneri* Steyerm.
22322 Navia carnevalii L. B. Smith & Steyerm.
22407 **Remijia reducta Steyerm.**
22473 Ilex aracamuniana Steyerm.
22559 Pochota aracamuniana Steyerm.
22622 Hexapterella steyermarkii Maas & Maas

LIGGETT, W. E. (William)

1 Echinacea purpurea f. *liggettii* Steyerm.

LINDHEIMER, F. (Ferdinand Jacob)

255 Grindelia microcephala var. adenodonta Steyerm.

LITTLE, E. L. (Elbert Luther)

9533 Pagamea guianensis var. macrocarpa Steyerm.
15238 Psychotria aubletiana var. andina f. pubescens Steyerm.
15354 Simira erythroxylon var. meridensis Steyerm.
15372 Guettarda steyermarkii f. pilosior Steyerm.

LUNDELL, C. L. (Cyrus Longworth)

2012 Solanum decurtatum Standl. & Steyerm.
2213 Annona primigenia Standl. & Steyerm.
3153 Lisianthius petenensis Standl. & Steyerm.
6193 Psychotria schippii Standl. & Steyerm.

LUTEYN, J. L. (James Leonard)

9413 Raveniopsis cowaniana Steyerm. & Luteyn
9610 Connellia smithiana Steyerm. & Luteyn

MADRIZ, A.

37 Trigonia costanensis Steyerm. & Badillo

MAGUIRE, B. (Bassett)

2874 Catostemma ebracteolatum Steyerm.
3558 Dendrosipanea wurdackii Steyerm.
4612 Borreria cataractarum Steyerm.
23072 Coussarea fanshawei Steyerm.
23204 Utricularia kaieteurensis Steyerm.
23249 Utricularia *maguirei* Steyerm.
24361 Retiniphyllum *maguirei* var. reticulatum Steyerm.
24393 Duroia eriopila var. tafelbergensis Steyerm.
24530 Malanea tafelbergensis Steyerm.
24874 Malanea sarmentosa f. tomentosa Steyerm.
27324 Sipanea pratensis var. dichotoma f. brachycarpa Steyerm.
27485 Ouratea ornata Maguire & Steyerm.
27631 Ouratea sipapoensis Maguire & Steyerm.
27674 Sloanea sipapoana Steyerm.
27756 Schefflera guanayensis subsp. sipapoensis Maguire, Steyerm. & Frodin
27864 Psychotria everardii subsp. sipapoensis Steyerm.
27869 Retiniphyllum laxiflorum var. longilobum Steyerm.
27895 Schradera brevipes Steyerm.
27971 Chimarrhis brevipes Steyerm.
28013 Remijia sipapoensis Steyerm.
28243 Meruma coccocypseloides Steyerm.
28349 Thibaudia smithiana Maguire, Steyerm. & Luteyn
28399 Matayba oligandra var. occidentalis Steyerm.
28409 Panopsis cuaoensis Steyerm.
28454 Schefflera pauciradiata Maguire, Steyerm. & Frodin
28458 Retiniphyllum tepuiense Steyerm.
28471 Schefflera sipapoensis Maguire, Steyerm. & Frodin
28483 Rudgea sipapoensis Steyerm.
28516 Piper politii subsp. sipapoense Steyerm.
28536 Pagamea velutina Steyerm.
28615 Talisia caudata Steyerm.
28626 Chimarrhis bathysoides Steyerm.
28656 Rhamnus sipapoensis Steyerm.
28741 Catostemma ebracteolatum Steyerm.
28743 Malanea sipapoensis Steyerm.
28778 Psychotria sipapoensis Steyerm.

29079 Remijia densiflora f. glabricalyx Steyerm.
29137 Sabicea velutina subsp. duidense Steyerm.
29242a Borreria pygmaea var. robusta Steyerm.
29253 Ouratea evoluta Maguire & Steyerm.
29469 Randia amazonasensis Steyerm.
29529 Perissocarpa umbellifera Steyerm. & Maguire
29543 Tepuianthus sarisarinamensis subsp. duidensis Maguire & Steyerm.
29546 Schefflera pedicelligera Maguire, Steyerm. & Frodin
29564 Thibaudia longipes Maguire, Steyerm. & Luteyn
29573 Pagamea capitata subsp. conferta f. breviloba Steyerm.
29786 Psychotria lourteigiana Steyerm.
29851 Psychotria adenophora Steyerm.
29859 Symbolanthus huachamacariensis Steyerm.
30001 Styrax tepuiensis subsp. huachamacarii Maguire & Steyerm.
30253 Schefflera huachamacarii Maguire, Steyerm. & Frodin
30285 Laplacea pubescens var. minor Steyerm.
30458 Sipanea glomerata var. paucinervia Steyerm.
30557 Ochthocosmus multiforus var. angustifolius Steyerm. & Luteyn
30632 Bonnetia tristyla subsp. nervosa Steyerm. (superfluous, illegitimate)
30683 Tepuianthus yapacanensis Maguire & Steyerm.
30766 Ouratea rotundipetala Maguire & Steyerm.
30878 Sipaneopsis morichensis Steyerm.
30881 Rudgea morichensis Steyerm.
30886 Perama galioides var. hispida f. cinerea Steyerm.
30945 Orthaea thibaudioides Maguire, Steyerm. & Luteyn
31740 Schefflera guanayensis Maguire, Steyerm. & Frodin
31823 Psychotria glandulicalyx subsp. camaniensis Steyerm.
32219 Calycophyllum spectabile Steyerm.
32329 Faramea fanshawei Steyerm.
32339 Orthaea pubifolia Maguire, Steyerm. & Luteyn
32351 Mapania *maguireana* T. Koyama & Steyerm.
32357 Faramea *maguirei* Steyerm.
32430 Cavendishia salicifolia Maguire, Steyerm. & Luteyn
32456 Gonzalgunia dicocca var. guianensis Steyerm.
32618 Psychotria puberulenta Steyerm.
32629 Ouratea gillyana subsp. pachypoda Maguire & Steyerm.
32758 Styrax tepuiensis subsp. guaiquinimae Maguire & Steyerm.
32974 Schradera *maguirei* Steyerm.
33070 Pagamea brevipedunculata Steyerm.
33427 Pagamea magniflora Steyerm.
33700 Chalepophyllum guianense var. cuneatum Steyerm.
34531 Retiniphyllum schomburgkii subsp. occidentale Steyerm.
34923 Tocoyena guianensis var. glabriuscula Steyerm.
35092 Psychotria duricoria var. longiloba Steyerm.
35143 Matayba yutajensis Steyerm.
35149 Thibaudia dolichandra Maguire, Steyerm. & Luteyn
35154 Schefflera reticulata subsp. yutajensis Maguire, Steyerm. & Frodin
35287 Hillia *maguirei* Steyerm.
35304 Peperomia yutajensis Steyerm.
35344 Gleasonia duidana var. latifolia Steyerm.
35356 Schradera yutajensis Steyerm.
35635 Schefflera pimichinensis Maguire, Steyerm. & Frodin
36188 Portulaca pygmaea Steyerm.
36259 Stachyarrhena reticulata Steyerm.
36518 Psychotria rosea f. calvescens Steyerm.
36657 Ouratea discophora subsp. pervenulosa Maguire & Steyerm.
36800 Ferdinandusa neblinensis Steyerm.
36889 Peperomia foveolata Steyerm.
36891 Peperomia yatuensis Steyerm.
36921 Psychotria speluncae subsp. exserta Steyerm.
36948 Pagameopsis *maguirei* subsp. neblinensis var. angustifolius Steyerm.
36975 Geophila orbicularis var. neblinae Steyerm.
37011 Neblinathamnus glabratus Steyerm.
37040 Rhamnus neblinensis Maguire & Steyerm.
37040 Rhamnus microreticulata Maguire & Steyerm., ined. ms.
37103 Macrocarpaea neblinae Maguire & Steyerm.
37130 Pagameopsis *maguirei* subsp. neblinensis Steyerm.
37148 Psychotria speluncae subsp. brevicalyx Steyerm.
37230 Rhamnus psilocarpa Maguire & Steyerm.
37254 Cavendishia neblinae Maguire, Steyerm. & Luteyn
37328 Dioscorea neblinensis Maguire & Steyerm.
37354 Schefflera globulifera Maguire, Steyerm. & Frodin
37483 Psychotria barnebyana Steyerm.
37490 Palicourea glabriflora Steyerm.
37570 Sipaneopsis pacimoniensis Steyerm.
37592 Dendrosipanea revoluta Steyerm.
37639 Sipaneopsis wurdackii Steyerm.
40009 Alibertia myrciifolia var. tepuiensis Steyerm.
40573 Psychotria pakaraimensis Steyerm.
40637 Chalepophyllum longilobum Steyerm.
40666 Platycarpum eglandulosum Steyerm.
40799 Ixora aluminicola Steyerm.
41438 Sipaneopsis *maguirei* Steyerm.

41496 Remijia argentea Steyerm.
41860 Retiniphyllum schomburgkii subsp. occidentale var. hirticalyx Steyerm.
41909 Ouratea brevipedicellata Maguire & Steyerm.
41996 Psychotria pallidinervia Steyerm.
42025 Amaioua guianensis var. macrantha Steyerm.
42031 Psychotria venezuelensis Steyerm.
42062 Dendropanax neblinae Maguire, Steyerm. & Frodin
42068 Guapira neblinensis Maguire & Steyerm.
42072 Neea neblinensis Maguire & Steyerm.
42084 Kotchubaea neblinensis Steyerm.
42096 Celiantha bella Maguire & Steyerm.
42120 Neblinathamnus argyreus Steyerm.
42134 Tapeinostemon longiflorum Maguire & Steyerm.
42226 Weinmannia neblinensis Maguire & Steyerm.
42266 Psychotria everardii subsp. neblinensis Steyerm.
42319 Dioscorea abysmophila Maguire & Steyerm.
42350 Orthaea wurdackii Maguire, Steyerm. & Luteyn
42378 Symplocos neblinae Maguire & Steyerm.
42379 Schefflera tremuloidae Maguire, Steyerm. & Frodin
42449 Psychotria leiantha Steyerm.
42467 Cephalodendron globosum Steyerm.
42469 Remijia *maguirei* Steyerm.
42475 Psychotria wurdackii Steyerm.
42493 Ladenbergia puberula Steyerm.
42496 Rhamnus acuminata Maguire & Steyerm.
42496 Rhamnus subpedunculata Maguire & Steyerm., ined. ms.
42515 Faramea neblinae Steyerm.
42597 Platycarpum *maguirei* Steyerm.
44713 Palicourea rigida f. microphylla Steyerm.
46152a Remijia roraimae var. guianensis Steyerm.
46814 Schradera bipedunculata Steyerm.
46864 Cephaëlis tepuiensis Steyerm.
46872 Psychotria aligera Steyerm.
46876 Sterigmapetalum exappendiculatum Steyerm. & Liesner
53562 Cephaëlis sandwithiana Steyerm.
53608 Thymocarpus cannoides Nicolson, Steyerm. & Sivadasan
53676 Duroia strigosa Steyerm.
53731 Maytenus longistipitata Steyerm.
53864 Macrocentrum *steyermarkii* Wurdack
54440 Psychotria officinalis subsp. wilhelminensis Steyerm.
60071 Duroia *maguirei* Steyerm.
60073 Psychotria adderleyi Steyerm.
60181 Scleronema neblinense Steyerm.
60295 Amphidasya neblinae Steyerm.
60477 Befaria neblinensis Maguire, Steyerm. & Luteyn
60503 Schefflera pallens Maguire, Steyerm. & Frodin
60511 Psychotria celiae Steyerm.
65567 Baccharis schomburkkii subsp. occidentalis Steyerm. & Maguire
65587 Chionolaena breweri Steyerm. & Maguire
65593 Tapeinostemon breweri Steyerm. & Maguire
65616 Mikania marahuacensis Steyerm. & Maguire
65641 Cottendorfia marahuacae L. B. Smith, Steyerm. & H. Robinson
65705 Navia lactea L. B. Smith, Steyerm. & H. Robinson

MANARA, B. (Bruno)

s.n. Paullinia *manarae* Steyerm.
s.n. Peltastes *manarae* Steyerm.
s.n. Peperomia *manarae* Steyerm.
s.n. Piper pubivaginatum Steyerm.
51 Siparuna *manarae* Steyerm.

MARCANO BERTI, L. (Luis)

54-979 Guapira glabriflora Steyerm.
119-979 Talisia Sancarlosiana Steyerm.
209 Guapira *marcano-bertii* Steyerm.
418 Sloanea megacarpa Steyerm. & Marcano Berti
447 Sloanea subpsilocarpa Steyerm.
519-979 Hillia *marcano-bertii* Steyerm.
532-979 Rudgea *marcano-bertii* Steyerm.
551 Guapira amacurensis Steyerm.

MATUDA, E. (Eizi)

1741 Galactia acuminata Steyerm.
2260 Jatropha standleyi Steyerm.
5330 Schismocarpus *matudai* Steyerm.

MCCONNELL

663 Schefflera rugosifolia Maguire, Steyerm. & Frodin

MEDINA, E. (Ernesto)

534 Ouratea *medinae* Maguire & Steyerm.

MELLO BARRETO, H. L.

226 Mendoncia *mello-barretoana* Steyerm.

METCALFE, O. B.

744 Grindelia arizonica var. dentata Steyerm.

MEXIA, Y. (Ynez)

8783 Salpianthus standleyi Steyerm.
8855 Paullinia *mexiae* Steyerm.

MOORE, G. E. (George)

s.n. Anemone virginiana f. plena Palmer & Steyerm.
s.n. Cirsium altissimum f. *moorei* Steyerm.

MOORE, J. A.

3488 Haplopappus gymnocephalus f. albus Steyerm. & Moore
3515 Polygala rimulicola Steyerm.
3528 Valeriana texana Steyerm.
3547 Laphamia quinqueflora Steyerm.
3607 Grindelia havardii Steyerm.

3686 Grindelia blakei Steyerm.
3687 Grindelia stricta var. procumbens Steyerm.
3768 Grindelia squarrosa f. depressa Steyerm.
3784 Grindelia revoluta Steyerm.
3795 Cladothrix lanuginosa var. carnosa Steyerm.

MORALES, R. J.
1106 Tradescantia disgrega f. pubescens Standl. & Steyerm.

MORI, S. (Scott)
15027 Talisia glandulifera Steyerm.

MORILLO, G. (Gilberto)
3339 Talisia *morilloi* Steyerm.
3355 Rinorea oraria Steyerm. & Fernández
3903 Sabicea *morillorum* Steyerm.
4070 Sabicea grandifolia Steyerm.
4136 Piper papilliferum Steyerm.
4192 Remijia *morilloi* Steyerm.
5510 Piper *morilloi* Steyerm.
6716 Faramea *morilloi* Steyerm.
6811 Chomelia glabricalyx Steyerm.
8260 Portulaca insignis Steyerm.
10102 Cynanchum julianii Morillo

MORITZ, J. W. K. (Johann Wilhelm Karl)
1065 Epidendrum steyermarkii A. D. Hawkes

MUENSCHER, W. C.
12360 Solanum *muenscheri* Standl. & Steyerm.

MUNZ, P. A. (Philip Alexander)
11157 Grindelia camporum var. australis Steyerm.

MURCA PIRES, J. (or J. M. Pires)
122 Psychotria iodotricha subsp. multiflora Steyerm.
6063 Retiniphyllum parvifolium Steyerm.
15010(33) Lindmania *piresii* L. B. Smith, Steyerm. & Luteyn
15014(37) Navia *piresii* L. B. Smith, Steyerm. & H. Robinson
50285 Coussarea amapaensis Steyerm.
50386 Palicourea amapaensis Steyerm.
50632 Ixora *piresii* Steyerm.
51210 Ixora amapaenis Steyerm.
51371 Psychotria araguariensis Steyerm.
51601 Duroia amapana Steyerm.
52250 Psychotria *piresii* Steyerm.
52451 Genipa spruceana Steyerm.

NASCIMENTO, O. C.
20 Psychotria formosissima Steyerm.

NEE, M. (Mike)
30967 Remijia sessilis Steyerm.

NELSON, E. W. (Edward William)
6523 Grindelia sublanuginosa Steyerm.
6864 Grindelia *nelsonii* Steyerm.

NELSON, J. C.
1670 Grindelia integrifolia f. dentata Steyerm.

OLDEMAN
209 Chomelia glabriuscula Steyerm.

OLDERMAN, R. A. A.
B-627 Rudgea oldemanii Steyerm.

OLIVA ESTEVA, F. (Francisco)
s.n. Brocchinia oliva-estevae Steyerm. & L. B. Smith

ORCUTT, C. R. (Charles Russell)
1204 Grindelia greenei Steyerm.

OWNBEY
2739 Joosia macrocalyx Standl. ex Steyerm.

PALMER, E. (Edward)
163 Grindelia *palmeri* Steyerm.
316 Grindelia oxylepis f. eligulata Steyerm.
429 Menodora decemfida var. longifolia Steyerm.
469 Grindelia microcephala var. pusilla Steyerm.
471 Grindelia greenmanii Steyerm.
520 Grindelia oxylepis var. capitellata Steyerm.

PALMER, E. J. (Ernest Jesse)
16342 Quercus ×inaequalis Palmer & Steyerm.
18928 Sambucus canadensis f. rubra Palmer & Steyerm.
21923 Benzoin aestivale var. pubescens Palmer & Steyerm.
25421 Quercus ×vaga Palmer & Steyerm.
26069 Quercus ×mutabilis Palmer & Steyerm.
31083 Menodora scabra var. ramosissima Steyerm.
33590 Grindelia microcephala var. adenodonta f. angustior Steyerm.
35387 Cladrastis lutea f. tomentosa Steyerm.
39039 Rosa setigera f. inermis Palmer & Steyerm.
40317 Amelanchier canadensis f. nuda Palmer & Steyerm.
41450 Ludvigia alternifolia var. pubescens Palmer & Steyerm.
41642 Rosa setigera f. serena Palmer & Steyerm.
55411 Phlox divaricata var. laphamii f. candida Palmer & Steyerm.
59655 Rubus flagellaris f. roseo-plenus Palmer & Steyerm.
61259 Vernonia bladwinii f. albiflora Steyerm.
65070 Phacelia hirsuta f. albiflora Palmer & Steyerm.

PARISH, S. B. (Samuel Bonsall)
9795 Menodora spinescens var. mohavensis Steyerm.

PARRY, C. C. (Charles Christopher)
570pp Menodora helianthemoides var. magniflora Steyerm.
571pp Menodora helianthemoides var. humilis Steyerm.

PEGLER
950 Menodora heterophylla var. australis Steyerm.

PEÑA, B. S.
s.n. Psychotria fimbriflora Steyerm.

PENNELL, F. W. (Francis Whittier)
1676 Coccocypselum brevipetiolatum Steyerm.

PHELPS, K. D. (Kathleen Deery)
366 Pagamea reducta Steyerm.

PHILIPSON
2072 Joosia umbellifera subsp. macarensis Steyerm.

PINKUS, A. S.
90 Hiraea tepuiensis Steyerm.
92 Calycolpus roraimensis Steyerm.
277 Ouratea pseudotatei Maguire & Steyerm.

PIPOLY, J.
6838 Tepuianthus aracensis Steyerm. & Maguire

PITTIER, H. (Henrí Francois)
5178 Bertiera guianensis var. leiophylla Steyerm.
7911 Psychotria microdon var. meridionalis Steyerm.
9829 Borreria laevis var. edentata Steyerm.
9967 Guettarda crispiflora var. venezuelensis Steyerm.
10948 Faramea multiflora var. epedunculata Steyerm.
11995 Rondeletia venezuelensis Steyerm.
12192 Faramea occidentalis var. meridionalis Steyerm.
13498 Rudgea costanensis Steyerm.
14010 Psychotria berteriana subsp. venezuelica Steyerm.
14103 Hippotis lasseri Steyerm.

PLOWMAN, T. (Timothy)
13610 Maytenus neblinae Steyerm.

PRANCE, G. T. (Ghillean)
7606 Duroia hirsutissima Steyerm.
8985 Geophila *prancei* Steyerm.
9015 Psychotria *prancei* Steyerm.
10528 Sipanea *prancei* Steyerm.
14739 Rudgea *prancei* Steyerm.
29016 Raveniopsis aracaënsis Kallunki & Steyerm.
59234 Duroia *prancei* Steyerm.

PURPUS, C. A. (Carl Albert)
1318 Menodora intricata var. *purpusii* Steyerm.
5722 Grindelia robinsonii Steyerm.
12091 Aster bimater Standl. & Steyerm.
16201 Tinantia leiocalyx f. glabra Standl. & Steyerm.

RAMIA, M. (Mauricio)
5254 Chomelia *ramiae* Steyerm.

REDMOND, P. (Parker)
s.n. Erythrina poeppigiana f. *redmondii* Steyerm. & Lasser

ROADHOUSE, F. E.
65 Grindelia hirsutula var. calva Steyerm.

ROHL, E.
103 Chomelia venezuelensis Steyerm.

ROSA, N. A.
706 Pagamea acrensis Steyerm.

RUÍZ-TERÁN, L. E.
441 Elaeagia *ruiz-teranii* Steyerm.
1433 Tocoyena costanensis subsp. andina Steyerm.
2980 Psychotria blepharophora var. pubens Steyerm.
3199 Psychotria *ruiz-teranii* Steyerm.
3746 Palicourea angustifolia var. glabricaulis Steyerm.
4703 Rudgea *ruiz-teranii* Steyerm.
6461 Peperomia acuminata f. rubra Steyerm.
10907 Lantana *ruiz-teranii* López-Palacios & Steyerm.

RUNYON
875 Orthrosanthus chimboracensis var. exsertus f. albus Steyerm.

RUSBY, H. H. (Henry Hurd)
s.n. Psychotria occidentalis Steyerm.

SAER, J.
4 Chiococca alba subsp. parvifolia var. micrantha f. pilosa Steyerm.
635 Gonzalagunia ciliata Steyerm.
727 Rondeletia larensis Steyerm.

SASTRE, C. (Claude)
934 Sabicea *sastrei* Steyerm.
2392 Psychotria *sastrei* Steyerm.
6463 Psychotria cypellantha Steyerm.

SCHIPP, W. A.
674 Cynanchum stenomeres Standl. & Steyerm.

SCHLIM, L.
531 Faramea pseudospathacea Steyerm.

SCHMITT, W. F.
s.n. Grindelia arenicola f. trichophora Steyerm.

SCHNEE, L. (Ludwig)
1577 Xyris *schneeana* L. B. Smith & Steyerm.

SCHOMBURGK, R. (Robert Hermann)
282 Psychotria cordifolia subsp. perpusilla Steyerm.
924 Chomelia *schomburgkii* Steyerm.
955 Ferdinandusa goudotiana var. eciliata Steyerm.

SCHULTES, R. E. (Richard Evens)
46-357 Retiniphyllum truncatum var. angustifolium Steyerm.

8156 Coussarea hirticalyx var. glabrior Steyerm.
9100 Retiniphyllum glabrum Steyerm.
13075 Hillia *schultesii* Steyerm.
14475 Ferdinandusa *schultesii* Steyerm.
15031 Stenopadus colombianus Cuatr. & Steyerm.
15056 Tepuianthus colombianus Maguire & Steyerm.
19367 Pagamea coriacea var. acuta Steyerm.
19929 Platycarpum *schultesii* Steyerm. ex Schultes
20061 Perama *schultesii* Steyerm.

SHAFER, J. A. (John Adolf)
8805 Psychotria deflexa subsp. cubensis Steyerm.

SHANTZ, H. L. (Homer LeRoy)
597 Grindelia inornata var. angusta Steyerm.

SHREVE, F. (Forrest)
8035 Viguiera *shrevei* Steyerm.

SILVA N. T. (Nilo)
81 Psychotria quadribracteata Steyerm.
60606 Neea grandis Maguire & Steyerm.
60607 Psychotria heteroneura Steyerm.
60633 Psychotria brazoi Steyerm.
60678 Mollinedia neblinensis Maguire & Steyerm.
60700 Faramea *silvae* Steyerm.
60719 Capparis grandipetala Maguire & Steyerm.
60842 Psychotria maturacensis Steyerm.
60865 Sloanea parvifructa Steyerm.
60872 Psychotria *silvae* Steyerm.
60873 Ilex attenuata Steyerm.
60880 Pagameopsis maguirei subsp. neblinensis var. pirapucensis Steyerm.
60880 Psychotria canescens Steyerm.
60898 Maguireocharis neblinae Steyerm.
60903 Schefflera coriacea subsp. neblinae Maguire, Steyerm. & Frodin
60907 Neblinathamnus brasiliensis Steyerm.
60941 Schefflera plurispicata Maguire, Steyerm. & Frodin

SILVERIO LEVEL, J.
145 Faramea parvibractea Steyerm.
147 Duroia kotchubaeoides Steyerm.

SKUTCH, A. F. (Alexander Frank)
935 Chamaedorea *skutchii* Standl. & Steyerm.
982 Urera killipiana Standl. & Steyerm.
1367 Phoebe padiformis Standl. & Steyerm.
1453 Clethra *skutchii* Standl. & Steyerm.
1569 Rondeletia myriantha Standl. & Steyerm.
1660 Fraxinus cavekiana Standl. & Steyerm.
1811 Diolena calciphila Standl. & Steyerm.
2008 Mabea excelsa Standl. & Steyerm.
2073 Psychotria clivorum Standl. & Steyerm.
2110 Rondeletia *skutchii* Standl. & Steyerm.

SMART
213 Menodora scabra var. longituba Steyerm.

SMITH, A.
F1779 Licania costaricensis Standl. & Steyerm.

SMITH, A. C. (Albert Charles)
2384 Appunia longiloba Steyerm.
2618 Malanea macrophylla f. cuneata Steyerm.
2792 Duroia eriopila f. glabra Steyerm.
3066 Malanea sarmentosa f. sparsipilosa Steyerm.
10289 Schradera vahlii var. acutifolia Steyerm.

SMITH, C. P. (Charles Piper)
1016 Grindelia rubricaulis var. latifolia f. villosa Steyerm.

SMITH, H. H. (Herbert Huntington)
100 Pogonopus speciosus subsp. sandwithianus Steyerm.
320 Rondeletia purdiei var. glabrior Steyerm.
393 Psychotria horizontalis var. psilophylla Steyerm.
2628 Diodia teres var. angustata f. latior Steyerm.

SMITH, REV. L. C.
135 Grindelia microcephala var. montana Steyerm.

SMITH, R. F. (Robert)
V-6649 Coussarea terepaimensis Steyerm.

SPAULDING, REV.
s.n. Grindelia nana f. longisquama Steyerm.

SPRUCE, R. (Richard)
937 Ixora sandwithiana Steyerm.
3440 Psychotria maguireorum Steyerm.
4008 Psychotria adpressipilis Steyerm.
4109 Bertiera guianensis var. glabriflora Steyerm.

STANDLEY, P. C. (Paul Carpenter)
7884 Ipomoea ophioides Standl. & Steyerm.
12459 Siphonoglossa hondurensis Standl. & Steyerm.
58025 Tradescantia guatemalensis f. alba Standl. & Steyerm.
58597 Archibaccharis blakeana Standl. & Steyerm.
58674 Aphanactis *standleyi* Steyerm.
58732 Clematis caleoides Standl. & Steyerm.
59219 Sapranthus megistanthus Standl. & Steyerm.
59321 Salmea orthocephala Standl. & Steyerm.
59358 Tradescantia aguensis Standl. & Steyerm.
59934 Diospyros johnstoniana Standl. & Steyerm.
60082 Jacobinia umbrosa f. erythrantha Standl. & Steyerm.
60304 Eupatorium antiquorum Standl. & Steyerm.
61100 Eupatorium plethadenium Standl. & Steyerm.

61425 Pseudabutilon inornatum Standl. & Steyerm.
61803 Physalis chimalteca Standl. & Steyerm.
62109 Dalbergia pacifica Standl. & Steyerm.
62513 Schkuhria viscosissima Standl. & Steyerm.
63104 Chamaedorea pachecoana Standl. & Steyerm.
63209 Zanthoxylum aguilarii Standl. & Steyerm.
63743 Eupatorium carmonis Standl. & Steyerm.
63878 Hyperbaena vulcania Standl. & Steyerm.
65053 Erigeron aquarius Standl. & Steyerm.
65123 Clethra pachecoana Standl. & Steyerm.
65221 Mahonia volcania Standl. & Steyerm.
65479 Buddleja amplexicaulis Standl. & Steyerm.
65798 Eupatorium huehuetecum Standl. & Steyerm.
65862 Eupatorium ovillum Standl. & Steyerm.
67195 Lobelia laxiflora f. lutea Standl. & Steyerm.
67221 Eupatorium rojasianum Standl. & Steyerm.
67473 Solanum fontium Standl. & Steyerm.
67488 Physalis calidaria Standl. & Steyerm.
67540 Verbesina apleura var. foliolata Standl. & Steyerm.
67887 Clerodendron pithecobium Standl. & Steyerm.
68152 Conostegia volcanalis Standl. & Steyerm.
68931 Teucunumania quetzalteca Standl. & Steyerm.
69568 Eugenia patalensis Standl. & Steyerm.
69756 Solanum verapazense Standl. & Steyerm.
69922 Psychotria pachecoana Standl. & Steyerm.
70009 Phoebe macrophylla Standl. & Steyerm.
70317 Conostegia gleasoniana Standl. & Steyerm.
71125 Eupatorium hastiferum Standl. & Steyerm.
71421 Ocotea verapazensis Standl. & Steyerm.
72891 Rondeletia izabalensis Standl. & Steyerm.
72793 Souroubea micrantha Standl. & Steyerm.
73714 Aeschynomene tricholoma Standl. & Steyerm.
73715 Serjania lobulata Standl. & Steyerm.
73841 Mirabilis pulchella Standl. & Steyerm.
74367 Pithecolobium saxosum Standl. & Steyerm.
74420 Abutilon orientale Standl. & Steyerm.
74456 Esenbeckia echinoidea Standl. & Steyerm.
74569 Lonchocarpus phlebophyllus Standl. & Steyerm.
74623 Corallocarpus guatemalensis Standl. & Steyerm.
74673 Euphorbia steyermarkii Standl.
75245 Bursera permollis Standl. & Steyerm.
75307 Pachecoa guatemalensis Standl. & Steyerm.
75590 Zexmenia pinetorum Standl. & Steyerm.
75788 Eupatorium jejunum Standl. & Steyerm.
76007 Borreria vegeta Standl. & Steyerm.
76162 Fraxinus vellerea Standl. & Steyerm.
76321 Randia habrophlebia Standl. & Steyerm.
76561 Schultesia guianensis f. lutescens Standl. & Steyerm.
78534 Malvastrum guatemalense Standl. & Steyerm.
78584 Trigonia rasa Standl. & Steyerm.
79287 Ipomoea santae-rosae Standl. & Steyerm.
80408 Fraxinus bicolor Standl. & Steyerm.
80900 Psychotria aguilarii Standl. & Steyerm.
80907 Euphorbia guatemalensis Standl. & Steyerm.
81097 Gnaphalium *standleyi* Steyerm.
81113 Gentiana guatemalensis Standl. & Steyerm.
81651 Garrya corvorum Standl. & Steyerm.
82039 Agave huehueteca Standl. & Steyerm.
82330 Climacorachis guatemala Standl. & Steyerm.
82430 Struthanthus brachybotrys Standl. & Steyerm.
82538 Trixis amphimalaca Standl. & Steyerm.
82597 Phoradendron huehuetecum Standl. & Steyerm.
82871 Vernonia mima Standl. & Steyerm.
82921 Verbesina petzalensis Standl. & Steyerm.
83332 Cardamine balnearia Standl. & Steyerm.
83528 Abutilon pachecoanum Standl. & Steyerm.
84001 Eupatorium cupressorum Standl. & Steyerm.
84404 Eupatorium vetularum Standl. & Steyerm.
84556 Gentiana lewisiae Standl. & Steyerm.
85146 Eupatorium mimicum Standl. & Steyerm.
85228 Tagetes sororia Standl. & Steyerm.
85603 Bonifazia quezalteca Standl. & Steyerm.
86226 Bouvardia pachecoana Standl. & Steyerm.
86270 Rubus hadrocarpus Standl. & Steyerm.
86890 Chamaedorea aguilariana Standl. & Steyerm.
87159 Chamaedorea quezalteca Standl. & Steyerm.
87473 Vernonia medialis Standl. & Steyerm.
87781 Pedilanthus camporum Standl. & Steyerm.
89560 Aphelandra gigantiflora f. lutea Standl. & Steyerm.
90160 Chamaedorea carchensis Standl. & Steyerm.
90328 Piper frioense Standl. & Steyerm.
90532 Calyptranthes macrantha Standl. & Steyerm.
90524 Rheedia macrantha Standl. & Steyerm.

90762 Cecropia sylvicola Standl. & Steyerm.
91207 Stillingia cruenta Standl. & Steyerm.

STEIN, B. A. (Bruce)

1553 Psychotria *steinii* Steyerm.

STERGIOS, B. (Basil)

2804 Chomelia *stergiosii* Steyerm.
8611 Neea cedensis Steyerm.

STEYERMARK, J. A. & G. AGOSTINI

8 Psychotria *agostinii* Steyerm.
17 Schradera glabriflora Steyerm.

STEYERMARK, J. A. & L. ARISTEGUIETA

4 Calycophyllum venezuelense Steyerm.
5 Malanea hypoleuca Steyerm.
17 Stegolepis *steyermarkii* Maguire
25 Platycarpum rugosum Steyerm.
59 Phoradendron insigne Steyerm.
102 Elaeagia maguirei var. pubens Steyerm.

STEYERMARK, J. A. & S. NILSSON

41 Columnea *steyermarkii* Morton
135 Psychotria parvibractea Steyerm.
176 Piper vitaceum var. venezuelense Steyerm.
178 Solanum rufistellatum Steyerm.
185 Solanum puberuloba Steyerm.
196 Schradera *nilssonii* Steyerm.
237 Selenipedium *steyermarkii* Foldats
382 Duroia retrorsipila Steyerm.
385 Malanea ueiensis Steyerm.
392 Hillia psammophila Steyerm.
426 Ladenbergia venamoensis Steyerm.
428 Guzmania *steyermarkii* L. B. Smith
429 Schefflera quinquestylorum Steyerm.
449 Ilex wurdackiana Steyerm.
450 Chorisepalum acuminatum Steyerm.
473 Phoradendron aphyllum Steyerm.
483 Schefflera quinquecarinata Steyerm.
561 Perama dichotoma var. hirsutula Steyerm.
732 Lisianthius acutilobus Steyerm.
767 Emmeorrhiza umbellata subsp. septentrionalis Steyerm.
768 Pouteria spectabilis Steyerm.

STEYERMARK, J. A. & J. J. WURDACK

116 Talisia tiricensis Steyerm. & Maguire
330 Rudgea phaneroneura Steyerm.
347 Ilex brevipetiolata Steyerm. & Wurd.
374a Lisianthius chimantensis Steyerm. & Maguire
377 Adenanthe bicarpellata Maguire, Steyerm. & Wurd.
387 Tepuia tatei var. chimantana Steyerm. & Maguire
426 Tetrapterys phylladenophora Maguire & Steyerm.
458 Notopora smithiana Steyerm. & Maguire
511 Chimantaea similis Maguire, Steyerm. & Wurd.
574 Chimantaea espeletoidea Maguire, Steyerm. & Wurd.
633 Bonnetia huberiana Steyerm.
640 Psychotria glandulicalyx Steyerm.
652 Stenopadus chimantensis Maguire, Steyerm. & Wurd.
669 Vaccinium chimantense Maguire, Steyerm. & Luteyn
675 Quelchia eriocaulis Maguire, Steyerm. & Wurd.
680 Bonnetia chimantensis Steyerm.
681 Achnopogon virgatus Maguire, Steyerm. & Wurd.
683 Quelchia bracteata Maguire, Steyerm. & Wurd.
713 Remijia pilosinervula Steyerm.
737 Ledothamnus decumbens Maguire, Steyerm. & Luteyn
747 Chimantaea humilis Maguire, Steyerm. & Wurd.
748 Chimantaea rupicola Maguire, Steyerm. & Wurd.
756 Quelchia ×grandifolia Maguire, Steyerm. & Wurd.
781 Daphnopsis *steyermarkii* Nevling
819 Myriocladus *steyermarkii* Swallen
821 Chimantaea mirabilis Maguire, Steyerm. & Wurd.
825 Mycerinus chimantensis Maguire, Steyerm. & Luteyn
826 Notopora chimantensis Steyerm. & Maguire
827 Lindmania *steyermarkii* L. B. Smith
851 Verbesina angusta Maguire, Steyerm. & Wurd.
861 Macrocarpaea rugosa Steyerm.
879 Laplacea fruticosa var. chimantae Steyerm.
921 Phoebe *steyermarkiana* C. K. Allen
921 Ocotea *julianii* van der Werff
953 Ledothamnus luteus Maguire, Steyerm. & Luteyn
954 Panicum *steyermarkii* Swallen
990 Bonnetia tepuiensis subsp. minor Steyerm.
1020 Pagameopsis maguirei Steyerm.
1028 Styrax tepuiense Steyerm. & Maguire
1036 Panopsis ornatinervia Steyerm.
1047 Bonnetia toronoensis Steyerm.
1059 Pterozonium *steyermarkii* Vareschi
1096 Xyris *steyermarkii* Maguire & Steyerm.
1100 Symplocos chimantensis Steyerm. & Maguire
1103 Euplassa chimantensis Steyerm.
1104 Neea tepuiensis Steyerm.
1105 Roupala chimantensis Steyerm.
1133 Cupania tepuiensis Steyerm. & Maguire
1136 Gongylolepis fruticosa Maguire, Steyerm. & Wurd.
1172 Palicourea perquadrangularis var. guayanensis Steyerm.
1197 Piper politii subsp. toronoense Steyerm.
1225 Cladium *steyermarkii* T. Koyama
1227 Tapeinostemon rugosum Maguire & Steyerm.
1340 Sabicea velutina subsp. chimantensis Steyerm.
1346 Piper tepuiense Steyerm.
1370 Passiflora bomareifolia Steyerm. & Maguire

STEYERMARK, J. A. (Julian Alfred)

4599a Houstonia pusilla f. rosea Steyerm.
5606 Hypericum pseudomaculatum f. flavidum Steyerm.
5779 Psoralea tenuiflora f. alba Steyerm.
6058 Ruellia caroliniensis f. alba Steyerm.
8522 Rhododendron roseum f. albidum Steyerm.
11261 Taxodium distichum f. confusum Palmer & Steyerm.
11345 Rudbeckia hirta f. homochroma Steyerm.
11390 Apios americana f. pilosa Steyerm.
11461 Carya buckleyi var. arkansana f. glabra Palmer & Steyerm.
12318 Quercus falcata f. angustior Palmer & Steyerm.
12414 Cardamine bulbosa f. fontinalis Palmer & Steyerm.
12491 Salix cordata f. mollis Palmer & Steyerm.
12548 Salix sericea f. glabra Palmer & Steyerm.
18628 Trillium ozarkanum Palmer & Steyerm.
20910 Salix cordata f. subintegra Palmer & Steyerm.
22499 Camassia scilloides f. petersenii Steyerm.
25927 Impatiens pallida f. dichroma Steyerm.
26652 Arenaria patula f. robusta Steyerm.
27665 Penstemon digitalis f. baueri Steyerm.
28324 Camassia scilloides f. variegata Steyerm.
28797 Echinacea pallida f. albida Steyerm.
29018 Mimosa zacapana Standl. & Steyerm.
29136 Commelina erecta var. angustifolia f. cana Standl. & Steyerm.
29267 Commelina erecta f. candida Standl. & Steyerm.
29313 Aeschynomene eriocarpa Standl. & Steyerm.
29490 Diospyros zacapana Standl. & Steyerm.
29505 Verbesina guatemalensis var. glabrata Standl. & Steyerm.
29640 Galactia minarum Standl. & Steyerm.
29644 Commelina standleyi Steyerm.
29671 Bouvardia *steyermarkii* Standl.
29718 Oxalis minarum Standl. & Steyerm.
29722 Hieracium minarum Standl. & Steyerm.
29737 Perymenium inamoenum Standl. & Steyerm.
29751 Tradescantia disgrega f. glandulosa Standl. & Steyerm.
29870 Phyllonoma cacuminis Standl. & Steyerm.
29906 Rondeletia cordovana Standl. & Steyerm.
30004 Athenaea macrocardia Standl. & Steyerm.
30066 Jacquemontia guatemalensis Standl. & Steyerm.
30068 Bursera *steyermarkii* Standl.
30254 Ipomoea saxorum Standl. & Steyerm.
30415 Pectis flava Standl. & Steyerm.
30416 Hydrocleis standleyi Steyerm.
30448 Crumenaria *steyermarkii* Standl.
30689 Machaerium fruticetorum Standl. & Steyerm.
30698 Verbesina *steyermarkii* Standl.
30866 Stevia chortiana Standl. & Steyerm.
30903 Eugenia cacuminum Standl. & Steyerm.
30926 Deppea amaranthina Standl. & Steyerm.
30987 Clusia lusoria Standl. & Steyerm.
31081 Saurauia veneficorum Standl. & Steyerm.
31269 Ageratum chortianum Standl. & Steyerm.
31327 Eugenia sasoana Standl. & Steyerm.
31341 Cosmos *steyermarkii* Sherff
31406 Chiococca semipilosa Standl. & Steyerm.
31430 Zanthoxylum nubium Standl. & Steyerm.
31433 Citharexylum *steyermarkii* Mold.
31453 Eugenia chiquimulana Standl. & Steyerm.
31489 Symplocos culminicola Standl. & Steyerm.
31534 Eupatorium macram Standl. & Steyerm.
31555 Lycianthes chiapensis var. sparsistellata Standl. & Steyerm.
31585 Miconia tixixensis Standl. & Steyerm.
31606 Viburnum mortonianum Standl. & Steyerm.
31696 Tradescantia standleyi Steyerm.
31758 Daphnopsis retifera Standl. & Steyerm.
31775 Eupatorium salinum Standl. & Steyerm.
31781 Asclepias woodsoniana Standl. & Steyerm.
31889 Phoradendron aguilarii Standl. & Steyerm.
31901 Bouvardia nubigena Standl. & Steyerm.
31913 Orthrosanthus chimboracensis var. centro-americanus Steyerm.
32041 Schaetzellia standleyi Steyerm.
32140 Sicyos guatemalensis Standl. & Steyerm.
32685 Perymenium jalapanum Standl. & Steyerm.
32767 Hieracium jalapense Standl. & Steyerm.
32808 Echeveria macrantha Standl. & Steyerm.
32823 Cacalia guatemalensis Standl. & Steyerm.
32868 Physalis lassa Standl. & Steyerm.
32945 Rhynchosia jalapensis Standl. & Steyerm.
33091 Arenaria altorum Standl. & Steyerm.
33124 Clethra licanioides Standl. & Steyerm.
33179 Canavalia munda Standl. & Steyerm.
33220 Rondeletia vulcanicola Standl. & Steyerm.
33244 Philodendron rojasianum Standl. & Steyerm.
33477 Roupala *steyermarkii* Sleumer
33448 Erblichia xylocarpa var. mollis Standl. & Steyerm.
33455 Aristolochia *steyermarkii* Standl.

33479 Chamaedorea rojasiana Standl. & Steyerm.
33501 Gymnanthes guatemalensis Standl. & Steyerm.
33533 Pseudocalymma standleyi Steyerm.
33605 Tinantia standleyi Steyerm.
33615 Marsdenia blepharodes Standl. & Steyerm.
33667 Hillia macrocarpa Standl. & Steyerm.
33743 Cyphomandra rojasiana Standl. & Steyerm.
33858 Sideroxylon *steyermarkii* Standl.
34047 Cyclanthera *steyermarkii* Standl.
34273 Sicydium glabrum Standl. & Steyerm.
34302 Psychotria altorum Standl. & Steyerm.
34304 Desmopsis guatemalensis Standl. & Steyerm.
34590 Viburnum detractum Standl. & Steyerm.
34609 Centaurium rosans Standl. & Steyerm.
34744 Eupatorium zunilanum Standl. & Steyerm.
34757 Stevia vulcanicola Standl. & Steyerm.
34760 Hypericum *steyermarkii* Standl.
34772 Lysimachia *steyermarkii* Standl.
34815 Hieracium culmenicola Standl. & Steyerm.
34860 Hieracium guatemalense Standl. & Steyerm.
34933 Cacalia pinetorum Standl. & Steyerm.
35001 Buddleja stenoptera Standl. & Steyerm.
35020 Odontonema *steyermarkii* Leonard
35489 Gentiana pumilio Standl. & Steyerm.
35810 Matelea *steyermarkii* Woodson
35835 Rojasianthe superba Standl. & Steyerm.
36019 Marsdenia *steyermarkii* Woodson
36044 Hydrangea *steyermarkii* Standl.
36067 Physalis campanula Standl. & Steyerm.
36075 Eupatorium saxorum Standl. & Steyerm.
36110 Pernettia saxicola Standl. & Steyerm.
36128 Hieracium tacanense Standl. & Steyerm.
36137 Juniperus standleyi Steyerm.
36175 Physalis amica Standl. & Steyerm.
36181 Polymnia standleyi Steyerm.
36207 Persea vesticula Standl. & Steyerm.
36210 Eugenia *steyermarkii* Standl.
36237 Chiococca *steyermarkii* Standl.
36258 Thalictrum standleyi Steyerm.
36268 Arenaria guatemalensis Standl. & Steyerm.
36286 Rondeletia brachistantha Standl. & Steyerm.
36291 Heliocereus heterodoxus Standl. & Steyerm.
36341 Eupatorium mendax Standl. & Steyerm.
36381 Ilex anodonta Standl. & Steyerm.
36386 Rhynchanthera medialis Standl. & Steyerm.
36426 Hoffmannia *steyermarkii* Steyerm.
36543 Liabum tajumulcense Standl. & Steyerm.
36575 Thalictrum *steyermarkii* Standl.
36576 Fissidens *steyermarkii* Bartram
36690 Hieracium ostreophyllum Standl. & Steyerm.
36787 Vernonia corae Standl. & Steyerm.
36801 Styrax vulcanicola Standl. & Steyerm.
36931 Casimiroa emarginata Standl. & Steyerm.
37004 Calea standleyi Steyerm.
37061 Persea *steyermarkii* C. K. Allen
37187 Campelia standleyi Steyerm.
37276 Buddleja astralis Standl. & Steyerm.
37381 **Chamaedorea stricta Standl. & Steyerm.**
37440 Pithecolobium zollerianum Standl. & Steyerm.
37583 Ficus cabusana Standl. & Steyerm.
37661 Gonolobus *steyermarkii* Woodson
37735 Chamaedorea vulgata Standl. & Steyerm.
37738 Rondeletia zolleriana Standl. & Steyerm.
37759 Cobaea *steyermarkii* Standl.
37766 Physalis carnosa Standl. & Steyerm.
37945 Calathea coccinea Standl. & Steyerm.
37953 Athenaea locuples Standl. & Steyerm.
37963 Anthurium titanium Standl. & Steyerm.
37974 Deppea inaequalis Standl. & Steyerm.
37982 Russelia laciniata Standl. & Steyerm.
38123 **Chamaedorea fusca Standl. & Steyerm.**
38170 Meliosma maxima Standl. & Steyerm.
38274 Eugenia simiarum Standl. & Steyerm.
38526 Lisianthius elatus Standl. & Steyerm.
38533 Jacquemontia pinetorum Standl. & Steyerm.
38658 Calea savannarum Standl. & Steyerm.
38839 Rudgea simiarum Standl. & Steyerm.
39165 Eugenia musarum Standl. & Steyerm.
39185 **Chamaedorea brachypoda Standl. & Steyerm.**
39288 Pancratium guatemalense Standl. & Steyerm.
39238 Lonchocarpus modestus Standl. & Steyerm.
39375 Chione guatemalensis Standl. & Steyerm.
39382 Duroia genipifolia Standl. & Steyerm.
39387 Capparis *steyermarkii* Standl.
39446 Mouriria *steyermarkii* Standl.
39448 Galipea guatemalensis Standl. & Steyerm.
39452 Bartholomaea mollis Standl. & Steyerm.
39454 Hyperbaena *steyermarkii* Standl.
39456 Mascagnia excelsa Standl. & Steyerm.
39516 Oecopetalum greenmanii Standl. & Steyerm.
39533 Coccoloba *steyermarkii* Standl.
39611 Crudia lacus Standl. & Steyerm.
39874 Dichapetalum bullatum Standl. & Steyerm.
39923 Sematophyllum *steyermarkii* Bartram
41543 Desmopsis izabalensis Standl. & Steyerm.
41748 Saurauia persifolia Standl. & Steyerm.
41819 Diolena rosiflora Standl. & Steyerm.
41864 Rondeletia macrocalyx Standl. & Steyerm.
41893 Chamaedorea stenocarpa Standl. & Steyerm.

41910 Hoffmannia racemifera Standl. & Steyerm.
41923 Ardisia apoda Standl. & Steyerm.
41928 Piper philodendroides Standl. & Steyerm.
41952 Palicourea phanerandra Standl. & Steyerm.
42212 Anthurium coibionii Standl. & Steyerm.
42487 Persea sessilis Standl. & Steyerm.
42489 Verbesina minarum Standl. & Steyerm.
42553 Greigia *steyermarkii* L. B. Smith
42600 Hoffmannia quadrifolia Standl. & Steyerm.
42649 Oreopanax *steyermarkii* A. C. Smith
42667 Piper minarum Standl. & Steyerm.
42931 Simsia *steyermarkii* Robinson & Brettell
42980 Russelia *steyermarkii* Carlson
42985 Calliandra carcerea Standl. & Steyerm.
43106 Psychotria minarum Standl. & Steyerm.
43145 Echeveria *steyermarkii* Standl.
43284 Microtropis ilicina Standl. & Steyerm.
43292 Mikania concinna Standl. & Steyerm.
43295 Vaccinium minarum Standl. & Steyerm.
43385 Phyllanthus minarum Standl. & Steyerm.
43439 Abutilon tridens Standl. & Steyerm.
43532 Eupatorium montigenum Standl. & Steyerm.
43583a Chamaedorea nubicum Standl. & Steyerm.
43622 Piper punctulatum Standl. & Steyerm.
43628 Buddleja euryphylla Standl. & Steyerm.
43747 Peperomia minarum Standl. & Steyerm.
43758 Mimosa canahuensis Standl. & Steyerm.
43806 Hoffmannia tuerckheimii var. glabra Standl. & Steyerm.
43837 Galactia sparsiflora Standl. & Steyerm.
43926 Serjania hispida Standl. & Steyerm.
44691 Eugenia cervina Standl. & Steyerm.
44757 Pilea killipiana Standl. & Steyerm.
44776 Anthurium radicosum Standl. & Steyerm.
44987 Piper ixocubvainense Standl. & Steyerm.
45142 Eugenia chinajensis Standl. & Steyerm.
45309 Sloanea petenensis Standl. & Steyerm.
45423 Monstera grandifolia Standl. & Steyerm.
45616 Capparis calciphila Standl. & Steyerm.
45627 Calea crassifolia Standl. & Steyerm.
45637 Rondeletia chinajensis Standl. & Steyerm.
45686 Oyedaea *steyermarkii* S. F. Blake
45710 Eugenia savannarum Standl. & Steyerm.
45712 Phoebe savannarum Standl. & Steyerm.
45738 Peperomia clavigera Standl. & Steyerm.
45827 Trichilia privigna Standl. & Steyerm.
46355 Guarea chirriactensis Standl. & Steyerm.
46398 Peperomia treleasei Standl. & Steyerm.
46624 Piper santae-clarae Standl. & Steyerm.
46653 Lycianthes barbatula Standl. & Steyerm.
46696 Piper lanciferum Standl. & Steyerm.
46773 Meliosma divers Standl. & Steyerm.
46862 Souroubea puberula Standl. & Steyerm.
47257 Mikania petrina Standl. & Steyerm.
47931 Hoffmannia vulcanicola Standl. & Steyerm.
48344 Cacalia pudica Standl. & Steyerm.
48334 Carex tunimanensis Standl. & Steyerm.
48413 Cerastium juniperorum Standl. & Steyerm.
48425 Viburnum euryphyllum Standl. & Steyerm.
48463 Symplocos vatteri Standl. & Steyerm.
48482 Symplocos abietorum Standl. & Steyerm.
48512 Monochaetum guatemalense Standl. & Steyerm.
48542 Carex *steyermarkii* Standl.
48554 Carex venosivaginata Standl. & Steyerm.
48558 Ardisia vatteri Standl. & Steyerm.
48564 Psychotria lilacina Standl. & Steyerm.
48572 Vaccinium haematinum Standl. & Steyerm.
48613 Peperomia huitzensis Standl. & Steyerm.
48621 Anthurium retiferum Standl. & Steyerm.
48631 Clerodendron mimicum Standl. & Steyerm.
48643 Solenophora abietorum Standl. & Steyerm.
48662 Mikania huitzensis Standl. & Steyerm.
48692 Spigelia carnosa Standl. & Steyerm.
48728 Diolena stenophylla Standl. & Steyerm.
48732 Coussarea mediocris Standl. & Steyerm.
48741 Pseudomedia simiarum Standl. & Steyerm.
48814 Hidalgoa *steyermarkii* Sherff
48831 Miconia echinoidea Standl. & Steyerm.
48843 Aegiphila hoffmannioides Standl. & Steyerm.
48934 Justicia *steyermarkii* Standl. & Steyerm.
49055 Carex huehueteca Standl. & Steyerm.
49104 Daphnopsis malacophylla Standl. & Steyerm.
49189 Ocotea laetevirens Standl. & Steyerm.
49270 Mendoncia guatemalensis Standl. & Steyerm.
49410 Peperomia dorstenioides Standl. & Steyerm.
49545 Ruyschia longistylis Standl. & Steyerm.
49556 Senecio *steyermarkii* Greenman
49712 Piper pinetorum Standl. & Steyerm.
49810 Saurauia cuchumatanensis Standl. & Steyerm.
49855 Viburnum brunnescens Standl. & Steyerm.

49859 Rubus hadrocarpus f. adenophorus Standl. & Steyerm.
49908 Castilleja altorum Standl. & Steyerm.
50061 Pinguicula clivorum Standl. & Steyerm.
50065 Hieracium clivorum Standl. & Steyerm.
50114 Siegesbeckia nudicaulis Standl. & Steyerm.
50132 Verbesina calciphila Standl. & Steyerm.
50143 Cardamine eremita Standl. & Steyerm.
50144 Romanschulzia alpina Standl. & Steyerm.
50150 Carex tojquianensis Standl. & Steyerm.
50157 Cirsium nigriceps Standl. & Steyerm.
50160 Hypericum calcicola Standl. & Steyerm.
50243 Drymaria minuscula Standl. & Steyerm.
50258 Oxalis calcicola Standl. & Steyerm.
50265 Commelina alpestris Standl. & Steyerm.
50280 Tauschia *steyermarkii* Math. & Const.
50303 Solanum alpicum Standl. & Steyerm.
50308 Montia calcicola Standl. & Steyerm.
50351 Dahlia coccinea var. *steyermarkii* Sherff
50501 Selaginella *steyermarkii* Alston
50569 Cardamine jejuna Standl. & Steyerm.
50672 Struthanthus oliganthus Standl. & Steyerm.
50739 Euphorbia senilis Standl. & Steyerm.
50818 Eucnide guatemalensis Standl. & Steyerm.
50876 Xylosma trinervium Standl. & Steyerm.
50908 Serjania phaseoloides Standl. & Steyerm.
50934 Echeveria huehueteca Standl. & Steyerm.
50936 Valeriana delicata Standl. & Steyerm.
50964 Eugenia papalensis Standl. & Steyerm.
50998 Bidens *steyermarkii* Sherff
51003 Smilacina crassipes Standl. & Steyerm.
51016 Zebrina huehueteca Standl. & Steyerm.
51039 Solanum huehuetecum Standl. & Steyerm.
51140 Juglans *steyermarkii* Manning
51269 Aristolochia mollis Standl. & Steyerm.
51340 Peperomia heterodoxa Standl. & Steyerm.
51398 Ophellantha *steyermarkii* Standl.
51498 Eupatorium crocodilium Standl. & Steyerm.
51538 Struthanthus tenuifolius Standl. & Steyerm.
51646 Euphorbia cuchumatanensis Standl. & Steyerm.
51666 Chamaedorea aequalis Standl. & Steyerm.
51672 Malaxis *steyermarkii* Correll
51683 Chamaedorea digitata Standl. & Steyerm.
51697 Hoffmannia huehueteca Standl. & Steyerm.
52104 Lycianthes orogenes Standl. & Steyerm.
52813 Aneilema ecuadoriensis Steyerm.
53095 Carex toreadora Steyerm.
53105 Carex azuayae Steyerm.
53576 Brunellia zamorensis Steyerm.
53769 Renealmia stellulata Steyerm.
53873 Brunellia paucijuga Steyerm.
54305 Elaeagia ecuadorensis Steyerm.
54475 Calceolaria *steyermarkii* Pennell
54506 Joosia aequatoria Steyerm.
54558 Joosia standleyana Steyerm.
54560 Tapeinostemon zamoranum Steyerm.
54664 Costus zamoranus Steyerm.
54825 Roupala obovata var. ecuadorensis Steyerm.
54873 Elleanthus *steyermarkii* Barringer
54901 Renealmia puberula Steyerm.
54967 Siparuna pittieri Steyerm.
55103 Symplocos lasseri Steyerm.
55176 Verbesina exalata Steyerm.
55217 Stellaria ovata f. paradoxa Steyerm.
55256 Cephaëlis tinctoria Standl. & Steyerm.
55291 Tofieldia sessiliflora var. robustior Steyerm.
55295 Conomorpha hieronymoides Steyerm.
55339a Orthrosanthus chimboracensis var. acorifolius f. albus Steyerm.
55346 Hypericum pseudocaracasanum Steyerm.
55371 Palicourea chimo Standl. & Steyerm.
55379 Sabazia urticifolia var. venezuelensis Steyerm.
55381 Fuschia adpressipilis Steyerm.
55392 Conomorpha larensis Steyerm.
55408 Chimarrhis venezuelensis Standl. & Steyerm.
55424 Banara larensis Steyerm.
55434 Dendropanax larensis Steyerm.
55470 Carex larensis Steyerm.
55506 Soliva anthemidifolia var. lanuginosa Steyerm.
55509 Rudgea hospes Standl. & Steyerm.
55528 Cajaphora larensis Steyerm.
55603 Bernardia venezuelana Steyerm.
55657 Lucilia venezuelensis Steyerm.
55824 Banara paucinervosa Steyerm.
55832 Maytenus parvifolia Steyerm.
55894 Azorella *julianii* Math. & Const.
55905 Elatine fassettiana Steyerm.
55906 Tillaea venezuelensis Steyerm.
55924 Euphorbia latazi var. glabra Steyerm.
55965 Guettarda steyermarkii f. latior Standl. & Steyerm.
55980 Conomorpha jajiensis Steyerm.
56061 Hypericum pseudomaculatum f. flavidum Steyerm.
56083 Heliconia schneeana Steyerm.
56124 Croton croizatii Steyerm.
56138 Lepidopilum *steyermarkii* Bartram
56162 Fuchsia meridensis Steyerm.
56232 Croton chamanus Steyerm.
56242 Oreopanax capitatus var. minor Steyerm.
56251 Eugenia meridensis Steyerm.
56268 Senecio *steyermarkii* Cuatr.
56272 Hypericum meridense Steyerm.
56300 Verbesina blakeana Steyerm.
56301 Cupania andina Steyerm.
56325 Ardisia meridensis Steyerm.
56333 Rustia venezuelensis Standl. & Steyerm.
56344 Saurauia meridensis Steyerm.

56411 Psychotria patria Standl. & Steyerm.
56412 **Palicourea canaguensis Steyerm.**
56441 Psychotria canaguensis Standl. & Steyerm.
56441 Rudgea nebulicola Steyerm.
56455 Turpinia multijuga Steyerm.
56502 Rudgea lucentifolia Standl. & Steyerm.
56507 Llagunoa venezuelana Steyerm.
56509 Maytenus coriacea Steyerm.
56513 Meriania *steyermarkii* Gleason
56516 Conomorpha frigidicola Steyerm.
56536 Drymaria firmula Steyerm.
56537 Baccharis meridensis Steyerm.
56539 Conomorpha densipapillata Steyerm.
56550 Rhynchospora paramora Steyerm.
56551 Myrcia sanisidrensis Steyerm.
56569 Dipterodendron venezuelense Steyerm.
56580 Zanthoxylum pallidum Steyerm.
56582 Ternstroemia acrodantha Kobuski & Steyerm.
56589 Calyptranthes meridensis Steyerm.
56591 Hillia microcarpa Steyerm.
56592 Havetia laurifolia var. venezuelana Steyerm.
56594 Cajaphora venezuelensis Steyerm.
56601 Guettarda *steyermarkii* Standl.
56614 Psychotria meridensis Steyerm.
56653 Ilex nervosa var. glabrata Steyerm.
56681 Psychotria standleyana Steyerm.
56727 Anthurium monsterioides Steyerm.
56792 Eupatorium *steyermarkianum* Badillo
56806 Croton larensis Steyerm.
56813 Phyllanthus larensis Steyerm.
56821 Croton deserticolus Steyerm.
56854 Phyllanthus croizatii Steyerm.
56869 Beloperone *steyermarkii* Leonard
56979 Ternstroemia camelliifolia var. minor Kobuski & Steyerm.
57005 Hieronyma croizatii Steyerm.
57019 Picramnia caracasana f. tomentella Steyerm.
57039 Uncinia meridensis Steyerm.
57040 Vesicarex collumanthus Steyerm.
57063 Hymenostephium viride Steyerm.
57066 Verbesina negrensis Steyerm.
57077 Viola venezuelensis Steyerm.
57084 Eupatorium stevioides Steyerm.
57111 Zanthoxylum tachirense Steyerm.
57136 Arachnothrix calycophylla Steyerm.
57137 Castilleja *steyermarkii* Pennell
57149 Verbesina tachirensis Steyerm.
57162 Cuphea serpyllifolia var. tachirensis Steyerm.
57170 Eugenia tachirensis Steyerm.
57172a Eugenia tamaensis Steyerm.
57175 Fuchsia verrucosa var. tamaensis Steyerm.
57192 Palicourea ensiformis Steyerm.
57198 Oreobolus venezuelensis Steyerm.
57204 Eugenia crebrifolia Steyerm.
57212 Hypericum ericifolium Steyerm.
57215 Hieracium frigidum f. tamaense Steyerm.
57217 Espeletia *steyermarkii* Cuatr.
57246 Pleurothallis *steyermarkii* Schweinf.
57253 Conomorpha sessilianthera Steyerm.
57255 Psychotria uberta Standl. & Steyerm.
57276 Casearia tachirensis Steyerm.
57298 Baccharis venulosa var. cuspidibracteata Steyerm.
57309 Psychotria tamaensis Standl. & Steyerm.
57310 Jungia reticulata Steyerm.
57321 Schefflera tamana Steyerm.
57335 Symplocos pittieriana Steyerm.
57336 Schefflera cuatrecasasiana Steyerm.
57340 Symplocos tamana Steyerm.
57359 Conomorpha tamana Steyerm.
57367 Carex tachirensis Steyerm.
57391 Rhynchospora tomentosa Steyerm.
57401 Carex tamana Steyerm.
57404 Rhynchospora tamana Steyerm.
57422 Fimbristylis tamaensis Steyerm.
57428 Rauwolfia *steyermarkii* Woodson
57435 Conomorpha sulcata Steyerm.
57441 Palicourea tachirensis Standl. & Steyerm.
57455 Stenospermatium pittieri Steyerm.
57456 Conomorpha liriensis Steyerm.
57481 Ranunculus nubigenus f. subintegrus Steyerm.
57519 Polymnia meridensis Steyerm.
57528 Pectis venezuelensis Steyerm.
57551 Dioscorea bolivarensis Steyerm.
57587 Rhynchospora trichochaeta var. venezuelensis Steyerm.
57629 Bulbostylis svensoniana Steyerm.
57649 Mauritia flexuosa var. venezuelana Steyerm.
57688 Phyllanthus bolivarensis Steyerm.
57713 Alseis trichocarpa Standl. & Steyerm.
57717 Chrysophyllum *steyermarkii* Monachino
57749 Eupatorium crassicaule Steyerm.
57807 Monotagma duidae Steyerm.
57820 Exochogyne *steyermarkii* Gilly
57821 Xyris esmeraldae Steyerm.
57835 Xyris capillaris Steyerm.
57835a Genlisea esmeraldae Steyerm.
57850 Drosera tenella var. esmeraldae Steyerm.
57853 Urospatha savannarum Steyerm.
57879 Doliocarpus esmeraldae Steyerm.
57888 Calathea duidae Steyerm.
57891 Phyllanthus orinocensis Steyerm.
57908 Bactris duidae Steyerm.
57919 Psychotria paupertina Standl. & Steyerm.
57920 Calathea lasseriana Steyerm.
57933 Bactris venezuelensis Steyerm.
57944 Desmoncus duidensis Steyerm.
57975 Tovomita duidae Steyerm.
57979 Lisianthius scabridulus Steyerm.
57986 Conomorpha apiculata Steyerm.
57989 Schefflera duidae Steyerm.
57994 Spathicarpa duidae Steyerm.
58001 Axonopus *steyermarkii* Swallen
58012 Navia *steyermarkii* L. B. Smith
58021 Sauvagesia duidae Steyerm.
58022 Ilex tateana Steyerm.
58038 Ilex stenophylla Steyerm.
58040 Stegolepis gleasoniana Steyerm.
58047 Oyedaea blakeana Steyerm.
58048 Psychotria duricoria Standl. & Steyerm.

58056 Psychotria avia Standl. & Steyerm.
58057 Smilax duidae Steyerm.
58061 Trichilia subsimplex Steyerm.
58099 Anthurium duidae Steyerm.
58117 Psychotria phaneroloma Standl. & Steyerm.
58123 Ilex retusa f. glabra Steyerm.
58125 Mikania auyantepuensis var. brevipedicellata Steyerm.
58127 Ilex retusa f. major Steyerm.
58168 Xyris scaridula Steyerm.
58176 Tofieldia duidae Steyerm.
58186 Bonnetia duidae Kobuski & Steyerm.
58191 Blepharandra cretacea var. composita Steyerm.
58225 Philodendron duidae Steyerm.
58229 Utricularia humboldtii f. cuneata Steyerm.
58233 Xyris culmenicola Steyerm.
58242 Styrax duidae Steyerm.
58254 Rhynchospora duidae Steyerm.
58262 Miconia *steyermarkii* Gleason
58265 Conomorpha lepidota f. acutata Steyerm.
58270 Vellozia duidae Steyerm.
58284 Ouratea duidae Steyerm.
58340 Ilex venezuelensis Steyerm.
58349 Ilex retusa f. glaucescens Steyerm.
58394 Remijia *steyermarkii* Standl.
58437 Xyris stenostachya Steyerm.
58442 Tocoyena orinocensis Standl. & Steyerm.
58445 Genlisea sanariapoana Steyerm.
58446 Utricularia oliveriana Steyerm.
58461 Pagamea anisophylla Standl. & Steyerm.
58466 Burmannia sanariapoana Steyerm.
58467 Sauvagesia miniata Steyerm.
58469 Rhynchospora sanariapensis Steyerm.
58472 Drosera sanariapoana Steyerm.
58488 Utricularia orinocensis Steyerm.
58504 Mandevilla *steyermarkii* Woodson
58505 Utricularia amazonasana Steyerm.
58520 Utricularia ayacuchae Steyerm.
58558 Malanea setulosa Steyerm.
58606 Clusia roraimana Steyerm.
58652 Rhynchospora tepuiana Steyerm.
58678 Oliganthes roraimensis Steyerm.
58759 Conomorpha roraimae Steyerm.
58761 Symplocos roraimensis Steyerm.
58848 Rapanea minima Steyerm.
58868 Eriocaulon *steyermarkii* Mold.
58870 Carex roraimensis Steyerm.
58943 Phthirusa roraimensis Steyerm.
58956 Eugenia rondonensis Steyerm.
58983 Rapanea reticulata Steyerm.
59000 Magnolia roraimae Steyerm.
59004 Mollinedia roraimensis Steyerm.
59065 Polygala balkeana Steyerm.
59072 Calea clematidifolia Steyerm.
59107 Cupania roraimae Steyerm.
59118 Rudgea bolivariensis Steyerm.
59136 Conomorpha leprosa Steyerm.
59182 Cupania kukenanica Steyerm.
59191 Utricularia bolivariana Steyerm.
59195 Utricularia congesta f. deminutiva Steyerm.
59227 Psychotria kukenanensis Steyerm.
59331 Microlicia *steyermarkii* Gleason
59333 Utricularia oliveriana f. parva Steyerm.
59335 Utricularia arenicola var. kavanayena Steyerm.
59336 Xyris lanulobractea Steyerm.
59342 Poecilandra pumila Steyerm.
59349 Abolboda macrostachya var. robustior Steyerm.
59351 Utricularia aureolimba Steyerm.
59359 Polygala appressa var. kavanayena Steyerm.
59361 Tetrapterys pusilla Steyerm.
59362 Nietneria paniculata Steyerm.
59363 Lagenocarpus *steyermarkii* Gilly
59369 Paepalanthus *steyermarkii* Mold.
59394 Ilex subrotundifolia Steyerm.
59396 Clusia pusilla Steyerm.
59403 Calea oliveri var. taeniotricha Steyerm.
59404 Utricularia congesta Steyerm.
59408 Calea lucidivenia f. lanceolata Steyerm.
59440 Psychotria ptariensis Standl. & Steyerm.
59452 Polygala sanariapoana Steyerm.
59482 Phyllanthus major Steyerm.
59483 Phoradendron ptarianum Steyerm.
59484 Ledothamnus *steyermarkii* A. C. Smith
59497 Grammadenia ptariensis Steyerm.
59504 Eupatorium tepuianum Steyerm.
59505 Eupatorium roupalifolium f. latifolium Steyerm.
59509 Anthurium ptarianum Steyerm.
59511 Ravenia ruellioides var. ptariana Steyerm.
59514 Stegolepis parvipetala Steyerm.
59517 Utricularia tepuiana Steyerm.
59521 Psychotria speluncae Standl. & Steyerm.
59527 Mikania phelpsii Maguire & Steyerm.
59534 Aulomyrcia bolivariensis Steyerm.
59537 Drimys brasiliense var. ptaritepuiensis Steyerm.
59547 Magnolia ptaritepuiana Steyerm.
59548 Malanea ptariensis Steyerm.
59549 Phthirusa ptariana Steyerm.
59570 Bonnetia *steyermarkii* Kobuski
59574 Ilex ptariana Steyerm.
59625a Utricularia venezuelana Steyerm.
59632 Conomorpha ptariensis Steyerm.
59634 Pagamea standleyana Steyerm.
59640 Cephalocarpus *steyermarkii* Gilly
59642 Ouratea ptaritepuiensis Steyerm.
59644 Genlisea nigrocaulis Steyerm.
59655 Stegolepis ptaritepuiensis Steyerm.
59658 Perama galioides var. intermedia Steyerm.
59660 Xyris setigera var. elongata Steyerm.
59677 Panopsis ptariana Steyerm.
59682 Philodendron ptarianum Steyerm.
59688 Phoradendron tepuianum Steyerm.
59695 Smilax staminea f. obtusata Steyerm.
59699 Clusia imbriata Steyerm.
59702 Clusia cerroana Steyerm.
59711 Siphoneugena densiflora var. tepuiensis Steyerm.
59719 Oedematopus ptarietepuiensis Steyerm.
59724 Aulomyrcia ptariensis Steyerm.

59734 Xyris albescens Steyerm.
59744 Pagamea *steyermarkii* Standl.
59753 Utricularia campbelliana var. minor Steyerm.
59759 Weinmannia *steyermarkii* Cuatr.
59760 Abolboda ptaritepuiana Steyerm.
59766 Heliamphora heterodoxa Steyerm.
59768 Gomidesia bonnetiasylvestris Steyerm.
59779 Leothrix *steyermarkii* Mold.
59781 Everardia *steyermarkii* Gilly
59830 Rhynchospora ptaritepuiana Steyerm.
59847 Brunellia integrifolia var. ptariana Steyerm.
59852 Utricularia aureomaculata Steyerm.
59858 Aspidosperma *steyermarkii* Woodson
59860 Mikania stictophora Steyerm.
59861 Tapeinostemon ptariense Steyerm.
59865 Eupatorium roupalifolium var. subintegrifolium Steyerm.
59866 Clusia hexacarpa var. ptaritepuiana Steyerm.
59869 Psychotria arenaria Standl. & Steyerm.
59913 Eriosorus paucifolius var. *steyermarkii* A. F. Tryon
59919 Xyris ptariana Steyerm.
59925 Croton roraimensis var. subintegrus Steyerm.
59926 Arthrostylidium *steyermarkii* McClure
59928 Baccharis ptariensis Steyerm.
59930 Utricularia heterochroma Steyerm.
59942 Hookeriopsis *steyermarkii* Bartram
59960 Aegiphila steyermarkii Mold.
59972 Doliocarpus ptariensis Steyerm.
59973 Tovomita atropurpurea Steyerm.
59974 Emmotum ptarianum Steyerm.
59979 Trichilia ptariana Steyerm.
59985 Moronobea ptaritepuiana Steyerm.
59987 Protium ptarianum var. angustior Steyerm.
59988 Panopsis tepuiana Steyerm.
59994 Protium ptarianum Steyerm.
59996 Piper *steyermarkii* Yuncker
60002a Coussapoa *steyermarkii* Cuatr.
60014 Mollinedia ptariensis Steyerm.
60015 Mikania hookeriana var. crassiculis Steyerm.
60021 Conceveibastrum ptarianum Steyerm.
60025 Couepia *steyermarkii* Maguire
60044 Dahlgrenia ptariana Steyerm.
60045 Euterpe ptariana Steyerm.
60046 Bactris ptariana Steyerm.
60089 Roupala sororopana Steyerm.
60090 Eupatorium pharcidodes var. sororopanensis Steyerm.
60094 Cyphomandra bolivariensis Steyerm.
60102 Myrcia sororopanensis Steyerm.
60119 Utricularia cuspidata Steyerm.
60121 Smilax lasseriana Steyerm.
60124 Dioscorea sororopana Steyerm.
60125 Diodia hyssopifolia var. leiocarpa Steyerm.
60127 Marcgravia sororopaniana Steyerm.
60129 Mahurea sororopantepuiana Steyerm.
60136 Daphnopsis dircoides Steyerm.
60161 Anguria simplicifolia Steyerm.
60175 Psychotria sororopanensis Standl. & Steyerm.
60184 Chiococca lucens Standl. & Steyerm.
60185 Cephaëlis bolivariensis Standl. & Steyerm.
60191 Psychotria heterocarpa Standl. & Steyerm.
60201 Matayba sororopaniana Steyerm.
60203 Matayba ptariana Steyerm.
60206 Rhynchospora bolivariana Steyerm.
60213 Aulomyrcia salticola Steyerm.
60215 Sauvagesia longipes Steyerm.
60234 Roupala minima Steyerm.
60237 Thesium tepuiense Steyerm.
60238 Hypolytrum tepuianum Steyerm.
60248 Eugenia tepuiensis Steyerm.
60251 Smilax pittieriana Steyerm.
60261 Sloanea pittieriana Steyerm.
60271 Buchenavia ptariensis Steyerm.
60272 Byrsonima bolivariana Steyerm.
60284 Myrcia tepuiensis Steyerm.
60285 Aulomyrcia parvifolia Steyerm.
60289 Humiria pilosa Steyerm.
60290 Ilex tepuiana Steyerm. ex Edwin
60310 Blepharandra ptariana Steyerm.
60312 Trattinickia glabra Steyerm.
60321 Oxythece *steyermarkiana* Monachino
60334 Rhynchospora karuaiana Steyerm.
60347 Brocchinia *steyermarkii* L. B. Smith
60354 Aulomyrcia amshoffiana Steyerm.
60359 Remijia stenopetala Standl. & Steyerm.
60365 Matayba reducta Steyerm.
60371 Erythroxylon venezuelense Steyerm.
60377 Palicourea aculeifera Steyerm.
60380 Psychotria cubitalis Standl. & Steyerm.
60385 Maytenus apiculata Steyerm.
60386 Croton kavanayensis Steyerm.
60406 Hyospathe maculata Steyerm.
60460 Protium puberulenta Steyerm.
60475 Tovomita angustata Steyerm.
60477 Utricularia subpeltata Steyerm.
60503 Ormosia *steyermarkii* Rudd
60541 Socratea albolineata Steyerm.
60542 Bactris kamarupa Steyerm.
60544 Sloanea caudata Steyerm.
60557 Ischnosiphon lasseriana Steyerm.
60566 Chrysochlamys pauciflora Steyerm.
60567 Philodendron krauseanum Steyerm.
60579 Paullinia mollicoma Steyerm.
60599 Eugenia ptariensis Steyerm.
60650 Micropholis *steyermarkii* Monachino
60652 Souroubea guianensis var. tomentella Steyerm.
60658 Sterigmapetalum guianense Steyerm.
60659 Phoradendron karuaianum Steyerm.
60660 Ilex karuaiana Steyerm.
60663 Matayba venezuelana Steyerm.
60665 Pourouma *steyermarkii* Standl. & Cuatr.
60668 Sloanea ptariana Steyerm.
60686 Hieronyma oblonga var. genuina f. glabra Steyerm.
60702 Aulomyrcia karuaiensis Steyerm.
60708 Caraipa longipedicellata Steyerm.
60735 Mikania lucida f. hirticaulis Steyerm.
60767 Lecythis karuaiensis Steyerm.
60768 Licania *steyermarkii* Maguire
60781 Bactris sororopanae Steyerm.
60789 Geonoma karuaiana Steyerm.

60813 Blepharodon *steyermarkii* R. Holm
60820 Diomma fruticosa Steyerm.
60822 Taralea *steyermarkii* Schery
60824 Euplassa venezuelana Steyerm.
60829 Cladium costatum Steyerm.
60831 Rhynchospora sororopana Steyerm.
60834 Trimezia fosteriana Steyerm.
60847 Anthurium krauseanum Steyerm.
60849 Senefelderopis croizatii Steyerm.
60863 Philodendron englerianum Steyerm.
60868 Rapatea *steyermarkii* Maguire
60871 Bonnetia tepuiensis Kobuski & Steyerm.
60875 Malanea microphylla Standl. & Steyerm.
60876 Podocarpus *steyermarkii* Buchh. & Gray
60879 Myrcia *exploratoris* McVaugh (dedicated to JAS)
60883 Byrsonima carraoana Steyerm.
60888 Pagamea pauciflora Standl. & Steyerm.
60892 Moronobea ptaritepuiana f. rosea Steyerm.
60898 Conomorpha depressa Steyerm.
60912 Cupania kavanayena Steyerm.
60914 Qualea ferruginea Steyerm.
60920 Drosera arenicola Steyerm.
60968 Desmoncus multijugus Steyerm.
60993 Homalium anzoateguiensis Steyerm.
61016 Sloanea onotillo Steyerm.
61039 Bactris bergantina Steyerm.
61317 Arachnothrix reflexa var. glandulifera Steyerm.
61373 Elaeagia laxiflora Standl. & Steyerm.
61424 Arachnothrix costanensis Steyerm.
61443 Freziera *steyermarkii* Kobuski
61513 Diospyros anzoateguiensis Steyerm.
61519 Abutilon pseudogiganteum Steyerm.
61523 Croizatia neotropica Steyerm.
61524 Meliosma pittieriana Steyerm.
61575 Styrax costanus Steyerm.
61612 Oyedaea verbesinoides var. glabrior Steyerm.
61626 Ternstroemia unilocularis Kobuski & Steyerm.
61659 Ilex vesparum Steyerm.
61665 Ternstroemia *steyermarkii* Kobuski
61726 Sloanea onotillo var. major Steyerm.
61731 Maytenus guianensis f. crenulata Steyerm.
61836 Dioscorea lasseriana Steyerm.
61874 Peperomia *steyermarkii* Yuncker
61914 Banisteria alternifolia Steyerm.
61919 Hasseltia monagensis Steyerm.
61950 Cinnamodendron venezuelense Steyerm.
61959 Quararibea *steyermarkii* Cuatr.
62017 Oreopanax venezuelense Steyerm.
62095 Oyedaea verbesinoides var. hypomalaca Steyerm.
62102 Duranta *steyermarkii* Mold.
62110 Rhynchospora culmenicola Steyerm.
62185a Xylobium *steyermarkii* Foldats
62189 Phyllanthus zanthoxyloides Steyerm.
62215 Sloanea breviseta Steyerm.
62216 Sloanea venezuelana Steyerm.
62225 Palicourea pustulata Steyerm.
62232 Alseis microcarpa Standl. & Steyerm.
62375 Aulomyrcia vinacea Steyerm.
62436 Melochia humboldtiana Steyerm.
62437 Clibadium surinamense var. macrophyllum Steyerm.
62491 Echeveria bicolor var. turumiquirensis Steyerm.
62532 Croton turumiquirensis Steyerm.
62539 Stylogyne turumiquirensis Steyerm.
62542 Hoffmannia costensis Standl. & Steyerm.
62548 Eugenia turumiquirensis Steyerm.
62573 Gnaphalium caeruleocanum Steyerm.
62579 Hypericum caracasanum var. turumiquirense Steyerm.
62583 Baccharis erectifolia Steyerm.
62605 Carex culmenicola Steyerm.
62611 Plinia fruticosa Steyerm.
62628 Myrtus myricoides var. turumiquirensis Steyerm.
62688 Tradescantia venezuelensis Steyerm.
62689 Abutilon turumiquirense Steyerm.
62691 Viburnum tinoides var. roraimense f. turumiquirense Steyerm.
62705 Carex turumiquirensis Steyerm.
62711 Befaria *steyermarkii* A. C. Smith
62739 Stellaria venezuelana Steyerm.
62752 Utricularia turumiquirensis Steyerm.
62800 Capparis guaguaensis Steyerm.
62875 Croton sucrensis Steyerm.
62880 Heteropterys quetepensis Steyerm.
62963 Excremis coarctata f. alba Steyerm.
65135 Aster anomalus f. albidus Steyerm.
66615 Heuchera puberula f. glabrata Steyerm.
67440 Viola triloba f. albida Steyerm.
67499 Pedicularis canadensis f. albescens Steyerm.
67915 Hydrophyllum appendiculatum f. album Steyerm.
67235 Mertensia virginica f. rosea Steyerm.
68024 Scutellaria nervosa f. alba Steyerm.
68254 Rhynchospora duidae Steyerm.
68397 Lysimachia quadriflora f. albescens Steyerm.
70292 Ruellia strepens f. alba Steyerm.
70126 Helianthus mollis f. flavida Steyerm.
72011 Rosa setigera f. alba Steyerm.
73223 Lithospermum canescens f. pallidum Palmer & Steyerm.
73886 Ledothamnus atroadenus Maguire, Steyerm. & Luteyn
74630 Palicourea tepuicola Steyerm.
74850 Anthurium *steyermarkii* Bunting
74652 Smilax chimantensis Steyerm. & Maguire
74656 Matayba chimantensis Steyerm. & Maguire
74781 Catostemma hirsutulum Steyerm.
74816 Struthuanthus chimantensis Steyerm. & Maguire
74877 Pagamea uniflora Steyerm.
74883 Graffenrieda *steyermarkii* Wurd.
74886 Ledothamnus atroadenus Maguire, Steyerm. & Luteyn
74980b Dicranoloma *steyermarkii* Bartram
75059 Phthirusa hippocrateoides Steyerm. & Maguire
75110 Stenopadus affinis Maguire, Steyerm. & Wurd.
75157 Markea reticulata Steyerm. & Maguire

75166 Malanea chimantensis Steyerm.
75358 Dacryodes chimantensis Steyerm. & Maguire
75406 Chiococca nitida var. chimantensis Steyerm.
75426 Phoradendron tenuiflorum Steyerm. & Maguire
75476 Piper toronotepuiense Steyerm.
75501 Ilex *steyermarkii* Edwin
75502 Begonia *steyermarkii* L. B. Smith & B. G. Schubert
75520 Alomia ballotifolia Maguire, Steyerm. & Wurd.
75534 Nothochlaena *steyermarkii* Vareschi
75544 Kotchubaea longiloba Steyerm.
75584 Rapatea chimantensis Steyerm.
75644 Hymenophyllopsis *steyermarkii* Vareshi
75701 Meliosma tepuiensis Steyerm. & Maguire
75733 Tepuia multiglandulosa Steyerm. & Maguire
75788 Didymopanax chimantensis Steyerm. & Maguire
75804 Myrica rotundata Steyerm. & Maguire
75830 Psychotria aubletiana var. cacuminis f. tomentella Steyerm.
75840 Magnolia chimantensis Steyerm. & Maguire
75912 Chimantaea lanocaulis Maguire, Steyerm. & Wurd.
75946 Rhamnus chimantensis Steyerm. & Maguire
75777 Clusia *steyermarkii* Maguire
78500 Viola viarum f. pilifera Palmer & Steyerm.
78703 Oenothera pilosella f. laevigata Palmer & Steyerm.
78868 Rubus pensilvanicus f. albinus Palmer & Steyerm.
79345 Calathea coccinea Standl. & Steyerm.
79674 Lobelia siphilitica f. purpurea Palmer & Steyerm.
80474 Silphium perfoliatum f. petiolatum Palmer & Steyerm.
82921 Muhlenbergia brachyphylla f. aristata Palmer & Steyerm.
84212 Rubus flagellaris var. occidualis f. roseus Steyerm.
86241 Randia aculeata var. dasyphylla Steyerm.
86323 Pittierothamnus elineolatus Steyerm.
86861 Psychotria lupulina subsp. rhodoleuca var. maypurensis f. pubens Steyerm.
87079 Isertia haenkeana var. mirandensis Steyerm.
87129 Dicranostyles imatacensis Steyerm.
87511 Stenospermation *steyermarkii* Bunting
87606 Dilkea magnifica Steyerm.
87782 Buettneria venezuelensis Steyerm.
87853 Rhynchospora *steyermarkii* T. Koyama
87964 Borreria bolivariensis Steyerm.
88149 Pavonia imatacensis Steyerm.
88277 Appunia venezuelensis Steyerm.
88425 Passiflora nuriensis Steyerm.
88591 Picramnia nuriensis Steyerm.
89005 Paullinia nuriensis Steyerm.
89276 Sipanea pratensis var. dichotoma f. breviflora Steyerm.
89464 Siparuna sancheziana Steyerm.
89491 Swartzia *steyermarkii* Cowan
89543 Stenospermation ammiticum Bunting
89565 Piper cuyunianum Steyerm.
89577 Stegolepis minor Steyerm.
89698 Navia arida L. B. Smith & Steyerm.
89802 Amaioua brevidentata Steyerm.
89813 Sicydium araguense Steyerm. & Trujillo
89875 Dichapetalum *steyermarkii* Prance
90199 Navia navicularis L. B. Smith & Steyerm.
90223 Navia connata L. B. Smith & Steyerm.
90269 Remijia densiflora var. minima Steyerm.
90428 Sterigmapetalum guianense subsp. ichunense Steyerm. & Liesner
90429 Remijia roraimae var. adpressa Steyerm.
90467 Qualea apodocarpa Steyerm.
90647 Henriettiella *steyermarkii* Wurd.
90798 Diodia hyssopifolia f. psiloclada Steyerm.
90823 Smilax auraimensis Steyerm.
90883 Tapirira dunstervilleorum Steyerm., Aristeg. & Wurd.
90919 Coccocypselum trinitense Steyerm.
90939 Macrolobium *steyermarkii* Cowan
90967 Meliosma nubicola Steyerm. & Lasser
91026 Cestrum pariense Steyerm.
91084 Topobea *steyermarkii* Wurd.
91120 Ixora agostiniana Steyerm.
91126 Malanea pariensis Steyerm.
91450 Piptocarpha *steyermarkii* Aristeg.
91499 Rytidostylis brevisetosa Steyerm.
91518 Coussarea pittieri Steyerm.
91538 Ilex *julianii* Edwin
91631 Psychotria sanmartensis var. costanensis Steyerm.
91874 Paullinia naiguatensis Steyerm.
91995 Connarus *steyermarkii* Prance
92077 Heisteria olivae Steyerm.
92079 Paullinia toxicodendroides Steyerm.
92131 Lacmellea costanensis Steyerm.
92333 Chrysophyllum monachinoanum Steyerm.
92336 Struthanthus mucronatus Steyerm.
92354 Dacryodes *steyermarkii* Sandw.
92379 Ochthocosmus grandifolius Steyerm.
92414 Pouteria venamoensis Steyerm.
92423 Orthaea venamensis Maguire, Steyerm. & Luteyn
92631 Piper venamoense Steyerm.
92657 Piper hippocrepiforme Steyerm.
92807 Peperomia microreticulata Steyerm.
92902 Vochysia pauciflora Steyerm.
92929 Psychotria coussareoides var. ciliata Steyerm.
92987 Cissus venezuelensis Steyerm.
93303 Parabignonia *steyermarkii* Sandw.
93230 Psychotria amplinoda Steyerm.
93238 Amanoa *steyermarkii* Jabl.
93361 Remijia roraimae var. auyantepuiensis Steyerm.
93413 Schoepfia tepuiensis Steyerm.
93431 Chrysophyllum ficoides Steyerm.
93476 Ocotea *steyermarkiana* C. K. Allen
93477 Notopora auyantepuiensis Steyerm.
93512 Achnopogon *steyermarkii* Aristeg.

93564 Cephaëlis cacuminis Steyerm.
93571 Sloanea *steyermarkii* C. E. Sm.
93652 Chiococca auyantepuiensis Steyerm.
93712 Heliamphora heterodoxa var. exappendiculata f. glabella Steyerm.
93737 Mandevilla subcarnosa var. angustata Steyerm.
93808 Stenopadus *steyermarkii* Aristeg.
93837 Utricularia *steyermarkii* P. Taylor
93844 Philacra *steyermarkii* Maguire
93889 Blepharodon auyantepuiense Steyerm.
93892 Cynanchum auyantepuiense Steyerm.
93895 Lindmania riparia L. B. Smith, Steyerm. & H. Robinson
93917 Pouteria auyantepuiensis Steyerm.
93980 Tepuia intermedia Steyerm.
93926 Didymopanax multiramosum Steyerm.
93974 Didymopanax auyantepuiense Steyerm.
94103 Malanea auyantepuiensis Steyerm.
94203 Qualea rubiginosa var. angustior Steyerm.
94382 Markea costanensis Steyerm.
94518 Lennoa madreporoides subsp. australis Steyerm.
94897 Piper pseudobredemeyeri Steyerm.
94923 Trichipteris *steyermarkii* Tryon
94956 Psychotria sucrensis Steyerm.
94962 Besleria mortoniana Steyerm.
95002 Piper pseudoaequale Steyerm.
95019 Psychotria pariensis Steyerm.
95022 Guzmania membranacea L. B. Smith & Steyerm.
95075 Psychotria humensis Steyerm.
95152 Sarcorhachis venezuelana Steyerm.
95187 Boehmeria ramiflora var. vinacea Steyerm.
95215 Psittacanthus costanensis Steyerm.
95246 Psychotria hyalina Steyerm.
95314 Psychotria costanensis var. pubibractea Steyerm.
95320 Vriesea splendens var. oinochroma Steyerm.
95355 Peperomia borburatensis Steyerm.
95374 Cinchona henleana var. trichophylla Steyerm.
95418 Selaginella gigantea Steyerm. & A. R. Smith
95456 Maripa stellulata Steyerm.
95463 Cestrum aristeguietae Steyerm.
95934 Palicourea perquadrangularis var. pubens Steyerm.
96039 Psychotria anceps var. robustior Steyerm.
96161 Rhodospatha *steyermarkii* Bunting
96216 Peperomia pariensis Steyerm.
96342 Elvasia *steyermarkii* Maguire
96472 Pitcairnia venezuelana L. B. Smith & Steyerm.
96653 Clidemia *steyermarkii* Wurd.
96715 Campylocentrum *steyermarkii* Foldats
96736 Manettia tachirensis Steyerm.
96816 Palicourea demissa var. chimo f. pubens Steyerm.
96951 Greigia ocellata L. B. Smith & Steyerm.
96993 Onicidium *steyermarkii* Foldats
97071 Manettia coccocypseloides var. glabrior Steyerm.
97090 Palicourea meridensis Steyerm.
97239 Manettia lindenii f. appendiculata Steyerm.
97243 Palicourea nubicola Steyerm.
97257 Piper canovillosum Steyerm.
97325 Anthurium *julianii* Bunting
97475 Chiococca naiguatensis Steyerm.
97655 Psychotria aneurophylloides Steyerm.
97664 Peperomia chapensis Steyerm.
97688 Psychotria yaracuyensis Steyerm.
97811 Schismatoglottis bolivariana Bunting & Steyerm.
97837 Maguireothamnus speciosus subsp. jauaensis Steyerm.
97851 Euceraea sleumeriana Steyerm. & Maguire
97852 Psychotria cerronis Steyerm.
97854 Tibouchina *steyermarkii* Wurd.
97857 Malanea jauaensis Steyerm.
97865 Navia intermedia L. B. Smith & Steyerm.
97865a Navia lasiantha L. B. Smith & Steyerm.
97878 Ledothamnus *steyermarkii* subsp. longisetus Maguire, Steyerm. & Luteyn
97881 Navia incrassata L. B. Smith & Steyerm.
97895 Lycopodium *steyermarkii* Ollgaard
97917 Stomatochaeta *steyermarkii* Aristeg.
97918 Ledothamnus jauaensis Maguire, Steyerm. & Luteyn
97928 Pagamea jauaensis Steyerm.
97944 Ledothamnus stenopetalus Maguire, Steyerm. & Luteyn
97945 Cardonaea jauaensis Aristeg., Maguire & Steyerm.
97958 Symbolanthus sessilis Steyerm. & Maguire
97979 Byrsonima *steyermarkii* Anderson
98016 Sipapoa *steyermarkii* Maguire
98049 Tyleria phelpsiana Maguire & Steyerm.
98054 Vaccinium puberulum var. jauaense Maguire, Steyerm. & Luteyn
98057 Psychotria glandulicalyx var. densipubens Steyerm.
98068 Lisianthius jauaensis Steyerm. & Maguire
98070 Psychotria phelpsiana Steyerm.
98072 Symplocos jauaensis Steyerm. & Maguire
98073 Smilax jauaensis Steyerm. & Maguire
98078 Schefflera reticulata subsp. jauaensis Maguire, Steyerm. & Frodin
98086 Aspidosperma decussata subsp. jauaensis Steyerm. & Maguire
98098 Psychotria jauaensis Steyerm.
98206 Pochota gracilis subsp. bolivariensis Steyerm.
98298 Manettia tamaensis Steyerm.
98345 Pachyphyllum *steyermarkii* Foldats
98381 Lepanthes *steyermarkii* Foldats
98384 Maxillaria *steyermarkii* Foldats
98558 Arcytophyllum nitidum f. hispidum Steyerm.

98568 Telipogon *steyermarkii* Foldats
98573 Dendrophthora *steyermarkii* Rizz.
98592 Brachionidium *steyermarkii* Foldats
98661 Stelis *steyermarkii* Foldats
98683 Psychotria aubletiana var. andina Steyerm.
98801 Palicourea dunstervilleorum Steyerm.
98939 Psychotria glabristipula Steyerm.
98951 Psychotria sanluisensis Steyerm.
98956 Piper galicianum Steyerm.
99218 Lepanthopsis *steyermarkii* Foldats
99251 Psychotria calciphila Steyerm.
99274 Hillia costanensis Steyerm.
99343 Palicourea venezuelensis Steyerm.
99348 Asketanthera *steyermarkii* Markgraf
99363 Malanea sanluisensis Steyerm.
99409 Sterigmapetalum heterodoxum Steyerm. & Liesner
99933 Piper heterobracteum Steyerm.
100217 Psychotria chapensis Steyerm.
100252 Rudgea buntingii Steyerm.
100263 Dicranostyles costanensis Steyerm. & Austin
100311 Asterogyne yaracuyense Henderson & Steyerm.
100371a Peperomia croizatiana Steyerm.
100391 Psychotria decurrens Steyerm.
100400 Hoffmannia aroensis Steyerm.
100402 Hoffmannia stenocarpa Steyerm.
100762 Psychotria dunstervilleorum Steyerm.
100763 Palicourea ctenocalyx Steyerm.
100818 Bulbophyllum *steyermarkii* Foldats
100883 Gomphicus *steyermarkii* Foldats
100884 Piper crenulatum Steyerm.
100940 Palicourea tamaensis var. psilophylla Steyerm.
101030 Psychotria norae Steyerm.
101055 Palicourea nana Steyerm.
101900 Palicourea buntingii Steyerm.
101939 Odontocarya *steyermarkii* Barneby
102035 Calidium *steyermarkii* Bunting
102360 Arcytophyllum venezuelanum Steyerm.
102431 Peperomia caraboboensis Steyerm. & Bunting
102603 Philodendron *steyermarkii* Bunting
102678 Heliconia *julianii* Barreiros
102757 Leandra *steyermarkii* Wurd.
102799 Sloanea maroana Steyerm.
102858 Ixora yavitensis Steyerm.
102860 Helianthostylis *steyermarkii* C. C. Berg
102933 Psychotria yavitensis Steyerm.
102939 Duroia maguirei var. patentinervia Steyerm.
103062 Monotagma yapacanensis Steyerm. & Bunting
103153 Bonnetia tristyla subsp. nervosa Steyerm.
103185 Symplocos yapancanensis Steyerm.
103186 Sloanea yapacanae Steyerm.
103267 Psittacanthus *julianus* Rizz.
103271 Ouratea papillata Maguire & Steyerm.
103322 Hoffmannia larensis Steyerm.
103352 Hoffmannia terepaimensis Steyerm.
103354 Psychotria manaraeana Steyerm.
103733 Peperomia aristeguietae Steyerm.
103752 Schradera andina Steyerm.
103937 Tapeinostemon longiflorum var. australe Maguire & Steyerm.
104418 Burmannia carrenoi Steyerm.
104454 Piper dunstervilleorum Steyerm.
104569 Sterigmapetalum resinosum Steyerm. & Liesner
104978 Piper longispicum f. tomentosum Steyerm.
104989 Piper nubigenum var. venezuelense Steyerm.
105009 Heteropterys *steyermarkii* Anderson
105045 Psychotria rosacea Steyerm.
105063 Palicourea puberulenta Steyerm.
105194 Cyathea *steyermarkii* Tryon
105222 Sloanea autanae Steyerm.
105237 Froesia venezuelensis Steyerm. & Bunting
105274 Distictis *steyermarkii* Gentry
105306 Peperomia buntingii Steyerm.
105390 Piper cernuum var. cernuum f. papillatum Steyerm.
105468 Drosera felix Steyerm. & L. B. Smith
105500 *Jasarum steyermarkii* Bunting
105658 Chimarrhis perijaënsis Steyerm.
105677 Panopsis perijensis Steyerm.
105721 Calceolaria yuparum Steyerm.
105747 Spermacoce perijaensis Steyerm.
105749 Psychotria perijaensis Steyerm.
105826 Piper dilatatum f. longipilum Steyerm.
106037 Psychotria glandulicalyx f. bracteifera Steyerm.
106178 Dichorisandra diederichsanae Steyerm.
106573 Styrax wurdackiorum Steyerm.
106763 Tillandsia *steyermarkii* L. B. Smith
106982 Neea parimensis Steyerm.
107033 Allophylus parimensis Steyerm.
107840 Erythroxylum *steyermarkii* Plowman
108741 Epiphyllum *steyermarkii* Croizat
108873 Stegolepis albiflora Steyerm.
108876 Raveniopsis jauaensis Steyerm.
108880 Navia scirpiflora L. B. Smith, Steyerm. & H. Robinson
108895 Navia jauana L. B. Smith, Steyerm. & H. Robinson
108921 Marcgravia *steyermarkii* de Roon
108938 Pochota tepuiensis Steyerm.
108984 Phainantha *steyermarkii* Wurd.
109039 Sloanea cavicola Steyerm.
109041 Liriosma tepuiensis Steyerm.
109076 Psammisia breweri Steyerm. & Maguire
109178 Virola *steyermarkii* Rodrigues, ined.
109181 Mycerinus viridiflorus Steyerm. & Maguire
109199 Daphnopsis nevlingiana Steyerm.
109237 Tepuianthus sarisarinamensis Maguire & Steyerm.
109252 Maytenus jauaensis Steyerm.
109255 Chorisepalum breweri Steyerm. & Maguire
109294 Ilex jauaensis Steyerm.
109298 Thibaudia carrenoi Steyerm. & Maguire
109315 Thibaudia breweri Steyerm. & Maguire
109373 Schefflera gracillima Steyerm. & Maguire

109389 Paepalanthus meseticola Mold. & Steyerm.
109390 Xyris jauana L. B. Smith & Steyerm.
109405 Paepalanthus venetifolius Mold. & Steyerm.
109428 Psychotria carrenoi Steyerm.
109447 Ouratea propinqua Maguire & Steyerm.
109485 Piptocarpha jauaensis Aristeg. & Steyerm.
109535 Tapeinostemon jauaensis Steyerm. & Maguire
109574 Styrax jauaensis Steyerm.
109584 Thibaudia jauaensis Steyerm. & Maguire
109596 Phyllanthus carrenoi Steyerm.
109633 Navia luzuloides L. B. Smith, Steyerm. & H. Robinson
109673 Matayba jauaensis Steyerm.
109689 Piper jauaense Steyerm.
109695 Sloanea jauaensis var. minor Steyerm.
109699 Sloanea carrenoi Steyerm.
109765 Maguireothamnus jauaensis var. breweri Steyerm.
109841 Sloanea jauaensis Steyerm.
109842 Cecropia *steyermarkii* Cuatr.
110148 Sloanea larensis Steyerm.
111182 Besleria *steyermarkiorum* Wiehler
111304 Blepharodon *julianii* Morillo
111402 Ilex altiplana Steyerm.
112181 Billbergia manarae Steyerm.
112735 Phthirusa *steyermarkiana* Rizz.
112797 Ouratea *steyermarkii* Sastre
112829 Dulacia redmondii Steyerm.
113200 Dipterx phaeophylla Steyerm.
113330 Croton subincanus var. guaiquinimensis Steyerm.
113438 Pakaraimaea dipterocarpacea subsp. nitida Maguire & Steyerm.
113463 Swartzia cowanii Steyerm.
113837 Ochthocosmus multiflorus var. canaripoensis Steyerm. & Luteyn
113851 Kunhardtia radiata Maguire & Steyerm.
113856 Guapira ayacuchae Steyerm.
114221 Piper cernuum var. araguense f. pubens Steyerm.
115564 Phoradendron *steyermarkii* Rizz.
115598 Sipanea carrenoi Steyerm.
115645 Bonnetia ptariensis Steyerm.
115968 Aphanocarpus steyermarkii f. glabrior Steyerm.
116093 Tepuianthus auyantepuiensis Maguire & Steyerm.
116166 Raveniopsis breweri Steyerm.
116180 Cottendorfia brachyphylla var. angustior L. B. Smith, Steyerm. & H. Robinson
117209 Piper pavasense Steyerm.
117221 Lubaria szczerbanii Steyerm.
117276 Ilex guaiquinimae Steyerm.
117298 Navia emergens L. B. Smith, Steyerm. & H. Robinson
117361 Navia ovoidea L. B. Smith, Steyerm. & H. Robinson
117393 Ouratea culmenicola Maguire & Steyerm.
117407 Stomatochaeta colveei Steyerm.
117421 Bonnetia guaiquinimae Steyerm.
117468 Aldina berryi Cowan & Steyerm.
117473 Croton guaiquinimae Steyerm.
117498 Sauvagesia guianensis subsp. guaiquinimensis Steyerm.
117569 Ochthocosmus longipedicellatus Steyerm. & Luteyn
117570 Ochthocosmus attenuatus Steyerm. & Luteyn
117615 Neea subglabrata Steyerm.
117841 Davilla *steyermarkii* Kubitzki
117920 Roupala griotii Steyerm.
117971 Neea guaiquinimae Steyerm.
117977 Daphnopsis guaiquinimae Steyerm.
117982 Cottendorfia atrorosea L. B. Smith, Steyerm. & H. Robinson
118338 Peperomia pseudojamesoniana Steyerm.
118651 Peperomia liesneri Steyerm.
118876 Sabicea liesneri Steyerm.
119027 Bartlettina liesneri King & H. Robinson
119958 Peperomia minarum Steyerm.
119971 Piper pseudohastularum Steyerm.
120032 Sterigmapetalum tachirense Steyerm. & Liesner
121697 Piper tacariguense Steyerm.
122132 Psychotria plowmanii Steyerm.
122197 Psychotria davidsei Steyerm.
122215 Sloanea cataniapensis Steyerm.
122318 Guettarda leiantha Steyerm.
122366 Neea brevipedunculata Steyerm.
122478 Navia igneosicola L. B. Smith, Steyerm. & H. Robinson
122730 Peperomia cyclophylla f. zulianensis Steyerm.
122876 Hillia zulianensis Steyerm.
123742 Psychotria trujilloi var. yaracuyensis Steyerm.
123808 Vriesea capituligera Steyerm.
123846 Navia geaster L. B. Smith, Steyerm. & H. Robinson
124311 Bonnetia euryanthera Steyerm.
124326 Tyleria breweriana Steyerm.
124383 Burmannia foliosa subsp. marahuacensis Maguire & Steyerm.
124406 Schefflera tremuloidea var. marahuacensis Maguire, Steyerm. & Frodin
124477 Cottendorfia discolor L. B. Smith, Steyerm. & H. Robinson, ined. ms. = Steyerbromelia discolor L. B. Smith & H. Robinson
124526 Cottendorfia geniculata var. minor L. B. Smith, Steyerm. & H. Robinson
124530 Sauvagesia guianensis subsp. sipapoensis Steyerm.
124582 Brewcaria duidensis L. B. Smith, Steyerm. & H. Robinson
124622 Bravaisia integerrima var. pilosa Steyerm.
124771 Piper linguliforme var. adpressipilum Steyerm.
124826 Piper marturetense f. pilosum Steyerm.
125483 Psychotria subimbricata Steyerm.
125174 Perissocarpa *steyermarkii* subsp. tachirensis Steyerm. & Maguire
125654 Navia aliciae L. B. Smith, Steyerm. & H. Robinson

125925 Oritrophium marahuacense Steyerm. & Maguire
125996 Cottendorfia arachnoidea L. B. Smith, Steyerm. & H. Robinson
126049 Rhamnus marahuacensis Steyerm. & Maguire
126328 Brewcaria marahuacae L. B. Smith, Steyerm. & H. Robinson
126381 Psychotria breweri Steyerm.
126421 Navia albiflora L. B. Smith, Steyerm. & H. Robinson
126472 Piper subsessilifolium var. morii Steyerm.
126510 Pitcairnia *steyermarkii* L. B. Smith
126610 Peperomia portuguesensis Steyerm.
127445 Piper tamayoanum Steyerm.
128062 Psychotria crassa f. alba Steyerm.
128071 Trimezia chimantensis Steyerm.
128104 Lindmania sessilis L. B. Smith, Steyerm. & H. Robinson
128465 Cottendorfia huberi L. B. Smith, Steyerm. & H. Robinson, ined. ms.
128465 Lindmania huberi L. B. Smith, Steyerm. & H. Robinson
128474 Lindmania imitans L. B. Smith, Steyerm. & H. Robinson
128500 Elaphoglossum *steyermarkii* Mickel
128611 Cottendorfia aurea L. B. Smith, Steyerm. & H. Robinson, ined. ms.
128611 Lindmania aurea L. B. Smith, Steyerm. & H. Robinson
128637 Adenanthe bicarpellata var. chimantensis Steyerm.
128815 Chimantaea huberi Steyerm.
128945 Lindmania saxicola L. B. Smith, Steyerm. & H. Robinson
128976a Vaccinium *steyermarkii* Luteyn
128992 Psychotria crassa f. angustior Steyerm.
129063 Navia pedemontana L. B. Smith, Steyerm. & H. Robinson
129067 Cottendorfia terramarae L. B. Smith, Steyerm. & H. Robinson
129067 Lindmania terramarae L. B. Smith, Steyerm. & H. Robinson
129197 Stegolepis terramarensis Steyerm.
129203 Cottendorfia delascioana L. B. Smith, Steyerm. & H. Robinson
129391 Calycolpus calophyllus var. angustifolius Steyerm.
129456 Mikania michelangeliana Steyerm.
129512 Brachionidium *julianii* Carnevali & Ramírez
129596 Guzmania terrestris L. B. Smith & Steyerm.
129646 Navia linearis L. B. Smith, Steyerm. & H. Robinson
129650 Scaphyglottis michelangeliorum Carnevali & Steyerm.
129798 Rutaneblina pusilla Steyerm. & Luteyn
129816 Phyllanthus jablonskianus Steyerm. & Luteyn
129924 Acopanea ahogadoi Steyerm.
129932 Chimantaea acopanensis Steyerm.
129962 Stegolepis maguireana Steyerm.
130072 Steyerbromelia diffusa L. B. Smith, Steyerm. & H. Robinson
130112 Ilex ignicola Steyerm.
130135 Tillandsia abysmophila L. B. Smith & Steyerm.
130228 Ochthocosmus berryi Steyerm.
130318a Navia berryana L. B. Smith, Steyerm. & H. Robinson
130328 Phyllanthus vacciniifolius var. vinillaensis Steyerm.
130339 Remijia delascioi Steyerm.
130410 Navia delascionis L. B. Smith, Steyerm. & H. Robinson
130425 Ilex marahuacae Steyerm.
130440 Remijia marahuacensis Steyerm.
130481 Ilex holstii Steyerm.
130531 Ilex brevipedicellata Steyerm.
130629 Gongylolepis terramarae Steyerm.
130637 Holstianthus barbigularis Steyerm.
130721 Schradera marahuacensis Steyerm.
130742a Peperomia marahuacensis Steyerm.
130878 Catostemma marahuacensis Steyerm.
130880 Lissocarpa stenocarpa Steyerm.
130907 Ouratea marahuacensis Maguire & Steyerm.
131659 Simira ignicola Steyerm.
131850 Navia grafii Steyerm. & Holst
131868 Symplocos acananensis Steyerm.
132006 Stegolepis humilis Steyerm.

SUKSDORF, W. N. (Wilhelm Nikolaus)

279 Grindelia hirsutala var. brevisquama f. tomentulosa Steyerm.

SWINK, F. A.

2775 Vernonia missurica f. *swinkii* Steyerm.

TAMAYO, F. (Francisco)

3133 Duroia gransabanensis Steyerm.
4509 Arcytophyllum nitidum subsp. caracasanum var. culmenicolum Steyerm.

TATE, G. H. H. (George Henry Hamilton)

424 Ilex culmenicola Steyerm.
431 Schefflera umbellata subsp. duidana Maguire, Steyerm. & Frodin
526 Ilex gleasoniana Steyerm.
567 Pagamea duidana Standl. & Steyerm.
1147 Borreria oligodonta Steyerm.
1365 Pagamea auyantepuiensis Steyerm.

THOMAS, W. W. (William Wayt)

3030 Navia plowmanii L. B. Smith, Steyerm. & H. Robinson
3261 Navia polyglomerata L. B. Smith, Steyerm. & H. Robinson
3245 Navia *thomasii* L. B. Smith, Steyerm. & H. Robinson

THURN, I. (Everard Ferdinand Im)

162 Schefflera monosperma Maguire, Steyerm. & Frodin

TILLETT, S. S. (Steven)

82 Croizatia naiguatensis Steyerm.
738-366 Manettia honigii Steyerm.
743-230 Peperomia atabapoensis Steyerm.
745-385 Sabicea *tillettii* Steyerm.
746-501 Manettia *tillettii* Steyerm.
746-798 Peperomia honigii Steyerm.
752-329 Siphocampylus *tillettii* Steyerm.
752-348 Duidaea marahuacensis Steyerm.

761-83 Peperomia *tillettii* Steyerm.
43934 Rudgea *tillettii* Steyerm.
43944 Merumea plicata Steyerm.
43946 Psychotria *tillettii* Steyerm.
43954 Psychotria boyanii Steyerm.
43996 Psychotria merumensis Steyerm.
44824 Retiniphyllum guianense Steyerm.
44825 Rudgea merumensis Steyerm.
44835 Duroia merumensis Steyerm.
44837 Calycophyllum merumense Steyerm.
44867 Orthaea merumensis Maguire, Steyerm. & Luteyn
44992 Schradera ternata Steyerm.
45007 Psychotria psittacina Steyerm.
45008 Psychotria urniformis Steyerm.
45057 Ceratostema glandulifera Maguire, Steyerm. & Luteyn
45059 Psychotria ayangannensis Steyerm.
45079 Psychotria multiramosa Steyerm.
45081 Malanea ciliolata Steyerm.
45085 Ixora intropilosa Steyerm.
45105 Psychotria amplinoda var. ayangannae Steyerm.
45180 Alibertia triloba Steyerm.
45184 Ferdinandusa goudotiana var. psilocarpa Steyerm.
45194 Retiniphyllum scabrum var. ayangannense Steyerm.
45114 Sipanea ayangannensis Steyerm.
45117 Rudgea enervia Steyerm.
45178 Schefflera ayangannensis Maguire, Steyerm. & Frodin
45182 Rudgea ayangannensis Steyerm.
45501 Piper perstipulare Steyerm.
45567 Calycophyllum intonsum Steyerm.

TORRES LEZAMAE, A.

203 Simira *lezamae* Steyerm.

TRACY, J. P. (Joseph Prince)

4669 Grindelia nana var. altissima Steyerm.

TRELEASE, W. (William)

s.n. Grindelia lanceolata f. latifolia Steyerm.

TRUJILLO, B. (Baltasar)

766 Psychotria fernandezii Steyerm.
1374 Psychotria avilensis Steyerm.
1921 Psychotria *trujilloi* Steyerm.
1955 Psychotria terepaimensis Steyerm.
2763 Faramea larensis Steyerm.
6555 Rudgea *trujilloi* Steyerm.
7594 Hoffmannia bernardii var. aracalensis Steyerm.
7919 Peperomia *trujilloi* Steyerm.

TUCKER, J. M.

979 Hyperbaena salvadorensis Steyerm.
1368 Bouvardia salvadorensis Steyerm.

ULE, E. (Ernst Heinrich Georg)

5386 Psychotria manausensis Steyerm.
6795 Joosia *ulei* Steyerm.

VAN DER WERFF, H. (Henk)

237 Peperomia ouabiane var. sanluisensis Steyerm.
548 Piper arieianum var. yaracuyense f. falconense Steyerm.
3642 Piper galicianum f. hirsutopetiolatum Steyerm.
5457 Faramea cazaderensis Steyerm.

VARADARAJAN, G. S.

1205 Connellia *varadarajanii* L. B. Smith & Steyerm.

VARESCHI, V. (Volkmar)

1386 Rudgea *vareschii* Steyerm.
4966 Tepuia *vareschii* Steyerm.
6850 Arcytophyllum *vareschii* Steyerm.
7790 Psychotria *vareschii* Steyerm.

VEILLON, J. P.

7 Dendropanax *veillonii* Steyerm.
14 Styrax andinus Steyerm.

VELASCO, R.

627 Palicourea flexiramea Steyerm.

VOGEL, S. (Stefan)

81 Psychotria caquetensis Steyerm.
290 Psychotria capitata f. trichophora Steyerm.
312 Palicourea *vogelii* Steyerm.

VOGL, PADRE C. (Cornelio)

41 Aspilia avilensis Aristeg. & Steyerm.

VON HAGEN, C. & W. (Cristine & Wolfgang)

2137 Chione panamensis Steyerm.

VON TUERCKHEIM, H. or von Türckheim (Hans)

1240 Struthanthus papillosus Standl. & Steyerm.
1617 Xylosma sessile Standl. & Steyerm.
1728 Elaterium macrophyllum Standl. & Steyerm.
1732 Polymnia verapazensis Standl. & Steyerm.
8410 Jungia guatemalensis Standl. & Steyerm.

WESSELS-BOER, J. G.

962 Psychotria *wessels-boeri* Steyerm.
1953 Schoenobiblus amazonicus Steyerm.

WHITEHOUSE, E. (Eula)

s.n. Selenia oinosepala Steyerm.

WHITTON, B. A.

120 Chiococca multipedunculata Steyerm.

WILLIAMS L. (Llewelyn)

10639 Utricularia *williamsii* Steyerm.
11505 Eugenia caurensis Steyerm.
11691 Myrciaria caurensis Steyerm.
12073 Palicourea rigida var. hirtibacca Steyerm.
12970 Chalepophyllum pungens Standl. & Steyerm.
12992 Psychotria calviflora Steyerm.
13178 Carex standleyana Steyerm.
13329 Rondeletia orinocensis Steyerm.
13650 Maytenus pittieriana Steyerm.
13853 Borreria macrocephala Standl. & Steyerm.
13918 Picramnia tristamina Steyerm.
13922 Philonotion *williamsii* Steyerm.
14026 Faramea yavitensis Steyerm.

14140 Caraipa ferruginea Steyerm.
14143 Clusia *williamsii* Steyerm.
14152 Ouratea venezuelensis Steyerm.
14154 Glandonia *williamsii* Steyerm.
14162 Vochysia steyermarkii Marcano Berti
14190 Pagamea plicatiformis Steyerm.
14312 Chaetocarpus *williamsii* Steyerm.
14321 Burdachia *williamsii* Steyerm.
14439 Amanoa pubescens Steyerm.
14525 Posoqueria *williamsii* Steyerm.
14587 Platycarpum decipiens Woodson & Steyerm.
14674 Rudgea carolina Standl. & Steyerm.
14898 Clusia reducta Steyerm.
14962 Eugenia llewelynii Steyerm.
14983 Psychotria ventuariana Standl. & Steyerm.
15067 Perama galioides f. quaternata Steyerm.
15532 Calathea acuminata Steyerm.
15564 Ryania casiquiarensis Steyerm.
15656 Sipanea pubinoda Steyerm.
16039 Tocoyena brevifolia Steyerm.

WILLIAMS, L. O. (Louis Otho)

11237 Psychotria aubletiana var. centro-americana Steyerm.
13178 Carex standleyana Steyerm.

WILSON, C. L. (Carl Louis)

175 Triolena izabalensis Standl. & Steyerm.
188 Tetrorchidium brevifolium Standl. & Steyerm.
272 Euphorbia verapazensis Standl. & Steyerm.
329 Hybanthus sylvicola Standl. & Steyerm.
356 Lisianthius calciphilus Standl. & Steyerm.

WINGFIELD, R. (Robert)

5495 Piper diffamatum var. angustius Steyerm.
6571 Piper pseudodivulgatum Steyerm.

WOOTON, E. O. (Elmer Ottis)

s.n. Grindelia acutifolia Steyerm.
2568 Grindelia arizonica var. stenophylla Steyerm.

WURDACK, J. J. (John Julius)

911 Hoffmannia parvifolia Steyerm.
961 Perama *wurdackii* Steyerm.
1817 Hippotis latifolia Steyerm.
2089 Hippotis *wurdackii* Steyerm.
2435 Pentagonia *wurdackii* Steyerm.
2461 Simira *wurdackii* Steyerm.
2523 Pentagonia parvifolia Steyerm.
34112 Eupatorium ibaguense var. indiscretum Maguire, Steyerm. & Wurd.
34201 Sauvagesia imthurniana subsp. chimantensis Maguire, Steyerm. & Wurd.
34225 Chimantaea eriocephala Maguire, Steyerm. & Wurd.
34262 Heliamphora heterodoxa var. exappendiculata Maguire & Steyerm.
39784 Alibertia latifolia var. pargueniana Steyerm.
39810 Gouania *wurdackii* Steyerm.
39823 Sipanea pratensis var. dichotoma f. glabrior Steyerm.
39858 Simira erythroxylon var. saxicola Steyerm.
40970 Chomelia monachinoi Steyerm.
41017 Sloanea *wurdackii* Steyerm.
41253 Toulicia anomala Steyerm.
41303 Randia venezuelensis Steyerm.
42698 Mitracarpus frigidus var. orinocensis Steyerm.
42701 Borreria confertifolia Steyerm.
42719 Ouratea *wurdackii* Maguire & Steyerm.
42727 Rudgea *wurdackii* Steyerm.
42824 Remijia *wurdackii* Steyerm.
42833 Sabicea brachycalyx Steyerm.
42915 Borreria *wurdackii* Steyerm.
42916 Sipanea pratensis var. dichotoma f. glabriloba Steyerm.
42988 Borreria intricata Steyerm.
43078 Coussarea revoluta Steyerm.
43148 Schefflera tamatamaensis Maguire, Steyerm. & Frodin
43316 Schradera hilliifolia Steyerm.
43383 Capirona *wurdackii* Steyerm.
43692 Perama galioides var. longiflora Steyerm.
43762 Euphronia acuminatissima Steyerm.

YUNCKER, T. G. (Truman George)

8323 Erblichia standleyi Steyerm.
8519 Mortoniodendron membranaceum Standl. & Steyerm.

APPENDIX III. *Family Index.* Numbers of taxa described by Steyermark arranged alphabetically by family.

Family	Genera	Species	Subspecies	Varieties	Forms	Miscellaneous
Acanthaceae	6	2	—	1	5	—
Actinidiaceae	1	9	—	—	—	—
Agavaceae	1	—	—	—	—	—
Amaranthaceae	1	—	1	—	—	—
Amaryllidaceae	1	1	—	—	—	—
Anacardiaceae	1	1	—	—	—	—
Annonaceae	3	4	—	—	—	—
Apocynaceae	4	2	1	1	—	—
Aquifoliaceae	1	37	—	2	3	—
Araceae	8	20	6	—	—	—
Araliaceae	4	29	—	2	—	—
Arecaceae	11	29	—	1	—	1
Aristolochiaceae	1	1	—	—	—	—
Asclepiadaceae	4	5	—	—	—	—
Asteraceae	58	136	1	39	36	11
Balsaminaceae	1	—	—	—	1	—
Berberidaceae	3	2	—	—	1	—
Betulaceae	1	—	—	—	1	—
Bignoniaceae	1	1	—	—	—	—
Bombacaceae	3	14	—	—	2	1
Boraginaceae	2	—	—	—	2	—
Brassicaceae	3	5	—	—	1	—
Bromeliaceae	14	64	—	1	—	6
Brunelliaceae	1	4	—	—	—	—
Burmanniaceae	1	2	1	—	—	—
Burseraceae	4	5	—	1	—	—
Cactaceae	2	2	—	—	—	1
Campanulaceae	2	1	—	—	2	—
Canellaceae	1	1	—	—	—	—
Capparidaceae	1	3	—	—	—	—
Caprifoliaceae	2	4	—	1	1	—
Caryophyllaceae	4	7	—	—	3	—
Cecropiaceae	1	1	—	—	—	—
Celastraceae	3	13	—	—	1	—
Chrysobalanaceae	1	1	—	—	—	—
Clethraceae	1	6	—	—	—	—
Clusiaceae	10	22	—	3	2	—
Combretaceae	1	1	—	—	—	—
Commelinaceae	6	11	—	1	6	—
Connaraceae	2	2	—	—	—	—
Convolvulaceae	5	9	—	—	—	1
Crassulaceae	2	3	—	1	—	—
Cucurbitaceae	8	8	—	—	—	2
Cunoniaceae	11	—	—	—	—	—
Cupressaceae	1	1	—	—	—	—
Cyperaceae	10	32	—	1	—	1
Dichapetalaceae	1	1	—	—	—	—
Dilleniaceae	1	2	—	—	—	—
Dioscoreaceae	1	5	—	—	—	—
Dipsacaceae	1	—	—	—	1	—
Dipterocarpaceae	1	—	1	—	—	—
Droseraceae	1	3	—	1	—	—
Ebenaceae	1	3	—	—	1	—
Elaeocarpaceae	1	24	—	2	—	—
Elatinaceae	1	1	—	—	—	—
Ericaceae	12	31	1	2	1	—

APPENDIX III. Continued.

Family	Genera	Species	Subspecies	Varieties	Forms	Miscellaneous
Eriocaulaceae	1	3	—	—	—	—
Erythroxylaceae	1	1	—	—	—	—
Euphorbiaceae	20	54	—	1	—	3
Fabaceae	20	23	—	—	4	1
Fagaceae	1	—	—	—	1	3
Flacourtiaceae	9	10	—	—	—	1
Garryaceae	1	1	—	—	—	—
Gentianaceae	10	27	—	1	1	—
Gesneriaceae	2	2	—	—	—	—
Grossulariaceae	11	—	—	—	—	—
Gunneraceae	1	1	—	—	—	—
Heliconiaceae	1	1	—	—	—	—
Humiriaceae	1	1	—	—	—	—
Hydrophyllaceae	2	—	—	—	2	—
Icaciniaceae	2	2	—	—	—	—
Iridaceae	2	2	—	3	1	—
Ixonanthaceae	1	5	—	2	—	—
Juglandaceae	1	—	—	—	1	—
Lamiaceae	1	—	—	—	1	—
Lauraceae	4	7	—	1	—	—
Lecythidaceae	1	1	—	—	—	—
Lennoaceae	1	—	1	—	—	—
Lentibulariaceae	3	25	—	2	3	—
Liliaceae	6	4	—	1	5	1
Limnocharitaceae	1	1	—	—	—	—
Lissocarpaceae	1	1	—	—	—	—
Loasaceae	3	3	—	—	—	—
Loganiaceae	2	5	—	—	—	—
Loranthaceae	3	12	—	—	—	—
Lythraceae	1	—	—	1	—	—
Magnoliaceae	1	3	—	—	—	—
Malpighiaceae	9	12	—	1	—	1
Malvaceae	4	8	—	—	—	—
Marantaceae	4	8	—	—	—	—
Marcgraviaceae	3	4	—	1	—	—
Melastomataceae	6	10	—	—	—	—
Meliaceae	2	9	—	—	—	—
Mendonciaceae	1	2	—	—	—	—
Menispermaceae	1	2	—	—	—	—
Monimiaceae	2	7	—	—	—	—
Moraceae	2	2	—	—	—	—
Myricaceae	1	1	—	—	—	—
Myrsinaceae	5	12	—	—	1	—
Myrtaceae	10	39	—	—	—	—
Nyctaginaceae	4	30	—	—	—	—
Ochnaceae	6	38	3	7	—	7
Olacaceae	4	5	—	—	—	—
Oleaceae	3	5	—	10	—	—
Onagraceae	3	2	—	2	1	—
Orchidaceae	1	1	—	—	—	—
Oxalidaceae	1	2	—	—	—	—
Passifloraceae	2	3	—	—	—	—
Piperaceae	3	35	2	10	13	—
Poaceae	1	—	—	—	1	—
Polemoniaceae	1	—	—	—	1	—
Polygalaceae	1	4	—	1	—	—

APPENDIX III. Continued.

Family	Genera	Species	Subspecies	Varieties	Forms	Miscellaneous
Portulacaceae	2	3	—	—	—	—
Primulaceae	1	—	—	—	1	—
Proteaceae	3	13	—	1	—	—
Quiinaceae	1	1	—	—	—	—
Ranunculaceae	4	3	—	—	3	—
Rapateaceae	3	13	—	—	—	—
Rhamnaceae	3	9	—	—	—	3
Rhizophoraceae	1	5	1	—	—	2
Rosaceae	3	1	—	1	7	—
Rubiaceae	93	555	29	113	46	49
Rutaceae	11	16	—	1	3	1
Sabiaceae	1	5	—	—	—	—
Salicaceae	1	—	—	—	3	—
Santalaceae	1	1	—	—	—	—
Sapindaceae	9	35	2	1	—	—
Sapotaceae	2	5	—	—	—	—
Sarraceniaceae	1	1	—	1	2	—
Saxifragaceae	1	—	—	—	1	—
Scrophulariaceae	5	3	—	—	2	—
Selaginellaceae	1	1	—	—	—	—
Simaroubaceae	1	2	—	—	1	—
Smilacaceae	1	6	—	—	1	—
Solanaceae	8	27	—	1	—	—
Staphyleaceae	1	1	—	—	-	—
Sterculiaceae	2	2	—	—	—	—
Styracaceae	1	8	2	—	—	—
Symplocaceae	1	11	—	—	—	—
Taxodiaceae	1	—	—	—	1	—
*Tepuianthaceae	1	6	1	—	—	—
Theaceae	4	13	2	3	—	2
Thymelaeaceae	2	7	—	—	—	—
Tiliaceae	1	2	—	—	—	1
Trigoniaceae	1	2	—	—	—	—
Turneraceae	1	1	-	1	—	—
Urticaceae	3	3	—	1		—
Valerianaceae	1	2	—	—	—	—
Velloziaceae	1	1	—	—	—	—
Verbenaceae	3	4	-	—	—	—
Violaceae	4	3	—	—	2	1
Viscaceae	1	9	—	—	—	1
Vitaceae	1	1	—	—	—	—
Vochysiaceae	3	4	—	1	—	—
Winteraceae	1	—	—	1	—	—
Xyridaceae	3	11	—	2	–	2
Zingiberaceae	2	3	—	—	—	—

SYSTEMATICS OF *ZAPOTECA* (LEGUMINOSAE)[1]

Héctor M. Hernández[2]

Abstract

Zapoteca (Leguminosae: Mimosoideae) is a relatively well-circumscribed genus belonging to the tribe Ingeae distributed from the southwestern United States and northern Mexico to northern Argentina and the West Indies. The highest concentration of taxa occurs in the dry forests of southern Mexico and, to a lesser extent, in Central America and the northern Andes. The predominance of allopatric distributions and the apparent low frequency of hybrids suggest that speciation in this genus has primarily arisen from genetic differentiation of geographically isolated populations. The recent climatic episodes of the Pleistocene appear to have had a prominent role on the current distributional patterns of *Zapoteca* species. *Zapoteca* species have similar reproductive biologies. All probably have nocturnal anthesis and are pollinated by unspecialized settling moths. Self-compatibility appears to be widespread in the genus, *Z. tetragona* being the only known self-incompatible species. Andromonoecy is another widespread component of the breeding system of *Zapoteca* species. This probably maximizes the use of reproductive energy without reducing pollinator attraction. The basic chromosome number of *Zapoteca* ($x = 13$) and some of the generalized characters of the polyads (i.e., acalymmate, discoid, 16-grained polyads) indicate a relationship between *Zapoteca* and the remaining genera of the Ingeae, with the exception of *Calliandra* sensu stricto, which is cytologically and morphologically isolated in this tribe. I recognize 17 species in *Zapoteca*, three of which (*Z. alinae*, *Z. andina*, and *Z. tehuana*) are newly described. Eleven subspecies are recognized, of which *Z. portoricensis* subsp. *pubicarpa* is newly described. A subgeneric classification is proposed, where taxa are grouped into four morphologically distinct subgenera: *Nervosa*, *Zapoteca*, *Aculeata*, and *Amazonica*. The subgenera are based primarily on differences in vegetative characters: number of pairs of pinnae, number of leaflet pairs per pinna, leaflet size, leaflet texture, venation patterns, and stipule type.

Resumen

Zapoteca (Leguminosae: Mimosoideae) es un género relativamente bien delimitado que pertenece a la tribu Ingeae. Se distribuye desde el suroeste de los Estados Unidos y el norte de México hasta el norte de Argentina y las Antillas. La más alta concentración de taxa se da en los bosques tropicales secos del sur de México y, en menor medida, en Centro América y en la porción norte de los Andes. La predominancia de distribuciones alopátricas, en combinación

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con la aparente baja frecuencia de híbridos, sugiere que la especiación en este género ha sido el resultado de un proceso de diferenciación genética de poblaciones aisladas geográficamente. Los episodios climáticos recientes de Pleistoceno posiblemente tuvieron un papel determinante sobre los patrones de distribución actuales de las especies de *Zapoteca*. Las especies de *Zapoteca* son bastante uniformes en los rasgos generales de su biología reproductiva. Todas tienen posiblemente flores con antesis nocturna y son polinizadas por palomillas no especializadas. Los sistemas de auto-compatibilidad genética parecen estar bién representados en el género, *Z. tetragona* siendo la única especie en donde la auto-incompatibilidad ha sido demostrada. La andromonoecia es otro componente común de los sistemas reproductivos de las especies de *Zapoteca*; este fenómeno se interpreta como un medio para maximizar el uso de la energía reproductiva, sin reducir la atracción a los polinizadores. El número cromosómico básico de *Zapoteca* (x = 13), en asociación con algunos caracteres generalizados de las políades (ej., políades acalimadas, discoides, con 16 granos), reflejan relaciones entre *Zapoteca* y el resto de los géneros de la tribu Ingeae, con la excepción de *Calliandra* sensu stricto, género que es fuertemente atípico desde el punto de vista citológico y morfológico. En este trabajo se reconocen 17 especies en *Zapoteca*, de las cuales *Z. alinae*, *Z. andina* y *Z. tehuana* se describen aquí como nuevas para la ciencia. También se reconocen 11 subespecies, de las cuales *Z. portoricensis* subsp. *pubicarpa* se describe como nueva. En base a los patrones de variación en caracteres vegetativos (ej., número de pares de pinnas, número de pares de foliolos por pinna, tamaño de los foliolos, textura de los foliolos, patrones de vanación de los foliolos y tipo de estípulas) se propone una clasificación subgenérica, en donde las especies se agrupan en cuatro subgéneros distintos: *Nervosa*, *Zapoteca*, *Aculeata* y *Amazonica*.

Zapoteca (Leguminosae: Mimosoideae) is a genus of 17 species in the relatively specialized tribe Ingeae. Its species are mostly erect or scandent shrubs, of small to moderate size, found in vegetation types ranging from arid, scrubby thorn forests to wet, evergreen tropical forests, although most species occur in areas originally covered by tropical deciduous forests. *Zapoteca* ranges from southwestern United States and northern Mexico to the West Indies and southward through most of Mexico, Central America, and part of South America, to northern Argentina. It attains its greatest diversity in southern Mexico, although in some areas of Central America and the northern Andes diversity is also considerable.

Zapoteca was recently separated from the large genus *Calliandra* Benth. (Hernández, 1986a). Extensive analyses of the polyad characteristics, seedling morphology, chromosome numbers, and several reproductive features in *Calliandra* sensu Bentham revealed differential variation patterns among its neotropical species. These variation patterns were associated with two distinct taxonomic groups: the first, including the members of Bentham's series *Laetevirentes*, and the second, the remaining neotropical species, these belonging to series *Macrophyllae*, *Nitidae*, *Pedicellatae*, and *Racemosae*. The strongly divergent nature of these two groups, along with the absence of intermediate forms between them, suggested that *Calliandra*, as originally conceived by its author, is polyphyletic (Hernández, 1986a). In an accompanying paper Romeo (1986) provided supporting evidence based on differing patterns of nonprotein imino and sulphur amino acids in seeds and leaves of *Zapoteca* and *Calliandra*. Consequently, the new genus *Zapoteca* was proposed to include the species of series *Laetevirentes*. *Zapoteca* and *Calliandra* are compared in Table 1.

I consider all the species included by Bentham (1875) in *Calliandra* ser. *Laetevirentes* to be *Zapoteca*. When I originally proposed *Zapoteca* (Hernández, 1986a), the possibility of including *Calliandra amazonica* and *C. aculeata*, treated by Bentham in ser. *Macrophyllae*, was discussed. Since these two species share a number of reproductive characters with *Zapoteca* (i.e., compact, spherical, homomorphic capitula; 16-grained discoid polyads with lens-shaped thickenings; elastically dehiscent fruits with relatively thin valves), they are transferred in the present work to *Zapoteca*. The stipular spines of *Z. aculeata*, the compound pseudopanicles of *Z. amazonica*, and the small number and larger size of the leaflets in both species are interpreted as advanced characteristics. These species should not be considered by any means as intermediate between *Zapoteca* and *Calliandra*; they are specialized species within *Zapoteca*, with divergent morphological characters.

Zapoteca is defined by its compact, spherical, homomorphic capitula; acalymmate, 16-grained, discoid polyads with lens-shaped thickenings (excluding *Z. nervosa*); elastically dehiscent fruits with membranous or coriaceous valves; and basic chromosome number of x = 13. This combination of characters makes *Zapoteca* a well-circumscribed entity; however, with the exception of the distinctive circular thickenings in the polyads, each of these characters occurs independently in other genera of tribe Ingeae. The general characteristics of the *Zapoteca* polyads, its basic chromosome number, and some of its morphological characters reflect close relationships of this genus with some

TABLE 1. Comparison of *Zapoteca* and *Calliandra* (from Hernández, 1986a).

	Zapoteca	*Calliandra*
Leaflets	thin membranous, rarely coriaceous	chartaceous to coriaceous
Inflorescences	spherical heads; homomorphic	obconiform, racemose, rarely spherical; homomorphic or heteromorphic
Polyads	16-grained, discoid	8-grained, bisymmetric, with viscid appendage in "basal" grain
Stigmas	cup-shaped, with narrow area of polyad receptivity	expanded; discoid, or capitate
Pods	membranous to coriaceous	more rigid; coriaceous, ligneous, rarely membranous
Seedlings	cotyledons ovate, sessile, foliaceous, ephemeral	cotyledons sagittate, petiolate, fleshy, persistent
Chromosome numbers	$x = 13$	$n = 8, 11$

genera of the Ingeae, perhaps with members of the *Pithecellobium* complex; however, to establish definite generic affinities of *Zapoteca* is a difficult task due to our poor current understanding about generic delimitation within this complex. What seems clear is that *Zapoteca* has closer affinities with some of these genera than with *Calliandra* sensu stricto. Several characters in *Calliandra* (e.g., polyad features, chromosome numbers, floral morphology) are atypical in the tribe Ingeae and indicate that this genus is evolutionarily divergent from the other genera of the tribe.

This study provides an account of the morphology, biogeography, reproductive biology, cytogenetics, and taxonomy of *Zapoteca*. The taxonomic revision is based on over 4,000 herbarium specimens from the major collections of the world and on extensive field observations. Field studies were conducted in most of Mexico, Nicaragua, Costa Rica, and Panama during 1983–1985. In addition, individuals representing eight species and five subspecies of *Zapoteca* were grown from seed in a greenhouse at the Missouri Botanical Garden during 1982–1986; these plants provided information for the introductory chapters and served to complement the field observations and herbarium studies when taxonomic decisions had to be made. Based on the critical examination of correlated morphological characters, in combination with eco-geographical factors, I recognize 17 species and 11 subspecies in *Zapoteca* (Table 2). The species are classified into four subgenera, which represent different evolutionary lines.

THE PLANTS

VEGETATIVE MORPHOLOGY

Habit. The species of *Zapoteca* are relatively uniform in habit. Most are erect shrubs approximately 3–4 m tall with woody stems. In most cases the stems are rather thin (ca. 1–2 cm in diameter), although occasionally individuals of *Z. tetragona* and *Z. portoricensis* develop stems up to 20 cm in diameter. A few species are scandent or sub-

TABLE 2. Outline of the classification of *Zapoteca*.

I. Subgenus *Nervosa*
  1. *Z. nervosa*

II. Subgenus *Zapoteca*
  2. *Z. media*
  3. *Z. alinae*
  4. *Z. lambertiana*
  5. *Z. filipes*
  6. *Z. portoricensis*
    a. subspecies *portoricensis*
    b. subspecies *pubicarpa*
    c. subspecies *flavida*
  7. *Z. mollis*
  8. *Z. caracasana*
    a. subspecies *caracasana*
    b. subspecies *weberbaueri*
  9. *Z. tetragona*
  10. *Z. andina*
  11. *Z. costaricensis*
  12. *Z. formosa*
    a. subspecies *formosa*
    b. subspecies *salvadorensis*
    c. subspecies *gracilis*
    d. subspecies *rosei*
    e. subspecies *mollicula*
    f. subspecies *schottii*
  13. *Z. scutellifera*
  14. *Z. tehuana*

III. Subgenus *Aculeata*
  15. *Z. aculeata*

IV. Subgenus *Amazonica*
  16. *Z. microcephala*
  17. *Z. amazonica*

scandent. *Zapoteca portoricensis* subsp. *flavida* and *Z. amazonica* grow in moist thickets supported by neighboring shrubs. Similarly, *Z. caracasana* branches near the base of the primary stems and has spreading branches that become prostrate or subprostrate. The scandent and prostrate habits are found exclusively in warm, moist habitats.

Leaves. The leaves of all species of *Zapoteca* are stipulate and twice pinnate with opposite leaflets. The wide variation in leaf characteristics provides an excellent basis for classifying members of the genus. Mature leaflets vary in length from about 0.5 cm in *Z. alinae* and *Z. media* to a maximum of 22 cm in *Z. amazonica*. In addition, there is a clear tendency towards a reduction in number of leaflets concomitant with an increase in leaflet size. In all species of subg. *Zapoteca* the pinnae have from several to many pairs of leaflets; by contrast, in *Z. amazonica* the leaves have only one pair of pinnae with a single pair of large leaflets. Furthermore, all members of subg. *Zapoteca* have relatively membranous leaflets, whereas in the remaining species they are clearly chartaceous to coriaceous.

Extrafloral nectaries are uniformly present in *Z. filipes*, *Z. scutellifera*, and *Z. nervosa*. They are located between the insertion of the pinnae and, less frequently, between the distal pairs of leaflets. In *Z. scutellifera* and *Z. filipes* an additional nectary is located near the base of the petioles. The nectaries are more or less cup-shaped in *Z. scutellifera* and *Z. nervosa* and cylindrical in *Z. filipes*. According to Zimmerman's classification (Elias, 1983), all of these fall into the "Hochnektarien" category (elevated nectaries). Extrafloral nectaries have long been considered to be the focal point of a mutually beneficial relationship between the plants that possess them and certain groups of ants (see summary in Bentley, 1977). The ants exploit the nectar produced by these glands, which is rich in sugars, amino acids, proteins, and other compounds (Elias, 1983) and provide the plant with varying degrees of antiherbivore protection. However, such a relationship has not yet been demonstrated in *Zapoteca*.

Venation patterns. Despite the fact that leaves have numerous taxonomically useful characters, monographers generally limit themselves to superficial descriptions of the most conspicuous features of leaf architecture. In this section, I describe the venation pattern of the leaflets of several species of *Zapoteca*, in order to obtain a broad picture of the variation of this important component of the leaf architecture.

Mature leaflets of ten species of *Zapoteca*, representing all the subgenera (Table 3), were cleared following Dilcher (1974). The terminology follows Hickey (1973, 1977).

Variation in leaflet venation patterns is highly consistent with the subgeneric classification in *Zapoteca* and provides important information for phylogenetic interpretation. All members of the genus essentially have brochidodromous venation. The secondary veins usually depart from the primary vein at an acute to right angle, curving abruptly to join superadjacent secondaries to form a loop. In addition, loops are always enclosed by arches formed by higher-order veins. *Zapoteca nervosa* differs from the remaining examined species in having eucamptodromous venation in the basal half of each leaflet and brochidodromous venation in the upper half (Fig. 30). Furthermore, the tertiary domains in the leaflets of this species are elongate and parallel to the primary vein, and the free-ending veinlets are more abundant in the distal area and usually are once- or twice-branched.

The marginal venation is looped in all *Zapoteca* species with the exception of subg. *Amazonica*, where it is clearly fimbriated. Similarly, all species of the genus have incompletely closed areoles, except *Z. amazonica* and *Z. microcephala*, which have imperfectly developed areoles.

With the exception of *Z. tehuana*, all species of subg. *Zapoteca* are characterized by relatively fine, inconspicuous tertiary and higher-order veins that are difficult to discriminate even under a dissecting microscope. By contrast, leaflets of *Z. tehuana* and all species of the other subgenera (Table 3) have thicker and conspicuous tertiary and quaternary veins and free-ending veinlets. The venation patterns of *Z. tehuana* (subg. *Zapoteca*) and *Z. aculeata* (subg. *Aculeata*) are strikingly similar, reflecting taxonomic affinities between the two subgenera. These two species share the basic brochidodromous venation pattern of the genus; however, they differ in their marginal venation and in the orientation of their high-order veins and veinlets. Although the marginal venation of these two species is clearly looped, occasional free-ending marginal veins are present. The veinlets are characteristically oriented towards the admedial-basal area of the leaflets in these two species.

Zapoteca amazonica and *Z. microcephala* have several characters in their leaves that depart from the rest of the genus. The tendency towards the development of larger leaflets concomitant with a reduction in their number in these species is probably associated with an increase in the degree of organization of leaflet venation. Hickey (1977) pro-

TABLE 3. Characteristics of leaflet venation in *Zapoteca* species.

Taxon	Venation Type	Number of Primary Veins	Marginal Venation	Relative Thickness of Secondary and Tertiary Veins	Areole Development	Veinlets
Subgenus *Nervosa*	eucamptodromous basally and brochidodromous distally	1	looped	moderate	incompletely closed	1–2 branched
Subgenus *Zapoteca* (excluding *Z. tehuana*)	brochidodromous	1	looped	hairlike	incompletely closed	1–2 branched
Z. tehuana	brochidodromous	1	looped with free-ending veins	moderate	incompletely closed	admedially ramified dendroid
Subgenus *Aculeata*	brochidodromous	1	looped with free-ending veins	moderate	incompletely closed	admedially ramified dendroid
Subgenus *Amazonica*	brochidodromous	2	fimbriated	moderate	imperfect	dendroid

Material examined. Subgenus *Nervosa*: *Z. nervosa*, *Ekman 284*. Subgenus *Zapoteca*: *Z. formosa*, *H-959*, *H-210*, *H-230*, *H-217*; *Z. tehuana*, *H-950*; *Z. alinae*, *H-952*; *Z. mollis*, *Grayum 4201*; *Z. portoricensis*, *H-948*, *H-793*; *Z. tetragona*, *H-956*. Subgenus *Aculeata*: *Z. aculeata*, *Acosta 13599*. Subgenus *Amazonica*: *Z. amazonica*, *Woytkowski 5943*; *Z. microcephala*, *Haught 1711* (F). Collections in MO unless otherwise indicated.

posed a system of leaf classification based on increasing levels of regularity of venation (leaf ranks) which provides a useful scale here. The venation patterns of the two species of subg. *Amazonica* reflect an advanced condition because their tertiary veins have relatively regular courses (third rank; see Fig. 48). In contrast, the leaflets of the remaining species of *Zapoteca* fall in the second rank because their tertiary and higher-order veins are random in course and are usually not well differentiated from the lower orders. Of particular interest is the presence of two co-primary veins (Fig. 48) in the leaflets of *Z. amazonica* and *Z. microcephala*. This probably indicates leaflet fusion. Hickey & Wolfe (1975) reported that leaflet fusion is a common tendency in the Leguminosae.

Leaf pubescence. With few exceptions, pubescence type is not a reliable taxonomic character in *Zapoteca*, because in most of the species it is clearly variable within and between populations. *Zapoteca nervosa*, *Z. aculeata*, *Z. amazonica*, and *Z. microcephala* appear to be uniformly entirely glabrous or nearly glabrous, whereas *Z. mollis* is consistently pubescent throughout. In the remaining species of subg. *Zapoteca*, pubescence is variable, reaching an extreme of inconstancy in *Z. formosa* and *Z. portoricensis*. A microscopic survey of cleared leaflets of 13 of the species revealed three basic types of hairs (Figs. 1–4). Their taxonomic distribution is shown in Table 4 (terminology following Leelavathi & Ramayya, 1982).

(1) Unicellular conical hairs (Fig. 1) are the most abundant and are found at the base of leaflets and on the rachillas of *Z. aculeata*, along the leaflet margins of *Z. microcephala*, and on all leaf parts of all the pubescent species of subg. *Zapoteca*. A very similar type of hairs, unicellular clavate (Fig. 2), is occasionally found on the rachilla of *Z. alinae* (Table 4).

(2) Multicellular macroform conical hairs (Fig. 3) occur in all species of subg. *Zapoteca* except *Z. formosa* and *Z. alinae*. They are found, intermixed with other types of hair, primarily on leaflet margins and rachillas.

(3) Filiform capitate hairs and filiform clavate hairs (Fig. 4) usually have a uniseriate cylindrical foot formed by a variable number of cells of varied lengths, and a multiseriate (or rarely uniseriate?) head. These are usually restricted to leaflet margins and rachillas, and are found in all species of subg. *Zapoteca* except *Z. formosa*.

TABLE 4. Distribution of types of leaf trichomes in selected species of *Zapoteca*. Ia = unicellular conical, Ib = unicellular clavate; II = multicellular macroform conical, III = filiform capitate or filiform clavate. Relative abundance is indicated by: + = occasional, ++ = regular, +++ = abundant. All collections in MO unless otherwise indicated. H = author's collections.

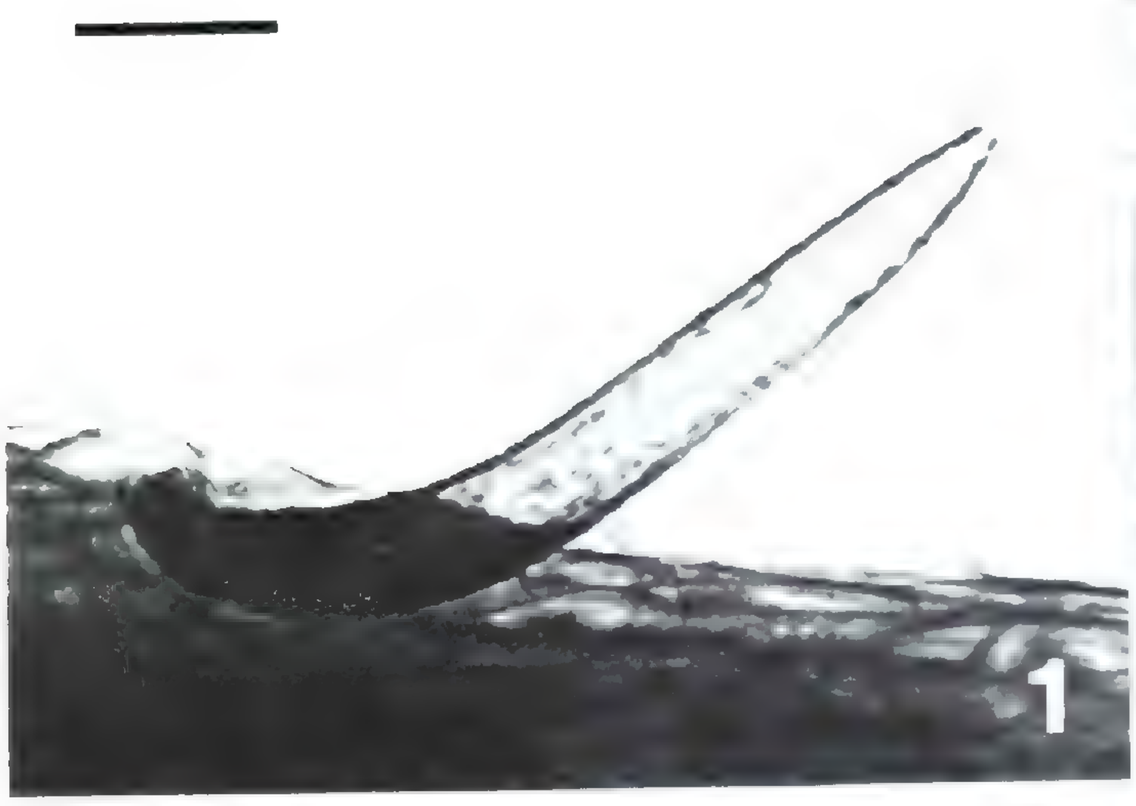
Taxon	Collection	Type			
		Ia	Ib	II	III
Subgenus *Nervosa*					
Z. nervosa	*Ekman 284*				
Subgenus *Zapoteca*					
Z. alinae	*H-949*	+	+	—	+
Z. formosa	*H-210*	+++	—	—	—
Z. formosa	*H-959*				
Z. formosa	*H-217*	+++	—	+	
Z. formosa	*H-230*	+++	—	—	—
Z. formosa	*Sousa 2563*	+++	—	—	—
Z. lambertiana	*Breedlove 37412*	++	—	+	+
Z. media	*H-951*	+++	—	++	++
Z. mollis	*Grayum 4201*	+++	—	++	++
Z. portoricensis	*H-948*	+++	—	++	++
Z. portoricensis subsp. *flavida*	*H-793*	+++	—	+	++
Z. tehuana	*H-950*	+++	—	+	+
Z. tetragona	*H-956*	++	—	++	++
Subgenus *Aculeata*					
Z. aculeata	*Acosta 13599*	+			
Subgenus *amazonica*					
Z. amazonica	*Woytkowski 5943*				
Z. microcephala	*Haught 1711* (F)	++			

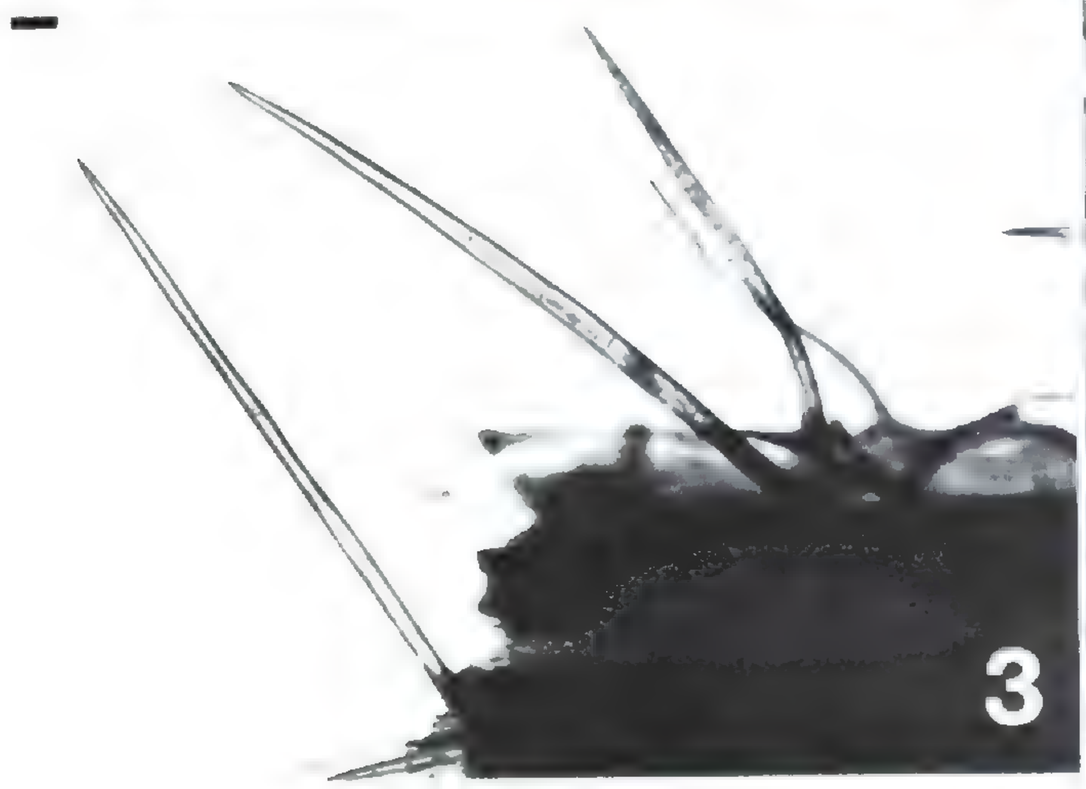
Stipules. The stipules are persistent, leafy, and possess a series of veins running parallel to the margins (Figs. 5, 6); in most species the stipules are conspicuous (e.g., *Z. amazonica*, *Z. tetragona*), although in some they are very small (e.g., *Z. tehuana*). Exceptional in this respect is *Z. aculeata*, which has spinescent stipules (Fig. 46), and *Z. nervosa*, whose stipules are reduced to small (< 1 mm) scales. Throughout the genus the stipules are adpressed and probably have a protective function during the early phases of leaf and inflorescence development. *Zapoteca andina* is exceptional by having descending or depressed stipules (Fig. 41). Moreover all species have stipels at the base of the distal pairs of pinnae and at the distal tip of every pinna.

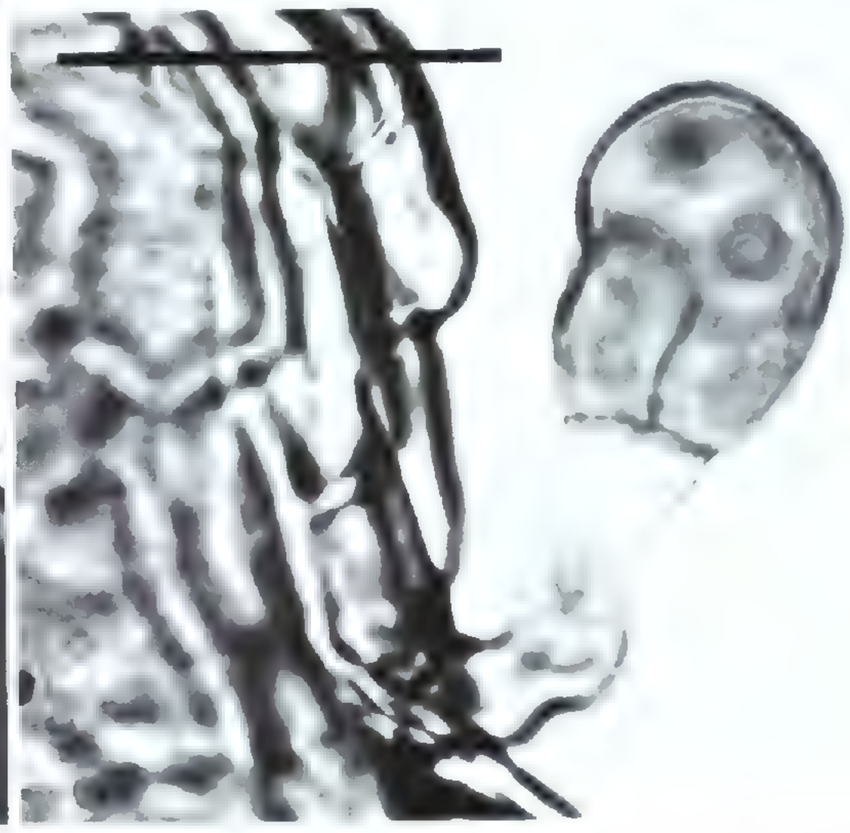
INFLORESCENCES AND FLOWERS

Inflorescences. The flowers are consistently arranged in compact, homomorphic, spherical, capitate inflorescences. In the basic plan of inflorescence organization, solitary or fasciculate peduncles are axillary and subtended by a leaf, as in *Z. alinae*, *Z. media*, and *Z. aculeata* (Fig. 7A). There is, however, an evolutionary trend toward the progressive reduction of the subtending leaves, which reaches its extreme in the two species of subg. *Amazonica*, where the leaves are always vestigial, and the inflorescence therefore appears to be an elongate panicle (Fig. 7D, E). Transitional forms between the two extremes are found in several species of subg. *Zapoteca* (Fig. 7B). For instance, in *Z. mollis*, *Z. portoricensis*, and additional species, the subtending leaves start developing during or after anthesis. Sometimes, however, the subtending leaves never develop, as in some individuals of *Z. caracasana* (Fig. 7C) and *Z. formosa*, in which the capitula are apparently aggregated in paniclelike inflorescences.

The trend towards retardation and suppression of leaf development that results in differences in foliation among the species of *Zapoteca* has also produced various patterns of inflorescence organization. I interpret these types as steps in a continuum of inflorescence specialization rather than as discrete and fundamentally different types. An indication of the derived character of the "paniculate" inflorescences of *Z. microcephala*, *Z. ama-*





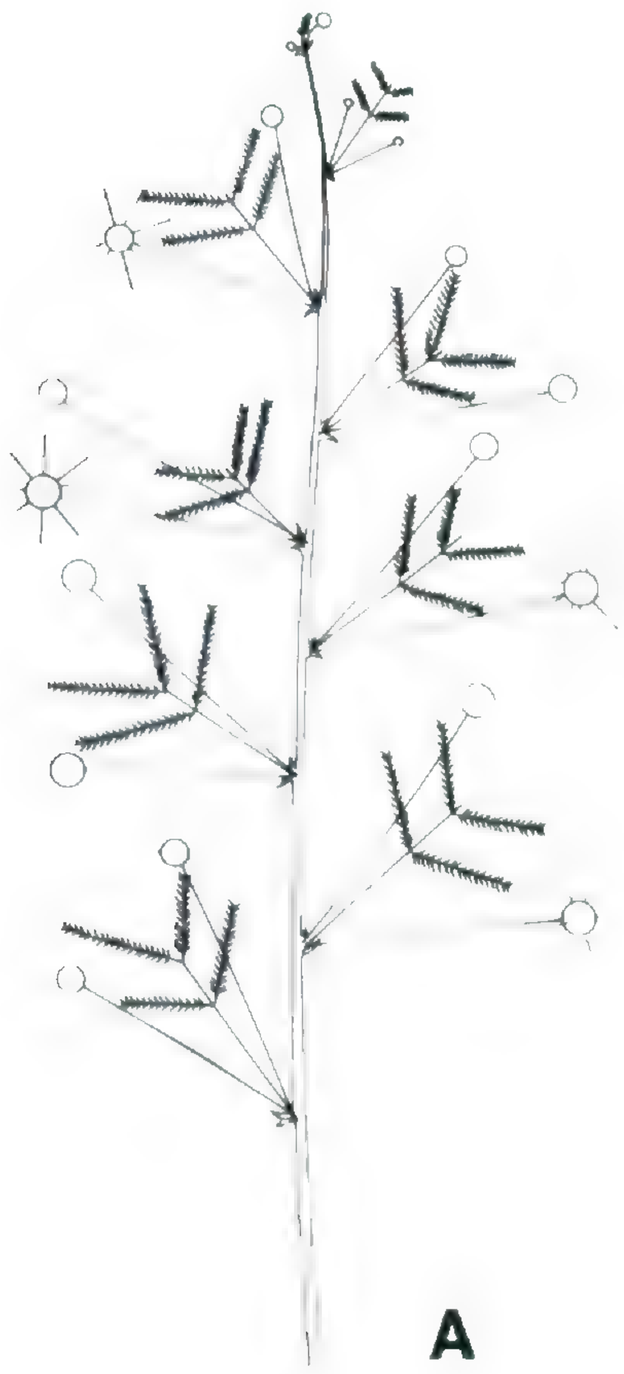


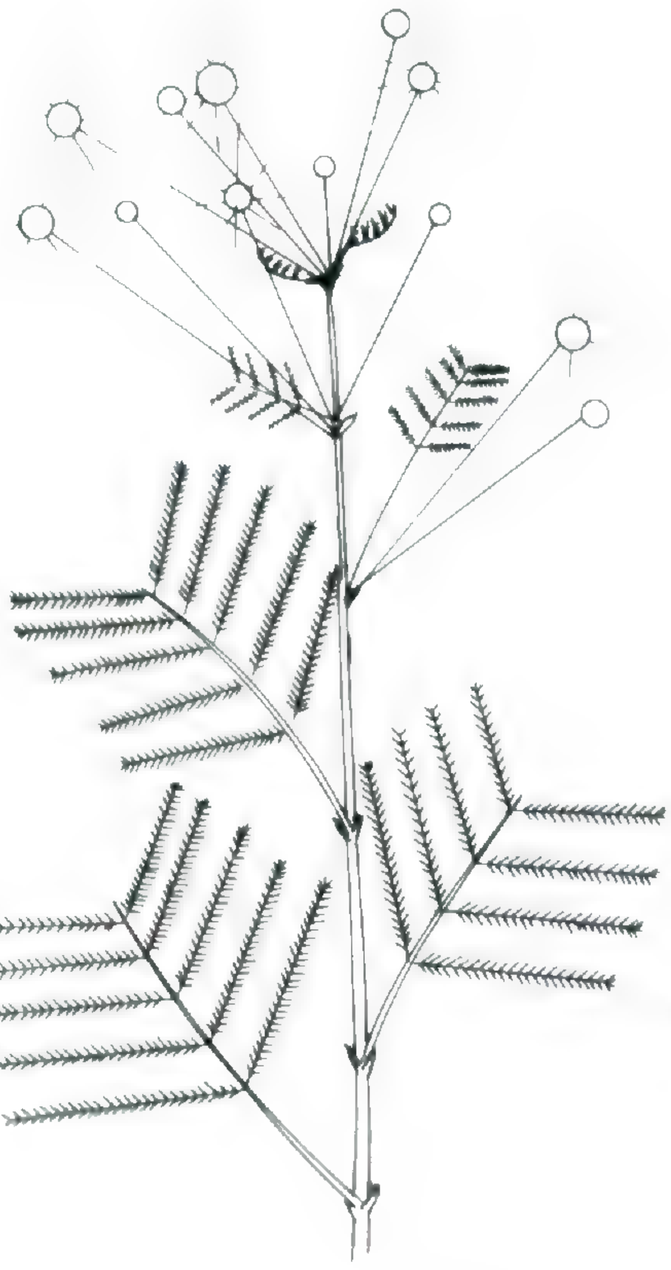
FIGURES 1–4. Leaf trichomes of *Zapoteca*. 1. Unicellular conical, *Z. alinae* (*H. Hernández* 952). 2. Unicellular clavate, *Z. alinae* (*H. Hernández* 952). 3. Multicellular macroform conical, *Z. mollis* (*Grayum* 4201). 4. Filiform capitate, *Z. tetragona* (*H. Hernández* 956). All collections at MEXU and MO. Scale bars = 100 μm.

zonica, and other species in subg. *Zapoteca* is the presence of persistent paired stipules at every node along the flowering system. These inflorescence types, therefore, cannot be considered strictly paniculate, and for this reason the term "pseudopanicle" will be used.

In summary, there has been an evolutionary trend of inflorescence modification in *Zapoteca*, where retardation and suppression of the subtending leaves has played a prominent role in changing the overall aspect of the flowering system. The axillary capitula subtended by a developed leaf

FIGURES 5, 6. Stipules of *Zapoteca*.—5. *Z. portoricensis* subsp. *portoricensis* (*H. Hernández* 948).—6. *Z. tetragona* (*H. Hernández* 956). Collections at MEXU and MO. Scale bars = 1 cm.





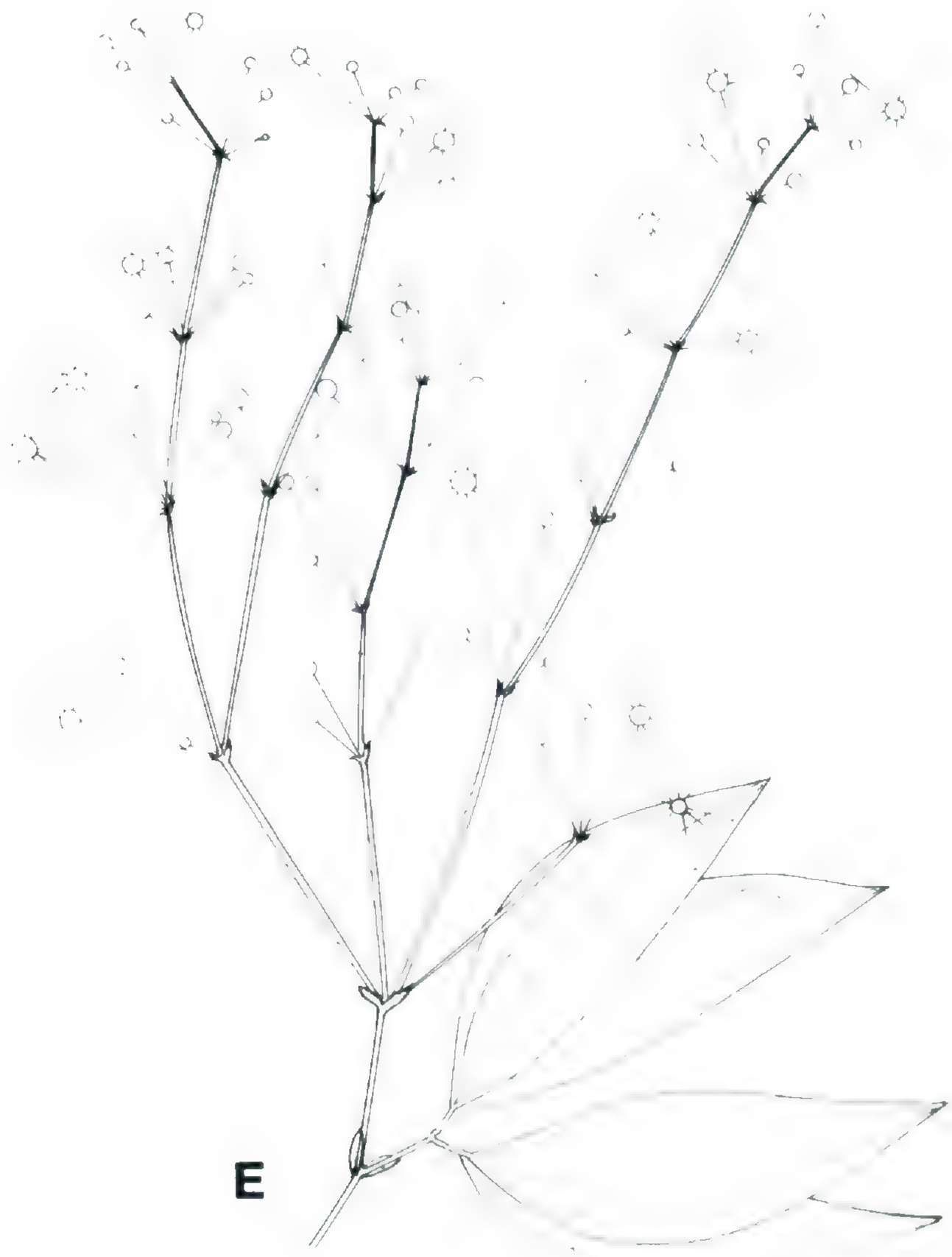


FIGURE 7. Patterns of inflorescence organization in *Zapoteca*.—A. The capitula at each node are subtended by a well-developed leaf, *Z. alinae* (*Sousa et al. 7846*, MO).—B. The capitula are subtended by late-developing leaves, *Z. portoricensis* (*Higgins 2578*, MICH).—C E. The subtending leaves are vestigial. C. *Z. caracasana* (*Asplund 15982*, LL). D. *Z. microcephala* (*Mutis 3800*, US). E. *Z. amazonica* (*Schunke 6913*, MO).

(leafy, axillary capitula) appear to represent the basic pattern. The paniclelike inflorescences of *Z. microcephala* and, especially, *Z. amazonica* (subg. *Amazonica*) are highly modified and are clearly derived from the basic type. Intermediate types exist in many species of subg. *Zapoteca*, where a single individual may have both leafy, axillary capitula and flowering branches with vestigial or late-developing subtending leaves.

Flowers. Aside from variation in size and in the relative proportions of their parts, the flowers of *Zapoteca* species are extremely constant. Details of floral morphology and certain aspects of floral biology are in the generic and specific descriptions and in the section on reproductive biology.

POLLEN

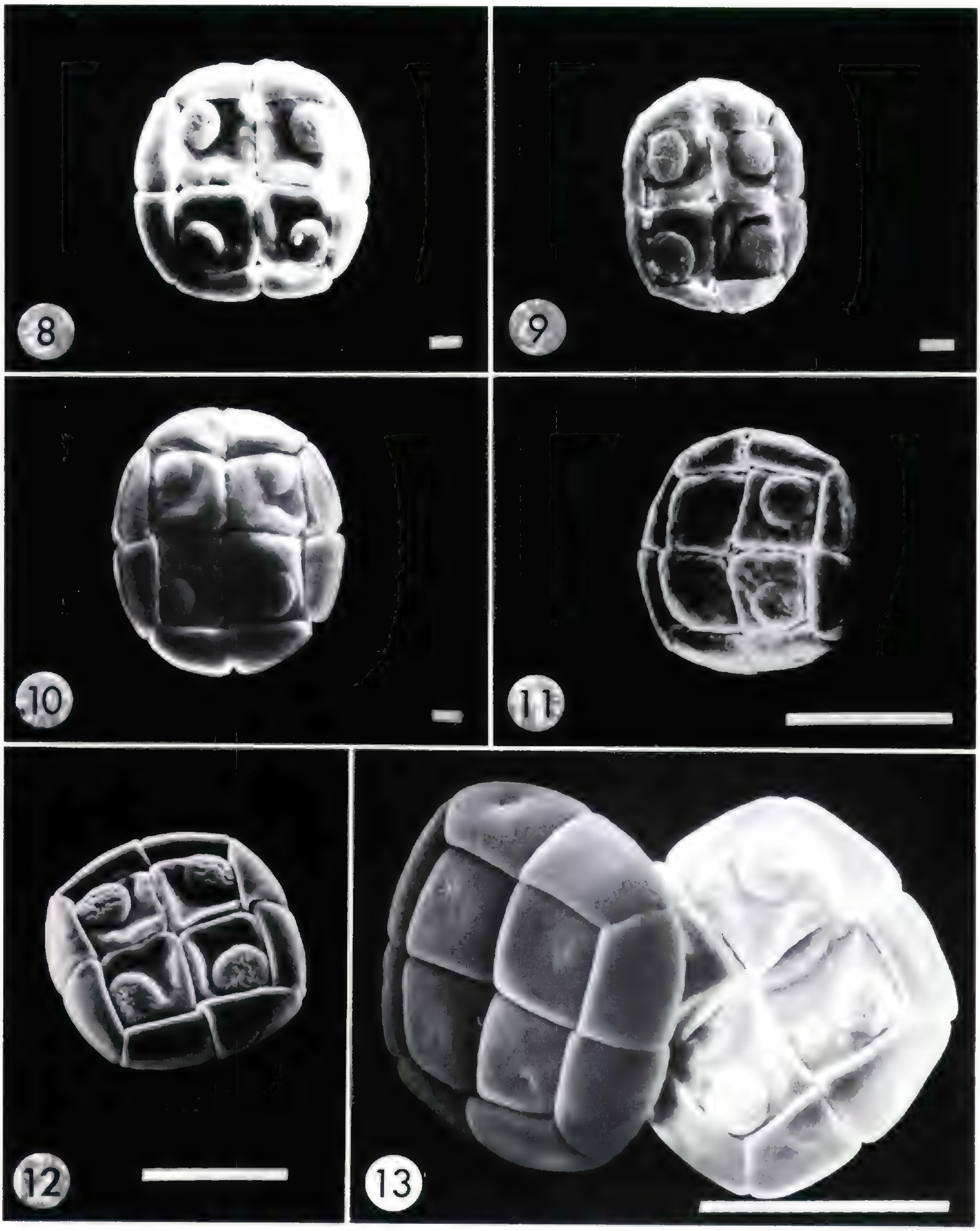
The diversity of pollen types in subfamily Mimosoideae has been studied extensively by several authors (Guinet, 1969, 1981—a review; Sorsa, 1969; Niezgoda et al., 1983). One of the outstanding features in this subfamily is the high frequency of permanently compound grains, these either in tetrads or more commonly in polyads. As Guinet (1981) and others pointed out, the basic polyad type in the Mimosoideae is the acalymmate type, in which the individual grains are more or less free from one another. This form of polyad cohesion is in contrast to the calymmate type, where the external layer of the exine is common to all cells. Calymmate polyads are found in *Calliandra*.

As discussed elsewhere (Hernández, 1986a), several comprehensive surveys on the pollen characteristics of *Calliandra* (Guinet, 1965, 1969, 1981; Guinet & Barth, 1969; Sorsa, 1969; Niezgoda et al., 1983) indicate the phyletic distinctness of *Zapoteca*. The basic plan of polyad organization here is the same as that in the other genera of tribe Ingeae, but unlike that of *Calliandra* sensu stricto. All the species in the genus have acalymmate, discoid, radially symmetrical, 16-grained polyads (Figs. 8–13). The eight central grains, which are distributed in two rows, are morphologically different from the peripheral grains (i.e., the pollen grains exhibit heteromorphy). The external layer of the exine has an undifferentiated granular structure, and the individual grains have internal apertures (see fig. 7 in Niezgoda et al., 1983). The size of the polyads ranges from 76 to 141 μm. One very striking diagnostic character, found nowhere else in Mimosoideae, is the occurrence of prominent lens-shaped structures in the central cells on one side of the polyad. These are found in all species of *Zapoteca* except *Z. nervosa*. In connection with this, Guinet (pers. comm., 1985) observed that the rounded lens-shaped areas occur on both sides of the polyads (on eight grains) in *Z. aculeata* and *Z. amazonica*; nevertheless, they are less pronounced on one side. Such areas sometimes occur on some or all of the peripheral grains of *Z. alinae* polyads (Fig. 9).

PODS, SEEDS, AND SEED DISPERSAL

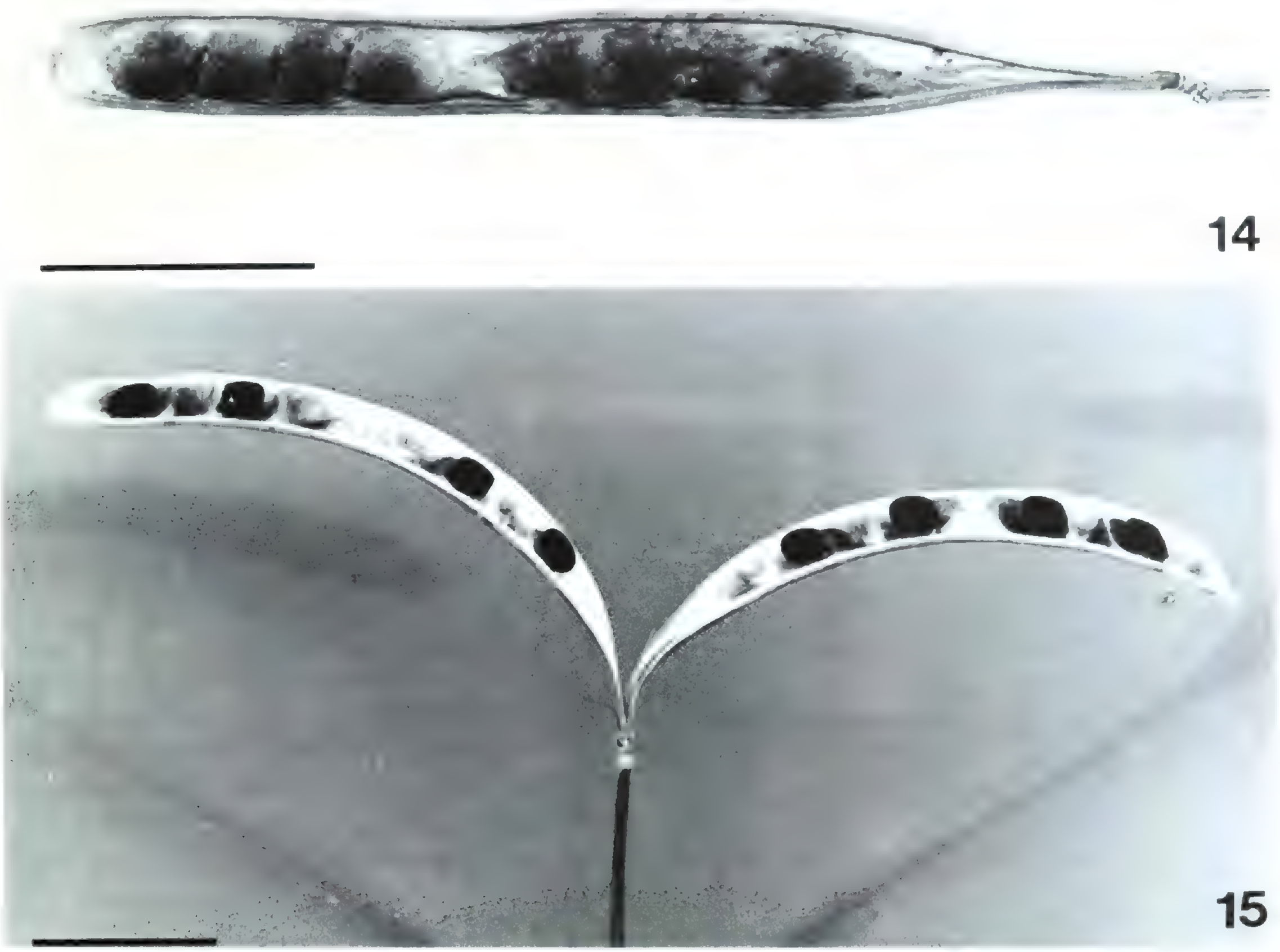
Pods. Pod morphology is relatively constant throughout *Zapoteca* (Figs. 14, 15). The pods are usually straight, linear, and flattened; they generally have unconstricted margins, visible seed chambers, and thickened sutures (terminology following Gunn, 1984). Pod size varies from 3.5 × 0.7 cm in *Z. formosa* subsp. *mollis* to 24 × 1.2 cm in *Z. amazonica*. There is some interspecific variation in the texture (density) of the valves, which is of taxonomic value. In this respect, the species may be arranged into three groups: 1) *Z. lambertiana* and *Z. filipes* with thin, membranous valves; 2) the remaining species of subg. *Zapoteca*, along with *Z. nervosa*, with thick, membranous valves; and 3) *Z. aculeata*, *Z. microcephala*, and *Z. amazonica*, with coriaceous valves. It is important to mention that the terminology of pod texture used here is relative, and as such its use is not applicable to other structures (e.g., leaflets). The pods are glabrous except those of *Z. caracasana* subsp. *weberbaueri*, *Z. mollis*, *Z. portoricensis* subsp. *pubicarpa*, and *Z. formosa* subsp. *salvadorensis*, which are short-pubescent, densely villous, puberulent, and pilose to densely pilose respectively.

Seeds. In all species of subg. *Zapoteca*, the seeds are widely ovoid to rhomboid and compressed and lack rupture lines, arils, or wings (Figs. 16, 17). In most members of this subgenus the testa is mottled, or dichrome, in which case the area encompassed by the pleurogram (areola) has a lighter color than the outside area. There is considerable interpopulational variability in seed size and the coloration of the testa, especially in *Z. formosa*; by contrast, *Z. tetragona* appears to be consistent in having dark, monochrome, ovate seeds. Another seed feature is the pleurogram, common in subfamily Mimosoideae (Gunn, 1984). Seeds of subg. *Zapoteca* usually have irregular, 90° pleurograms (sensu Gunn, 1984), although those of *Z. tetragona* are always regular. The seeds of *Z. amazonica* differ from those of subg. *Zapoteca* in being narrowly rhomboid to narrowly elliptic, larger, and in lacking the characteristic pleurogram.



FIGURES 8–13. Unacetolyzed 16-grained polyads of *Zapoteca* species. –8. *Z. media* (*R. Fernández 3163*). — 9. *Z. alinae* (*H. Hernández 206*); one of the peripheral grains has the lens-shaped structure characteristic of the central grains. — 10. *Z. lambertiana* (*H. Hernández 147*). — 11. *Z. tehuana* (*H. Hernández 950*). — 12. *Z. tetragona* (*H. Hernández 956*). 13. *Z. caracasana* subsp. *weberbaueri* (*Johnson 2494*, MO); both sides of the polyad are shown. All collections at MEXU unless otherwise indicated. Scale bars = 10 μm Figures 8 10; 50 μm Figures 11–13.

Seed dispersal. *Zapoteca* pods dehisce explosively with the valves splitting along both sutures from apex to base (Fig. 15). This is probably the prevalent short-range dispersal mechanism for species of *Zapoteca* over land and is probably effective over larger distances as a result of accumulative short-distance dispersal events over many generations.



FIGURES 14, 15. Pods of *Zapoteca tetragona* (*H. Hernández 956*).—14. Indehisced pod.—15. Dehisced pod. Scale bars = 2 cm.

This dispersal mechanism, however, does not explain the presence of species such as *Z. formosa*, *Z. caracasana*, and *Z. portoricensis* on islands, which they presumably reached by long-distance dispersal over water. *Zapoteca formosa*, for instance, occurs throughout the West Indies and on some islands off the Mexican Pacific coast (Revillagigedo Islands). Populations of this variable species frequently grow in coastal areas. Although experiments have shown that seeds and mature pods of *Z. formosa* subsp. *formosa* taken from a coastal population of the Yucatán Peninsula floated for only two to four days in seawater, the seeds are highly resistant to saline water. As shown in Figure 18, seeds from this population (*Hernández 946*) germinated after soaking in saline water (3.4% sodium chloride) for up to 70 days. Most of the seeds germinated normally when they were mechanically scarified and transferred to petri dishes in a medium moistened with fresh water. Ridley (1930) presented evidence that seeds and pods may disperse for considerable distances floating on debris. The great resistance to salinity of the seeds of *Z. formosa*, and presumably of *Z. caracasana* and *Z. portoricensis* as well, suggest that these species dispersed by flotation from the continental mainland. Further discussion about the distribution and dispersal of *Z. formosa* is provided below.

SEEDLINGS

The taxonomic importance of seedling characters has been recognized by legume researchers for a long time (De Candolle, 1825; Compton, 1912). Recently, such characters have been applied successfully in the construction of generic and infrageneric classifications in Leguminosae (Léonard, 1957; Vassal, 1969; Robbertse & van der Schiff, 1971; Kupicha, 1977; Guinet et al., 1980; and others). The distinctive seedlings of the species formerly assigned to ser. *Laetevirentes* indicated the heterogeneous nature of *Calliandra*

FIGURES 16, 17. Seeds of *Zapoteca* species showing the irregular pleurograms.—16. *Z. portoricensis* subsp. *portoricensis* (*H. Hernández 948*).—17. *Z. formosa* (*Torres 4063*). Collections at MEXU and MO. Scale bars = 500 μm.

(sensu Bentham) and provided evidence for recognition of *Zapoteca* (Hernández, 1986a).

Seedlings of 19 populations representing eight species of *Zapoteca*, all belonging to subg. *Zapoteca*, were studied (Table 5). About 10 mechanically scarified seeds per sample were germinated in petri dishes. After one to three days, when the radicles had emerged, the germinated seeds were transferred to individual pots. The seedlings were described following Duke & Polhill (1981).

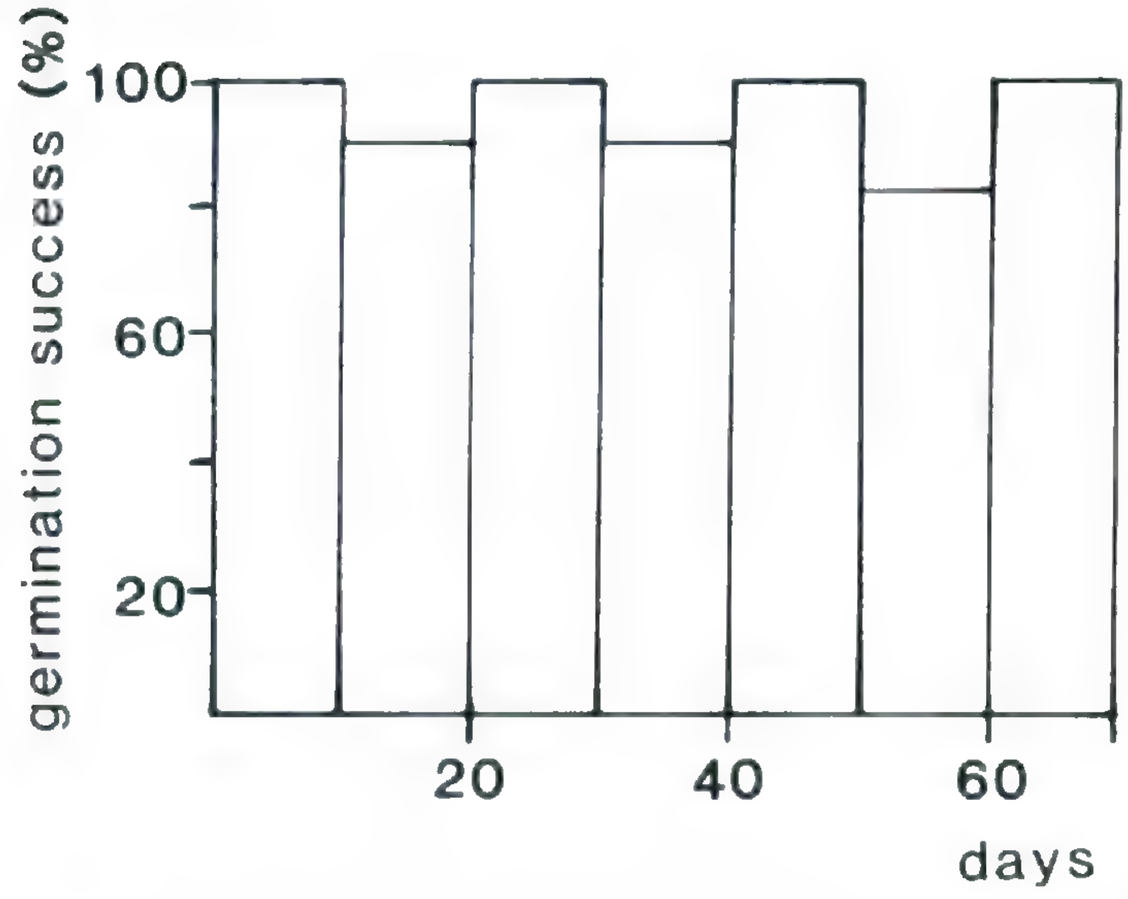


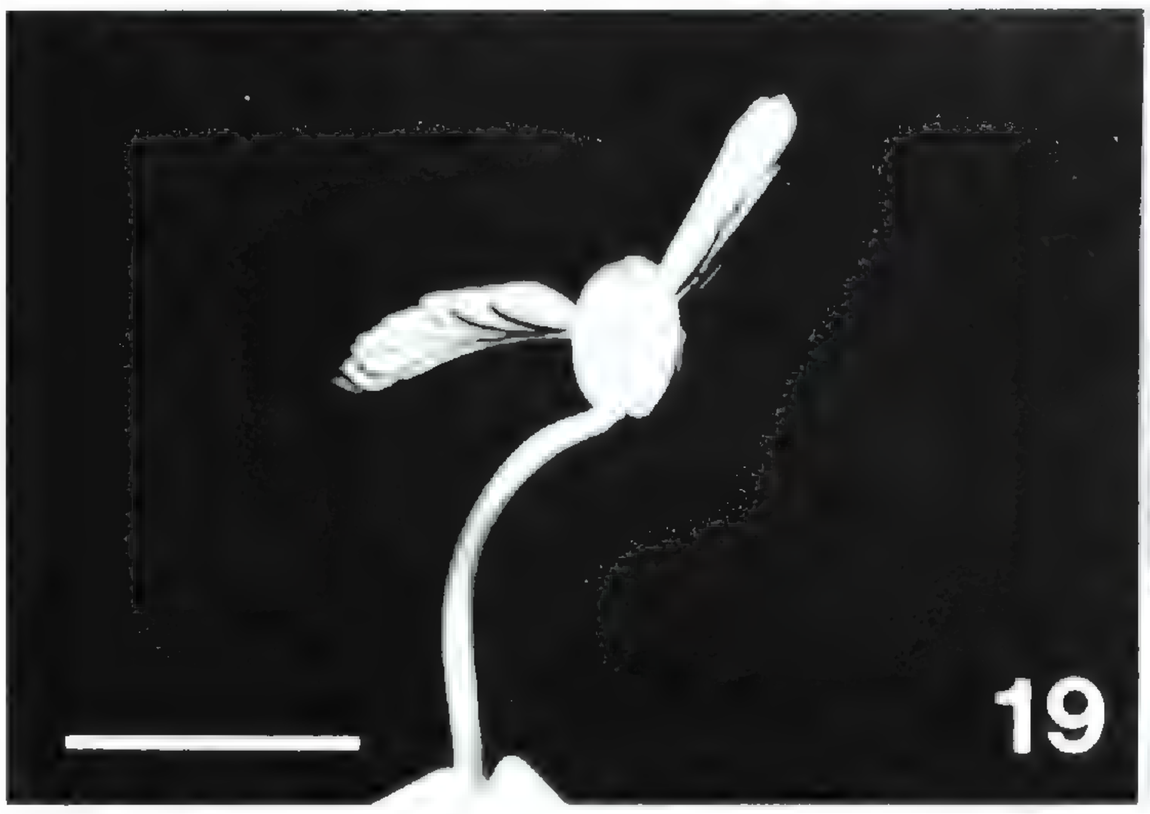
FIGURE 18. Resistance of *Zapoteca formosa* subsp. *formosa* seeds to saline water (3.4% sodium chloride). The bars indicate percent of germinated seeds. Ten seeds were tested at each time interval.

The principal characters used in the descriptions were: 1) position (whether epigeal, geal, or hypogeal), morphology, texture, and degree of persistence of the cotyledons, and 2) type (whether pinnate or bipinnate) and sequence (whether opposite or alternate) of the eophylls.

These samples were remarkably uniform, the seedlings of each species examined being essentially identical. Diagnostic characters at the species level, such as the square stems of *Z. tetragona* or the ovate leaflets of *Z. formosa*, became manifest above the third eophyll, as the first metaphylls arose. A brief description of the seedlings listed in Table 5 follows (Figs. 19, 20):

Germination phaneroepigeal; cataphylls absent. Cotyledons sessile, elliptic to elliptic-ovate, foliaceous, ephemeral (remaining functional for ca. one week). Leaves stipulate, glabrous; first two eophylls opposite and pinnate, the pinnae with 4–12 lanceolate to narrowly oblong leaflets; third eophyll alternate, bipinnate, with 1 pair of pinnae; fourth eophyll alternate, bipinnate, with 1, rarely 2 pairs of pinnae.

In summary, although the seedlings of subg. *Aculeata*, *Amazonica*, and *Vervosa* remain unknown, the seedlings that have been observed so far, all in subg. *Zapoteca*, display a high degree of inter- and intraspecific morphological homogeneity.



FIGURES 19, 20. Seedlings of *Zapoteca*. —19. Five-day-old seedling of *Z. tetragona* (*H. Hernández 956*). 20. Three-week-old seedling of *Z. portoricensis* subsp. *portoricensis* (*H. Hernández 948*). Collections at MEXU and MO. Scale bars = 1 cm.

PATTERNS OR MORPHOLOGICAL DIFFERENTIATION

There are several morphological features common to all *Zapoteca* species. Among the most important are: brochidodromous venation patterns in leaflets; persistent, leafy stipules (excluding *Z. aculeata*); homomorphic, spherical, capitate inflorescences; cup-shaped stigmas; 16-grained polyads with prominent lens-shaped thickenings (excluding *Z. nervosa*); and dry, linear, flattened pods with thickened margins and showing a particular mode of dehiscence.

The distribution of morphological features among the species of *Zapoteca* reflects four evolutionary lines, which correspond to the four subgenera proposed in the systematic treatment.

Subgenus *Nervosa* comprises *Z. nervosa*, which appears to be morphologically the most isolated species in the genus. Superficially, this species appears out of place within *Zapoteca*; however, the morphology and the type of dehiscence of its pods and the overall features of its inflorescences justify its placement within this genus.

Zapoteca nervosa exhibits several characters unique in the genus, the most important of which are: stems with fissured bark; large, coriaceous, grayish leaflets with a peculiar eucamptodromous brochidodromous venation; and 16-grained polyads

TABLE 5. Species of *Zapoteca* in which seedlings were studied. H = author's collections.

Taxon	Collection Data	Distribution
Z. alinae	*Torres 3947* (MO, MEXU)	Mexico, Oaxaca
Z. caracasana subsp. *weberbaueri*	*Johnson 2494-82* (MO)	Colombia, Valle
Z. formosa subsp. *formosa*	*Johnson 483-78* (MO)	Mexico, Yucatán
Z. formosa subsp. *formosa*	*Torres 4262* (MO, MEXU)	Mexico, Oaxaca
Z. formosa subsp. *formosa*	*Johnson 490-78* (MO)	Mexico, Yucatán
Z. formosa subsp. *rosei*	*Johnson 1270-79* (MO)	Mexico, Guerrero
Z. formosa subsp. *rosei*	*Torres 6612* (MEXU)	Mexico, Oaxaca
Z. formosa subsp. *schottii*	*Starr & Birgy 169* (MEXU)	Mexico, Sonora
Z. formosa subsp. *schottii*	*Felger 84-124* (MEXU)	Mexico, Sonora
Z. lambertiana	*Acosta 134* (MO, XAL)	Mexico, Veracruz
Z. lambertiana	*Martínez O. 284* (MEXU)	Mexico, Tamaulipas
Z. media	*Delgado 53* (MEXU)	Mexico, Hidalgo
Z. portoricensis subsp. *portoricensis*	*H-154* (MO, MEXU)	Mexico, Veracruz
Z. tehuana	*Torres 4167* (MO, MEXU)	Mexico, Oaxaca
Z. tetragona	*H-167* (MO, MEXU)	Mexico, Veracruz
Z. tetragona	*H-675* (MO, MEXU)	Costa Rica, Cartago
Z. tetragona	*H-800* (MO, MEXU)	Mexico, Veracruz
Z. tetragona	*H-827* (MO, MEXU)	Mexico, Veracruz
Z. tetragona	*Johnson 1582* (MO)	Mexico, Veracruz

without lens-shaped structures. In this connection, it is reasonable to hypothesize that *Z. nervosa* represents an evolutionary line that separated from the main stock early in the evolution of the genus, and its peculiar morphological features would be explained by divergent evolution. The lack of areolate, lens-shaped thickenings in the polyads of *Z. nervosa*, a character also absent in the remaining genera of the Ingeae, appear to represent a primitive condition within *Zapoteca* and suggests that this species is phylogenetically basal in this genus. Additional information on this critical species is needed in order to learn more about its phylogenetic relationships.

Subgenus *Zapoteca* is the most widespread and diversified subgenus in *Zapoteca*. Yet a number of morphological features common to all the species make this subgenus easily recognizable. All the species have pinnae with several to many pairs of thin, membranous leaflets, which show characteristic usually inconspicuous and simplified venation patterns. The highest diversity of hair types (three types) of the genus is found in subg. *Zapoteca*; the species of the remaining subgenera are characterized by having only the unicellular conical type (Table 4). Further, the valves in the pods in subg. *Zapoteca*, along with *Z. nervosa*, are consistently thick-membranous, whereas those of subg. *Aculeata* and *Amazonica* are coriaceous.

The pattern of leaflet venation in *Z. tehuana* differs from those of the other species in subg. *Zapoteca* and shows strong similarity with those of *Z. aculeata* (subg. *Aculeata*). This may indicate a phylogenetic link between the two subgenera.

Subgenus *Aculeata* contains only *Zapoteca aculeata*, which is characterized primarily by spinescent stipules (a characteristic that has clearly been derived within the genus), by an apparent arborescent habit, and by pinnae having fewer pairs of chartaceous-coriaceous leaflets than those of subg. *Zapoteca*. The coriaceous pods of *Z. aculeata* resemble those of subg. *Amazonica*.

Subgenus *Amazonica* is made up of *Z. amazonica* and *Z. microcephala*, which are characterized by having the most obvious combination of apomorphic features in *Zapoteca*. Their leaves are reduced to two or three large, coriaceous leaflets in each pinna. This is the result of an evolutionary trend toward reduction in the number of leaflets associated with increased leaflet size. This trend is also seen in other genera of Mimosoideae (e.g., *Calliandra*, *Mimosa*). Moreover, the leaflets in these species have a number of common architectural features reflecting an increased level of organization, which is also interpreted as an advanced condition. A progressive trend toward suppression of leaves subtending the inflorescence in *Zapoteca* has resulted in the highly specialized, elongate pseudopanicles of these species. Among other clearly apomorphic features of subg. *Amazonica* are the elongate seeds of *Z. amazonica*, which lack the characteristic pleurogram and are the largest in the genus.

Biogeography

Zapoteca ranges from the southwestern United States (southern Arizona and southwestern Texas) and northern Mexico, from about latitude 32°30′N, southward through most of Mexico, Central America, and much of South America (Venezuela, Colombia, Ecuador, Peru, Bolivia, Guyana, Brazil, Paraguay) to northern Argentina (ca. latitude 27°30′S). *Zapoteca* also occurs on most of the West Indies and in the Revillagigedo Islands (i.e., Isla Socorro and Isla Clarión).

Zapoteca species occur in a variety of environments, ranging from open, arid or semiarid, scrubby vegetation types (e.g., *Z. media*, *Z. alinae*, *Z. formosa* subsp. *mollicula*, and *Z. formosa* subsp. *schottii*) to the wet evergreen forests of Amazonian Peru (*Z. amazonica*). Most populations of *Z. portoricensis* subsp. *flavida* and *Z. tetragona* are found in relatively wet, lowland habitats, generally on disturbed sites. The greatest degree of diversification has occurred in areas covered by seasonal, tropical deciduous forests (sensu Breedlove, 1981). In addition to the species found in clearly arid regions, most populations of eight species of *Zapoteca* (*Z. nervosa*, *Z. lambertiana*, *Z. filipes*, *Z. mollis*, *Z. caracasana*, *Z. andina*, *Z. formosa*, and *Z. tehuana*) occur in tropical deciduous forests. In addition, *Z. portoricensis* subsp. *portoricensis* and subsp. *pubicarpa* primarily occur in middle-elevation oak, pine–oak, or subtropical montane moist forests.

The occurrence of three of the four subgenera of *Zapoteca* in South America (*Zapoteca*, *Aculeata*, and *Amazonica*), compared with only one in Mexico and Central America, is probably a consequence of the more ancient existence of *Zapoteca* in South America. Although only subg. *Zapoteca* is represented in Mexico and Central America, extensive diversification has taken place at the specific and subspecific levels, especially in Mexico. For instance, there are seven subspecific taxa in Mexico (i.e., *Z. portoricensis* subsp. *portoricensis*, *Z. portoricensis* subsp. *pubicarpa*, *Z.*

portoricensis subsp. *flavida*, *Z. formosa* subsp. *formosa*, *Z. formosa* subsp. *rosei*, *Z. formosa* subsp. *mollicula*, *Z. formosa* subsp. *schottii*), four of them restricted to this country. In contrast, only four subspecies of subg. *Zapoteca* occur in all of South America (*Z. portoricensis* subsp. *flavida*, *Z. caracasana* subsp. *caracasana*, *Z. caracasana* subsp. *weberbaueri*, and *Z. formosa* subsp. *formosa*), and only one of these, *Z. caracasana* subsp. *weberbaueri*, is endemic.

Viewed from a global perspective, there are no clear centers of species diversity in *Zapoteca*. The total number of species and the number of endemic species are roughly correlated with the size of each region (i.e., Mexico, 7 species/4 endemics; Central America, 6/2; West Indies, 4 1; and South America, 10/6. However, a more detailed analysis of the areas of species concentration and the distribution of endemic taxa revealed several regions with high diversity (Fig. 21).

Southern Mexico (Oaxaca and Chiapas, including southern Puebla) has the largest concentration of species and subspecies of *Zapoteca*. This relatively small region, characterized by its remarkable climatic and topographic diversity, contains seven species, and if subspecies are taken into account, the figure rises to eleven taxa (*Z. media*, *Z. alinae*, *Z. lambertiana*, *Z. portoricensis* subsp. *portoricensis*, *Z. portoricensis* subsp. *pubicarpa*, *Z. portoricensis* subsp. *flavida*, *Z. tetragona*, *Z. formosa* subsp. *formosa*, *Z. formosa* subsp. *rosei*, *Z. formosa* subsp. *mollicula*, and *Z. tehuana*). Four of these are endemics (*Z. alinae*, *Z. portoricensis* subsp. *pubicarpa*, *Z. formosa* subsp. *mollicula*, and *Z. tehuana*), especially to dry areas of Oaxaca and the arid valleys of the Pueblan–Oaxacan border region. The number of species and subspecies of *Zapoteca* suddenly decreases from this center in all directions (Fig. 21). On the Pacific slope of Mexico, from Guerrero northwards, there are four taxa (*Z. tetragona*, *Z. formosa* subsp. *formosa*, *Z. formosa* subsp. *rosei*, and *Z. formosa* subsp. *schottii*), decreasing to one in the northern portion. *Zapoteca media* and *Z. formosa* subsp. *formosa* are the only taxa that occur in the Central Plateau. Along the entire Atlantic slope, from Tabasco to Tamaulipas, together with the Yucatán Peninsula, there are only five taxa (*Z. lambertiana*, *Z. portoricensis* subsp. *portoricensis*, *Z. portoricensis* subsp. *flavida*, *Z. tetragona*, and *Z. formosa* subsp. *formosa*). *Zapoteca lambertiana* is the only one of these that is essentially endemic to this region.

In Central America, there are a total of eight taxa (*Zapoteca portoricensis* subsp. *portoricensis*, *Z. portoricensis* subsp. *flavida*, *Z. mollis*, *Z. caracasana*, *Z. tetragona*, *Z. costaricensis*, *Z. formosa* subsp. *formosa*, and *Z. formosa* subsp. *salvadorensis*). Diversity is quite uniform among the different countries (Fig. 21). *Zapoteca mollis* and *Z. costaricensis* are essentially endemic to Costa Rica, although a disjunct population of the former is known from Panama. *Zapoteca formosa* subsp. *salvadorensis* is restricted to southern Guatemala and El Salvador.

Six taxa of *Zapoteca* occur in the West Indies (*Z. nervosa*, *Z. portoricensis* subsp. *portoricensis*, *Z. portoricensis* subsp. *flavida*, *Z. caracasana* subsp. *caracasana*, *Z. formosa* subsp. *formosa*, and *Z. formosa* subsp. *gracilis*). Generally only a single species occurs on a particular island; however, in Hispaniola the four species, including the endemic and morphologically distinct *Z. nervosa*, occur together. Howard (1973) pointed out that Hispaniola and Cuba are the most floristically diverse islands in the West Indies and that they show great habitat diversity and highest percentage of endemism (Hispaniola with 33% of endemic genera). *Zapoteca formosa* subsp. *gracilis* is the second endemic entity in the West Indies. It is primarily restricted to coastal areas in Cuba, the Bahamas, Cayman Islands, and northwestern Haiti.

Eleven taxa of *Zapoteca* occur in South America. The greatest diversity occurs in the tropical Andean countries, Venezuela, Colombia, Ecuador, Peru, and Bolivia, where populations are primarily found in the foothills of the Andes, in the inter-Andean valleys, and less commonly in the Amazon Basin. As illustrated in Figure 21, the number of taxa in each of these countries ranges from four to six, with Colombia and Ecuador most diverse. Perhaps the most remarkable biogeographical feature of this whole area is the occurrence of five endemic taxa, which, excluding *Z. caracasana* subsp. *weberbaueri* and *Z. andina*, comprise the most highly advanced species in *Zapoteca*, each with a large number of derived morphological characters (i.e., *Z. aculeata*, Ecuadorean Andes; *Z. microcephala*, Median Valley of the Magdalena River; and *Z. amazonica*, Amazonian Peru). Outside this area, diversity is much lower, with one or two taxa occurring within Guyana, Brazil, Paraguay, and northern Argentina (Fig. 21). Within this large region, however, there are two extra-Andean endemic species: *Z. filipes*, restricted to the Brazilian states of Goiás and Minas Gerais, and *Z. scutellifera*, found in the states of Amazonas, Pará and Rondônia, Brazil, and in the departments of El Beni and Santa Cruz, Bolivia.

Zapoteca species are predominantly segregated geographically and/or ecologically, although a

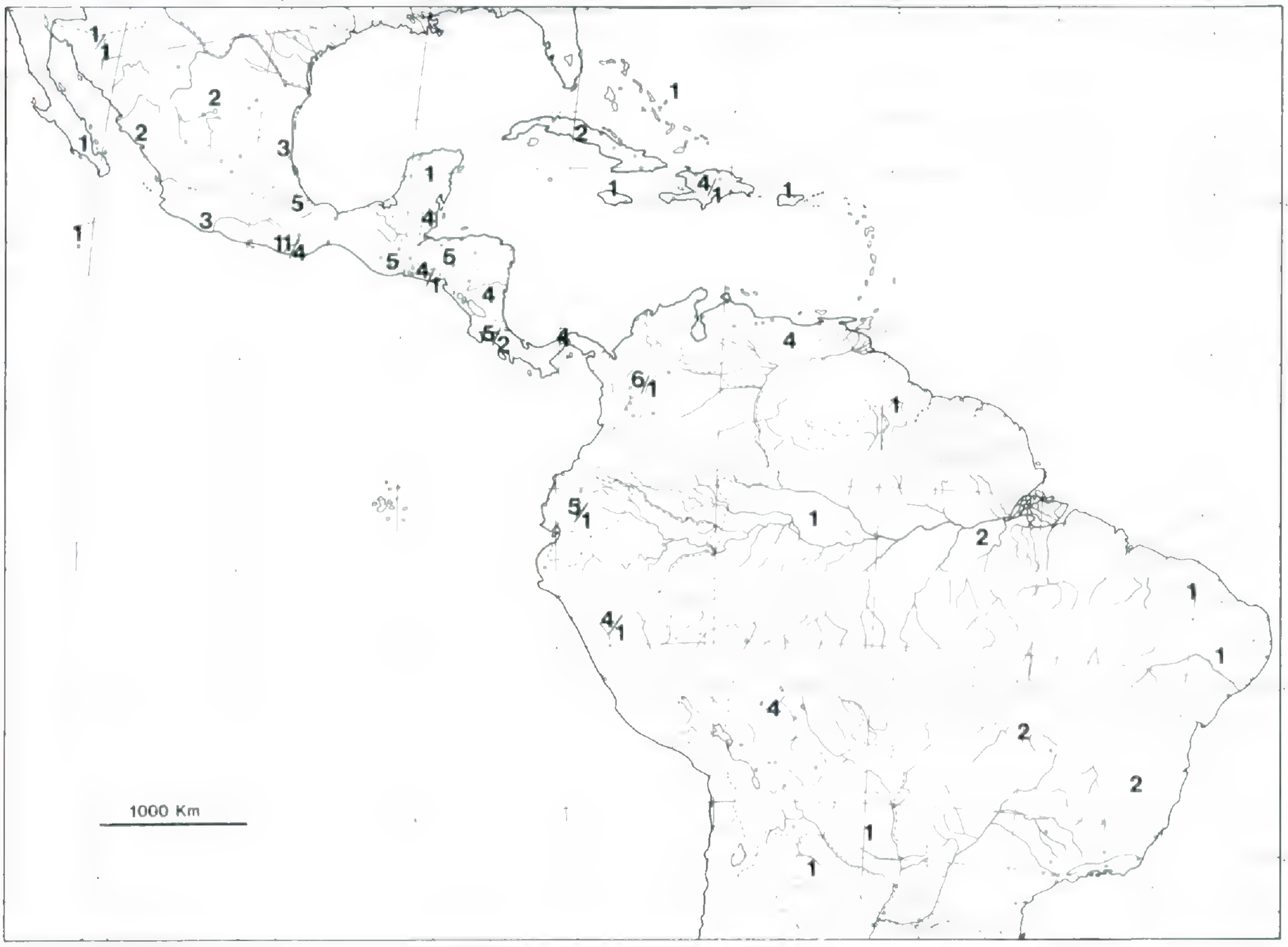


FIGURE 21. Number of *Zapoteca* species and subspecies per country. Mexican regions and Brazilian states are treated as separate units. Total number of taxa/endemic taxa.

number of cases of gross geographical overlap are known. However, only a few records of true sympatry exist: in the District of Tlacolula, Oaxaca, plants of *Z. alinae* (*H. Hernández & Ramírez 942*) have been found intermixed with plants of *Z. formosa* subsp. *rosei* (*H. Hernández & Ramírez 943*); in this same area of Oaxaca, *Z. formosa* subsp. *formosa* has occasionally been found growing alongside *Z. formosa* subsp. *rosei* (*H. Hernández & Torres 216*, *217* and *Magallanes 111*, *113*). Also, in the tropical deciduous forest of El Chorreadero, Chiapas, *Z. lambertiana* (*Breedlove 39694*, *H. Hernández & Ramírez 891*) and *Z. portoricensis* subsp. *portoricensis* (*Breedlove 11889*) have been collected; however, it is unclear whether these are narrowly sympatric.

There are some presumed hybrids. For example, in southern Guatemala and in southern Mexico, a number of collections provide evidence for extensive hybridization between *Z. portoricensis* subsp. *portoricensis* and *Z. tetragona*; in southern Puebla and northern Oaxaca, some plants with characters intermediate between *Z. media* and *Z. formosa* likewise suggest hybridization. In Guerrero populations of *Z. formosa* subsp. *formosa* and *Z. formosa* subsp. *rosei* come into close proximity, and there are a number of collections of probable hybrid origin.

The predominance of allopatric distributions and the apparent rarity of hybrids in *Zapoteca* suggest that hybridization has played an insignificant role in the evolution of the genus. The few cases of strict sympatry may represent secondary contact of previously differentiated populations. It could be hypothesized that speciation in *Zapoteca* has primarily resulted from genetic differentiation of geographically isolated populations.

There are wide disjunctions in the distribution of *Z. formosa* subsp. *formosa* in South America, from northern Colombia and Venezuela to Bolivia, southeastern Brazil, and Paraguay (Fig. 44). As elaborated below, its distribution was probably continuous across the Amazon Basin during the cool-dry phases of the Pleistocene, when a drier and presumably more suitable environment for this subspecies was widespread (Ab'Sáber, 1982; Absy, 1982; Bigarella & Andrade-Lima, 1982; van der Hammen, 1982; Prance, 1982). *Zapoteca scu-*

tellifera is closely related and is known from a few disjunct populations in the Amazon Basin (Fig. 44). Specialized characters in *Z. scutellifera* (e.g., scutelliform extrafloral nectaries, scandent habit) and its presumed edaphic specialization suggest that it was probably derived from *Z. formosa* subsp. *formosa*. *Zapoteca scutellifera* could have been derived from populations of *Z. formosa* subsp. *formosa* that became isolated after the return to the present-day, warm-wet climatic conditions.

This pattern, along with the patchy distributions of dry-forest species like *Z. lambertiana* and *Z. mollis*, supports Gentry's (1979, 1982) theory of reverse refuges. This theory assumes that the present discontinuities in the distribution of the dry forests (dry forest refuges) coupled with the existence of geographically restricted, morphologically differentiated dry-area populations, result from a shift towards more mesic conditions after the climatic deterioration in the Quaternary.

A second example of possible allopatric speciation in *Zapoteca* involves the two members of the highly specialized subg. *Amazonica*: *Z. microcephala* and *Z. amazonica*. *Zapoteca microcephala* is restricted to the Middle Magdalena River Valley, whereas *Z. amazonica* occurs in Amazonian Peru (Fig. 47). These two species, which are obviously closely related, probably differentiated as a consequence of a vicariance event caused by the uplift of the northern Andes, which reached their present elevation at the beginning of the Pleistocene some three million years ago (van der Hammen, 1982).

Additional evidence suggesting an allopatric model of speciation for *Zapoteca* is the relatively common occurrence of closely related taxa displaying contiguous or nearly contiguous distributions. This distribution pattern is shown by closely related species, such as *Z. tetragona* and *Z. andina* (Figs. 40, 42), and by virtually all the subspecies in the genus (Figs. 36, 39, 41).

Reproductive Biology

During the past few years a considerable body of data has accumulated on the diverse reproductive mechanisms of the Mimosoideae (Simpson et al., 1977; Kenrick & Knox, 1982; Koptur, 1983, 1984; Knox & Kenrick, 1983; Hopkins, 1984; Bernhardt, 1983). Entomophily was probably the original mode of pollination in the subfamily, as indicated by the presence of apparently insect, probably hymenopteran, pollinated mimosoid inflorescences in the Middle Eocene Claiborne Formation, Tennessee (Crepet & Dilcher, 1977), and in the Oligocene of the Texas Gulf Coast (Daghlian et al., 1980), and also by the wide distribution of this pollination system in the subfamily. It has been suggested (Raven & Polhill, 1981; Polhill et al., 1981) that Mimosoideae were already differentiated from the other subfamilies by the start of the Eocene (54 m.y. B.P.). Entomophily is widespread in tribe Mimoseae (e.g., *Desmanthus*, *Leucaena*, *Mimosa*, *Prosopis*), which is generally considered to be the basal tribe of the Mimosoideae. Furthermore, most species of *Acacia* (Acacieae) are insect-pollinated (Bernhardt, 1983; pers. obs.); however, bird pollination has been derived secondarily in some Australian species of this genus (Ford & Forde, 1976; Bernhardt, 1983; Kenrick et al., 1983). In contrast, *Parkia* (Parkieae) is primarily bat-pollinated (Baker & Harris, 1957; Hopkins, 1984), although a few species are pollinated by insects (see discussion in Hopkins, 1984).

High-energy pollination systems such as those involving hawkmoths, birds, and bats are concentrated among the genera of the more advanced tribe Ingeae (Cruden et al., 1976; Arroyo, 1981; Koptur, 1983; Hernández, 1986a; unpublished obs.). In the Ingeae, the transition from low-energy insect pollination to high-energy systems, which demand greater allocation to nectar and pollen, is associated with inflorescence modifications. For instance, connation of the staminal filaments to form a tube and increase in number and length of the filaments made it possible for the flowers to hold larger quantities of nectar necessary to satisfy the energy requirements of larger, homothermic pollinators. Similarly, changes in periodicities of nectar and aroma production, nectar quality, and timing of anthesis have enabled the plants to adjust to the physiological and behavioral characteristics of particular pollinators.

Mimosoideae have a number of additional reproductive traits that make them extremely interesting from an ecological and evolutionary point of view. Guinet (1969, 1981) discussed in detail that the most conspicuous feature of mimosoid pollen is the occurrence of permanent units of dispersal in the form of tetrads, octads, and polyads throughout the subfamily. Such units of pollination presumably provide the plants with a selective advantage in reproduction. As has been demonstrated for *Acacia* species (Kenrick & Knox, 1982; Knox & Kenrick, 1983), a single pollen unit is able to fertilize all the ovules in the ovary. Another widespread feature of the mimosoid inflorescences that is important in the breeding systems of the species is the occurrence of female sterile flowers. Viewed in an evolutionary perspective, these reproductive phenomena have great potential as characters on

which to base phylogenetic interpretations. Published reports concerning the reproductive biology of the species here assigned to *Zapoteca* are virtually nonexistent, and the present chapter is intended to provide an account, based on my own observations, of some of the reproductive features of these plants.

METHODS

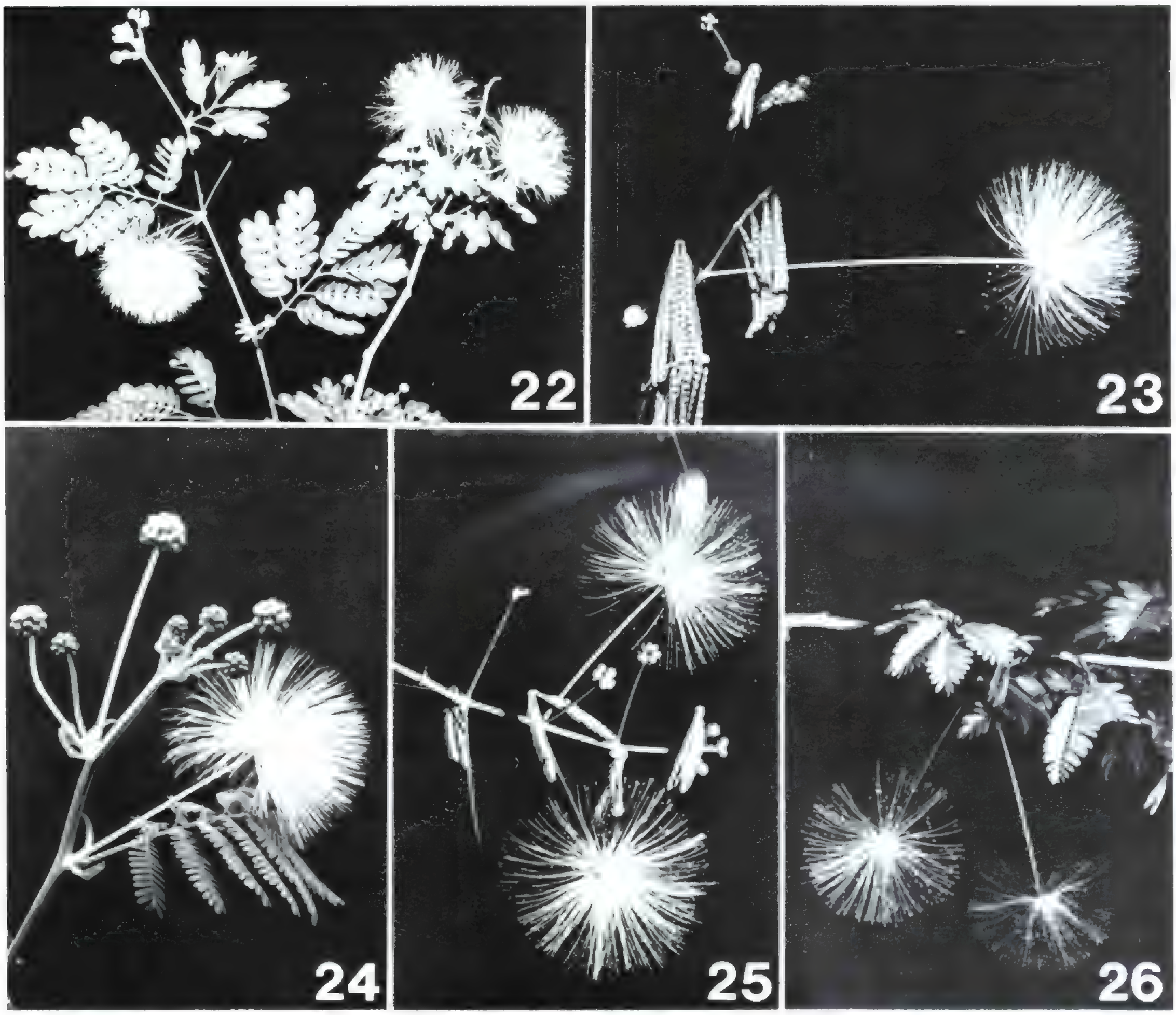
Nectar volumes were measured with calibrated micropipets, and sugar concentrations were determined using a temperature-compensated Erma hand refractometer. In a few cases, when the flowers were very small, a syringe was used to extract the nectar from the staminal tubes. All measurements were made in the greenhouse early in the morning in order to estimate the total amount of nectar produced per flower. Between four and ten individuals per population were examined. It is quite possible that the results in Table 6 might be lower volumes than would be found in the wild, since it has been shown that nectar volumes and sugar concentrations may be significantly lower in plants growing in greenhouse pots compared with wild plants (Cruden & Hermann, 1983). However, they allow species comparisons.

Field observations on flower visitors were carried out continuously during the first three to five hours of anthesis. Since all *Zapoteca* species flower at night, the behavior of flower visitors was observed with the aid of a head lamp. In most cases, visitors were successfully collected with insect nets. Insect voucher specimens are deposited in the Entomological Collection at the Instituto de Biología, UNAM.

The number of ovules per gynoecium was determined by squashing fixed ovaries in a drop of Alexander's stain (Alexander, 1969); the ovaries were examined with a compound light microscope within 15–20 minutes after staining. Sex expression was characterized for each population by dissecting fixed flowers and counting the proportion of hermaphrodite and female-sterile flowers in each inflorescence. Self-compatibility was assessed on plants growing in the greenhouse using the techniques outlined by Bawa (1974). Pollinations were accomplished using a fine brush within four hours of the beginning of anthesis, once the anthers were dehiscent. Anther dehiscence was determined by touching the anthers with a clean microscope slide; a large number of polyads on the slide revealed open thecae. Given the small size of the flowers, the inflorescence was taken as a unit in the pollination treatments. In every population, a determined number of inflorescences were artificially cross- and self-pollinated, and several additional inflorescences were left untreated (open) to test for autogamy. Due to the difficulty involved in emasculating the delicate flowers of *Zapoteca*, the possibility of apomixis was not tested. For the cross-pollinations, mixtures of polyads from several individuals were used whenever possible. For the self-pollinated inflorescences, the pollen donor was taken from the same inflorescence or from other inflorescences in the same individual; therefore, a great number of these flowers were geitonogamously pollinated. Treated inflorescences were marked with hanging labels. As the greenhouse was insect-free, inflorescence manipulation was minimized by avoiding the need to bag inflorescences. Sample size varied from two to nine individuals per population. After each treatment, brushes and hands were sterilized with ethanol. Since pod abortion occurs in *Zapoteca* species at several stages of pod development, the resulting pods were counted only if they matured fully. Seed set was estimated in every population by calculating the average number of fully developed seeds in mature pods.

FLOWERING PHENOLOGY

Although it is difficult to characterize the phenological behavior of a given species throughout its range, I shall attempt to draw some generalizations about the flowering patterns in *Zapoteca*. This discussion is based primarily on species restricted to Mexico and Central America. In wide-ranging species such as *Z. tetragona*, flowering times vary from one region to another. This species, which usually grows in secondary vegetation derived from lowland tropical wet forests, flowers mostly during the dry season; nevertheless, in the Mexican state of Morelos, where a more seasonal climate exists, the populations flower primarily during the rainy season. *Zapoteca portoricensis* subsp. *flavida*, which grows in wet habitats, also flowers during the dry season. By contrast, the species growing in drier habitats (thorn forests, tropical deciduous forests, and tropical semideciduous forests) tend to flower predominantly during the second half of the rainy season (e.g., *Z. formosa*, *Z. lambertiana*, *Z. media*, *Z. alinae*). The species from drier areas have shorter, more synchronized flowering periods than species living in wetter habitats (e.g., *Z. amazonica* and *Z. tetragona*), which continue to produce flowers for longer periods. Finally, *Z. portoricensis* subsp. *portoricensis*, which generally grows in montane mesophyllous forests (terminology following Rzedowski, 1978), also flowers in the wet season.



FIGURES 22–26. Inflorescences of *Zapoteca* species at anthesis; all photographs were taken at night. 22. *Z. formosa* subsp. *formosa* (right) and *Z. formosa* subsp. *rosei* (left) (*H. Hernández 216*, *217*, respectively).—23. *Z. portoricensis* subsp. *portoricensis* (*H. Hernández 948*).—24. *Z. tetragona* (*H. Hernández 956*).—25. *Z. media* (*H. Hernández 951*). 26. *Z. tehuana* (*H. Hernández 950*). All collections at MEXU and MO.

A possible explanation for this differential flowering pattern is that in wet areas excessive rains may have destructive effects on the delicate inflorescences of *Zapoteca* and may reduce the activity of potential pollinators (Janzen, 1967). I observed the devastating effects of rain on inflorescences of several *Zapoteca* species in wet and dry forests. These effects are clearly reduced in areas of less precipitation.

As far as I have observed, species of *Zapoteca* display two distinct flowering strategies. Most species (e.g., *Z. formosa*, *Z. media*, *Z. portoricensis*, *Z. tetragona*) have a very generalized flowering behavior. Here regular numbers of inflorescences open every night over several months. By contrast, *Z. alinae* exhibits a more specialized strategy. Individuals of this species intermittently produce relatively large numbers of inflorescences on scattered nights throughout its flowering period, from July to September. This specialization is similar to the "multiple-bang" strategy described by Gentry (1974) for tropical Bignoniaceae. It differs, however, in that the flowering is not synchronized among the different individuals that make up a given population of *Z. alinae*. One possible adaptive value of this strategy is that these flowering bursts produce conspicuous visual and olfactory stimuli, thus increasing the chances of pollinator attraction.

THE INFLORESCENCE AS THE UNIT OF POLLINATOR ATTRACTION

Species of *Zapoteca* always have their flowers arranged in compact, homomorphic, capitate inflorescences, which act as units of attraction (Figs. 22–26). In each flower, the numerous elongate

TABLE 6. Volume and sugar density of nectar in selected species of *Zapoteca*. All collections in MO. H = author's collections.

Taxon	Collection Data	Volume (μl) $\bar{x}$ (±S.D.)	Sugar density (%) $\bar{x}$ (±S.D.)
Z. alinae	Mexico, Oxaca, *H-949*	< 1	17.27
Z. formosa	Mexico, Jalisco, *H-230*	< 1	13.9
Z. lambertiana	Mexico, Chiapas, *H-891*	< 1	
Z. portoricensis	Mexico, Tamaulipas, *H-146*	< 1	14.8
Z. portoricensis	Mexico, Veracruz, *H-948*	1.04(0.8)	18.43(3.4)
Z. tetragona	Mexico, Veracruz, *H-956*	3.05(2.0)	19.83(2.5)
Z. tetragona	Mexico, Veracruz, *H-960*	5.12(2.0)	20.32(3.2)

filaments, which give the inflorescences their attractive powder puff aspect, are fused basally, forming a tube in which nectar accumulates.

Anthesis and the process of flower presentation. Field and greenhouse observations have shown that species of *Zapoteca* display predictable flowering mechanisms. All members of the genus exhibit nocturnal anthesis and a remarkable synchrony in floral behavior during flower presentation. Usually the filaments of all the flowers in a head become erect in a springlike fashion late in the evening (ca. 17:00–18:00 hours), during the last two hours of daylight. Subsequently, when the filaments are completely erect (ca. 18:00 19:00 hours), the anthers dehisce. At about the same time, nectar secretion begins, accompanied by production of a sweet aroma. Each head remains functional for only one night and the filaments wilt within approximately the first two hours of daylight.

Attractants: filament color and aroma. With few exceptions, the color of the staminal filaments is constant in a given species of *Zapoteca* and thus is of taxonomic value. The filaments may be white (e.g., *Z. alinae*, *Z. portoricensis*, *Z. tetragona*), red-purple (*Z. lambertiana*), or a combination of white in the basal half and pink or red-purple in the distal half (e.g., *Z. amazonica*, *Z. caracasana*, *Z. media*). The widespread *Z. formosa* shows some geographical variation in filament color, and the recognition of subspecies within this species is based in part on this feature. This character is nearly always stable at the population level in *Z. formosa*; however, in a population observed in eastern Oaxaca a mixture of plants with white (*H. Hernández & Torres 216*) and white/pink filaments (*H. Hernández & Torres 217*) turned up. Similarly, individual plants of *Z. tehuana* with either white or white/pink filaments were observed in a greenhouse population (*H. Hernández 950*). The flowers of all species of *Zapoteca* produce a delicate, sweet fragrance, which presumably functions as does the color of the stamens in attracting pollinators (Brantjes, 1978).

Rewards: nectar production. The amount of nectar produced by individual flowers varies among the species of *Zapoteca*, perhaps as a function of the size of the nectaries and the physical capacity of the staminal tube. As shown in Table 6, all the species analyzed except *Z. tetragona* produce quantities of nectar below or slightly above one microliter (μl) per flower. In the two populations of *Z. tetragona* (the species with essentially the most massive flowers in the genus), the nectar volumes were substantially higher (Table 6). The nectar of *Zapoteca* species has rather low sugar concentrations, ranging from 13.9 to 20.3%. The nectar volumes and sugar concentrations in the flowers of *Zapoteca* species reported here agree with those reported by Opler (1983) and Baker & Baker (1983) for settling moth-pollinated flowers.

FLOWER VISITORS

Inflorescences of *Zapoteca* species are well adapted for pollination by moths. Field observations conducted in ten different populations representing five species of *Zapoteca* clearly showed that the flowers are consistently visited and pollinated by a variety of settling moths, mostly of families Noctuidae, Pyralidae, and Geometridae (Table 7). The moths were usually observed to visit the inflorescences after some nectar had accumulated in the staminal tube and after floral fragance was detected by observers. Moths usually landed in the upper part of the inflorescence, where the underside of their bodies contacted the anthers and the stigmatic surfaces (Fig. 27). Moths generally moved from one part of the inflorescence to another in search of nectar, and the length of time they remained on an inflorescence was often up to 20 30 minutes. Aside from the species in Table 7, a substantial

number of species of smaller moths were excluded because they were considered to be ineffective pollinators.

Many species of moths were observed to exploit the nectar of *Z. tetragona* (population J) illegitimately. They extracted nectar by standing on the peduncles without touching the anthers and stigmas. However, five species of moths were observed to visit the flowers of this species legitimately; among these, *Palpita flegia* (Fig. 27) and *Diaphania jairusalis* may be considered the primary pollinators on the basis of their abundance (Table 7). The color of the wings of these two species is strikingly similar to that of the white filaments of *Z. tetragona*. In contrast, the nectar robbers, along with the few other occasional pollinators, have wings with a variety of color patterns.

Although inflorescences of *Zapoteca* species display the typical syndrome of characteristics associated with hawkmoth pollination (Faegri & van der Pijl, 1979), hawkmoths were rarely observed as visitors. During the course of my observations, only two hawkmoths were observed, one visiting the flowers of *Z. formosa* (population C) and one on *Z. lambertiana* (population J). A possible explanation for this is that the individual flowers produce rather small amounts of nectar, making the visits energetically unprofitable to hawkmoths. According to Opler (1983) and Haber & Frankie (in press), hawkmoth-pollinated flowers usually produce much greater amounts of nectar (maximum available nectar $\bar{x}$ = 130.5 μl; Opler, 1983) compared with the relatively smaller amounts found in the flowers of *Zapoteca* (Table 6).

Two unidentified species of crab spiders (Araneida: Thomisidae) were observed preying on moths visiting the inflorescences of *Z. formosa* subsp. *rosei* and *Z. portoricensis* subsp. *portoricensis*. These light-colored spiders would be inconspicuous on the inflorescences of *Zapoteca* species, where their cryptic coloration permits them to prey on flower visitors. Given that the spiders occurred in very low numbers, their negative impact on the reproductive potential of the plants is probably unimportant. Such an association between crab spiders and flowers has been reported by other authors (Wickler, 1968; Kevan, 1972; Gertsch, 1979, and others).

FIGURE 27. *Palpita flegia* visiting the flowers of *Zapoteca tetragona* in a population near Catemaco, Veracruz (*H. Hernández 799*, MEXU, MO).

POLLINATION RELATIONSHIPS

All species of *Zapoteca* have very delicate, cup-shaped stigmas, and as indicated elsewhere (Hernández, 1986a), the concave area of receptivity is so narrow that only a single 16-grained polyad can be held (see fig. 11 in Hernández, 1986a). Considering that the likelihood of a pollen unit reaching the stigma is directly proportional to the receptive area of the stigma (Cruden & Miller-Ward, 1981), one might anticipate that the chances of successful pollination in species of *Zapoteca* are rather low. As pointed out earlier, however, the settling moths that were recorded visiting species of *Zapoteca* normally remain on the inflorescences for considerable periods of time. The chances of successful pollination are also affected by the time the body of a particular pollinator makes contact with the stigma; therefore, the relatively long visits by settling moths compared with hawkmoths might be understood as a compensating factor to the intrinsic low chances of a polyad reaching the stigma in *Zapoteca*.

The average number of ovules per ovary in *Zapoteca* species is highly correlated with the number of pollen grains in the polyads. As indicated in Table 8, the number of ovules ranges from 11 to 15 and never exceeds the number of grains in the polyad (16). Therefore, the ratio of grains per polyad to the number of ovules is close to one,

TABLE 7. Pollinators of *Zapoteca* species. Capital letters designate populations and the figures in parenthesis the numbers of individuals collected from inflorescences. FORMO = *Z. formosa*, LAMB = *Z. lambertiana*, MEDIA = *Z. media*, PORTO = *Z. portoricensis*, TETRA = *Z tetragona*.

Pollinator	FORMO	LAMB	MEDIA	PORTO	TETRA
Noctuidae					
Rhizagrotis malefida Guenee				H(1)	
Heliothis zea Boddie			E(1)		
Autographa biloba Steph.				I(1)	
Pseudoplusia includens Walker			E(1)		
Prodenia ornithogalli Guenee					J(1)
Gonitis edetrix Guenee		D(1)			
Leucania sp.					J(1)
unidentified spp.				G(1)	J(4)
Pyralidae					
Pilocrocis tripunctata Fabr.	B(1)	D(1)			
Conchylodes platinalis Guenee	B(3)	D(1)			
C. alcifera Hampson	B(4)				
Diaphania jairusalis Walker		D(2)			J(4)
Palpita flegia Cramer	C(1)			I(1)	J(35)
Lineodes mesodonta Dyar	A(1)				
unidentified spp.	B(2)			H,I(10)	
Geometridae					
Mecoceras aulis Druce				G(1)	
Ametris mitocris Cramer	B(2)				
Apicia medusa Druce				F,G(3)	J(2)
unidentified spp.	A,B(3)	D(1)		F,G(2)	
Arctiidae					
Agaraea longicornis H. Sch.		D(5)			
Ctenuchiidae					
Psilopleura vittata Walker				G(1)	

Populations. A. Mexico, Michoacán (*H-185*); B. Mexico, Jalisco (*H-230*); C. Mexico, Oaxaca (*H-207*); D. Mexico, Chiapas (*H-891*); E. Mexico, Hidalgo (*H-133*); F. Mexico, Hidalgo (*H-122*); G. Mexico, Hidalgo (*H-136*); H. Mexico, Veracruz (*H-154*); I. Mexico, Veracruz (*H-165*); J. Mexico, Veracruz (*H-799*). Collections in MEXU and MO.

ranging from 1.04 in *Z. formosa* to 1.45 in *Z. alinae*. An almost identical situation has been reported by Kenrick & Knox (1982) and Knox & Kenrick (1983) for species of *Acacia*. In this genus, however, the range of variation in the ratio of number of grains to number of ovules is somewhat broader than in *Zapoteca*, but the species of *Acacia* with 16-grained polyads also have ratios approaching one (Kenrick & Knox, 1982). In *Calliandra* (sensu Hernández, 1986a) ratios also vary around one; however, in several species of the highly advanced ser. *Racemosae*, the number of ovules greatly exceeds the eight grains found in the polyads (Nevling & Elias, 1971; Cruden, 1977; Hernández, 1984, and unpublished results). This reduction in the ratio of number of grains to number of ovules is probably associated with the highly modified fungiform, discoid, or capitate stigmas found in *Calliandra*, which have a greater area of receptivity than the representatives of the other genera mentioned (Hernández, 1986a).

BREEDING SYSTEMS

Sex expression. In species of *Zapoteca*, sex expression and genetic self-incompatibility systems are the primary components of the breeding system that affect pollination and fertilization. Analysis of the inflorescences of several species has shown that morphologically expressed andromonoecy resulting from abortion of the gynoecium is widespread in the genus (Table 9). Functionally male flowers with an aborted gynoecium are irregularly distributed among populations. Generally, individual plants have inflorescences with varying proportions of hermaphroditic and functionally male flowers; however, individuals with inflorescences composed entirely of hermpahroditic flowers are not uncommon.

TABLE 8. Average number of ovules in ovaries of *Zapoteca* species. Collections in MO. H = author's collections.

Species	Collection	Number of Ovules $\bar{x} \pm$ S.D. (N)	Polvad Ovule Ratio
Z. alinae	*H-206*	11.0 ± 1.02 (46)	1.5
Z. formosa subsp. *formosa*	*H-954*	13.6 ± 0.71 (37)	1.2
Z. formosa subsp. *rosei*	*H-185*	13.3 ± 0.77 (32)	1.2
Z. formosa subsp. *rosei*	*H-209*	15.4 ± 0.50 (11)	1.0
Z. formosa subsp. *rosei*	*H-217*	12.3 ± 0.80 (30)	1.3
Z. formosa subsp. *rosei*	*H-230*	13.7 ± 0.65 (40)	1.2
Z. formosa subsp. *mollicula*	*H-218*	11.2 ± 0.94 (27)	1.4
Z. lambertiana	*H-147*	14.1 ± 0.86 (33)	1.1
Z. media	*H-192*	12.5 ± 0.68 (38)	1.3
Z. portoricensis subsp. *portoricensis*	*H-122*	14.2 + 0.62 (30)	1.1
Z. portoricensis subsp. *portoricensis*	*H-165*	12.1 ± 0.70 (35)	1.3
Z. tetragona	*Neill 5388*	13.4 ± 0.71 (32)	1.2

The ratios of hermaphroditic to female-sterile (functionally male) flowers change during the course of the flowering season in individual populations. Therefore, the figures provided in Table 9, which correspond to a single stage of the flowering cycle in each population for which data are enumerated, do not reflect the actual proportions of the two flower types.

Table 9 indicates a great amount of intra- and interspecific variation in sex expression among the species of *Zapoteca*. The ratios of hermaphroditic to female-sterile flowers varied from 0.4 to 77.5 in the studied populations. Thus far, I have been unable to establish any correlation between the nature of sex expression and factors such as altitude, frequency of pollinator visitation, and incompatibility systems. Nevertheless, a planned, detailed analysis of temporal variation in the ratios of hermaphroditic to female-sterile flowers in natural populations would probably contribute significantly to understanding this reproductive phenomenon.

Incompatibility systems. The results of the incompatibility experiments show that of the five species studied, only *Z. tetragona* is clearly genetically self-incompatible, as indicated by the inability of the flowers to set pod following the self- and open-pollinated treatments in the two populations (Table 10). In contrast, plants of the two populations of *Z. formosa* that were studied proved to be genetically self-compatible, and those from one additional population (*H. Hernández 959*) were partially autogamous, judging from the fact that a relatively high proportion of the untreated inflorescences (20%) set pods (Table 10).

Incompatibility studies on the remaining species (*Z. media*, *Z. alinae*, *Z. portoricensis*) were inconclusive but suggested that these species are genetically self-compatible, at least in part. In both *Z. media* and *Z. alinae*, pod set was significantly higher in untreated (open) inflorescences compared with the self-pollinated inflorescences (Table 10), although this may have been partly the result of mechanical damage to floral parts during the hand pollinations. In *Z. portoricensis*, the difference in pod set between the untreated and the self-pollinated inflorescences was less pronounced; however, the few pods that were derived from the hand self-

TABLE 9. Sex expression in flowers of *Zapoteca* species. Collections in MO. H = author's collections.

Taxon	Collection	Percent of ♂ Flowers (N)	♀ ♂ Ratio
Z. alinae	*H-206*	27.0 (211)	2.7
Z. formosa subsp. *rosei*	*H-209*	72.2 (54)	0.4
Z. formosa subsp. *rosei*	*H-217*	1.4 (144)	71.0
Z. formosa subsp. *rosei*	*H-230*	14.0 (107)	6.1
Z. formosa subsp. *mollicula*	*H-218*	1.3 (157)	77.5
Z. lambertiana	*H-165*	2.1 (143)	46.7
Z. lambertiana	*H-891*	1.5 (133)	66.5
Z. media	*H-192*	2.9 (175)	33.3
Z. portoricensis subsp. *portoricensis*	*H-165*	6.0 (181)	15.6
Z. tetragona	*Neill 5388*	11.0 (100)	8.1

TABLE 10. Results of incompatibility experiments in *Zapoteca* species. Pod set (%) is given as the percent of treated inflorescences (N) that developed at least one pod, and seed set as the average number of fully developed seeds per pod. SI = genetically self-incompatible; SC = genetically self-compatible. Collections in MO. H = author's collections.

Taxon	Collection	Individuals	Treatment	Pod Set %	Pod Set N	Average Number of Pods Per Inflorescence	Seed Set	Conclusion
Z. alinae	*H-949*	9	Open	8.5	71	2.3	9.3	SC
			Self	0.4	239	1.0	4.0	
			Cross	6.5	186	1.3	7.8	
Z. formosa	*H-954*	4	Open	0	98	—	—	SC
			Self	5.6	53	1.3	4.5	
			Cross	18.2	11	2.0	3.8	
Z. formosa	*H-959*	3	Open	20.0	20	1.0	5.6	SC
			Self	5.3	19	1.0	2.0	
			Cross	66.7	6	1.7	6.5	
Z. media	*H-951*	4	Open	15.6	167	1.4	6.9	SC
			Self	0	80			
			Cross	18.9	58	1.5	5.3	
Z. portoricensis	*H-948*	7	Open	2.7	221	1.3	2.8	SC(?)
			Self	1.6	122	2.0	0	
			Cross	13.2	128	2.2	4.7	
Z. tetragona	*H-956*	2	Open	0	24	—	—	SI
			Self	0	43			
			Cross	33.3	12	1.8	11.2	
Z. tetragona	*H-960*	4	Open	0	18	—	—	SI
			Self	0	14			
			Cross	100	1	1	8	

pollinated inflorescences developed no mature seeds. In contrast, the pods set in untreated inflorescences produced a relatively low average number of seeds per pod (2.8), which indicates some degree of genetic self-compatibility in *Z. portoricensis*. Presuming that there was no accidental transfer of polyads among the untreated plants, the individuals of all three species tested were at least in part genetically self-compatible.

CONCLUDING REMARKS

Zapoteca species are relatively consistent in several important features of reproductive biology. All the observed species exhibit nocturnal anthesis. The small flowers are organized in compact, capitate inflorescences, and there is remarkable synchrony among the flowers of a given capitulum in all the stages of flower presentation and in the patterns of aroma and nectar production. This suggests that ecologically the spherical capitula act as units of attraction. The particular combination of morphological and behavioral features in the inflorescences of species of *Zapoteca* is well adapted for pollination by settling moths. Moreover, the remarkable morphological correlation between the stigmas and the polyads in *Zapoteca*, along with the specific behavior of its pollinators, reflects a highly organized reproductive system. Reduction in the number of ovules in each ovary increases the reproductive efficiency of these species, giving a single polyad the potential of fertilizing all the ovules in an ovary. In other words, the high correlation between the number of ovules in an ovary and the number of pollen grains in a polyad is a reflection of the high probability of the ovules being fertilized by the pollen grains contained in a single polyad.

According to Arroyo (1981), about half of the genera of Mimosoideae are andromonoecious; this condition occurs especially in taxa with capitate inflorescences. The results presented in Table 9 indicate that andromonoecy is widespread in *Zapoteca*, and the presence of a vestigial gynoecium in functionally male flowers strongly suggests that andromonoecy is derived from hermaphroditism in

this genus. Several models have been developed to explain the selective basis for the evolution of andromonoecy (e.g., Heithaus et al., 1974; Ruiz & Arroyo, 1978; Primack & Lloyd, 1980; Dulberger et al., 1981; Bertin, 1982). The following discussion will be centered on the possible factors playing a selective role in the evolution and maintenance of female sterility in *Zapoteca*.

In species of *Zapoteca*, as in the majority of plant species (Stephenson, 1981), the number of flowers produced by individual plants is significantly larger than the number of pods reaching maturity. In natural populations, the vast majority of the capitula abscise after anthesis. Even in the remaining capitula, only a fraction of the fertile ovaries develop into pods. For instance, in a population of *Z. tetragona* near Catemaco, Veracruz (*H. Hernández 800*), it was estimated that each capitulum produced an average of 2.04 (± 1.3; N = 425) mature pods, comparatively few in relation to the average number of hermaphroditic flowers per head (17.8 ± 2.7; N = 100) in the same population. Thus, most of the flowers produced in *Zapoteca* serve only as attractive elements in the inflorescence and as pollen donors (Stephenson, 1981, and references therein).

Rather than being limited by pollinator activity, the inflorescences of the *Zapoteca* species are probably affected by energetic, and certainly by physical–architectural constraints, which set the upper limit for maximum pod production. In this connection, Stephenson (1981) reviewed the available evidence and suggested that "an upper limit to the number of pods that set is usually determined by resources rather than the number of morphologically female flowers, and . . . natural levels of pollination exceed pod set in many species." In this context, the adaptive nature of female sterility can be understood: given the lower pod set in *Zapoteca* populations, a reduction in the number of functional gynoecia in an inflorescence would not reduce pod set. Vestigial gynoecia must be energetically less expensive to produce than the larger, functional ones. Thus, andromonoecy should be understood as a system that makes more efficient use of reproductive energy without compromising pollinator attraction (Ruiz & Arroyo, 1978; Primack & Lloyd, 1980; Arroyo, 1981; Bertin, 1982) and as a means to increase the pollen ovule/ratios and, consequently, the chances of pollination.

Cytogenetics

According to Goldblatt (1981), the genera of the Ingeae consistently have basic chromosome numbers of $x = 13$, with the exception of the highly specialized *Calliandra*, in which $n = 11$ and $n = 8$ have been reported (see review in Hernández, 1986a). As discussed earlier, differential patterns in chromosome numbers and in morphological characteristics provided the justification for the segregation of *Zapoteca* from *Calliandra* sensu Bentham.

Methods

Somatic chromosome counts were obtained from actively growing root tips taken from germinating seeds or mature plants in the Experimental Greenhouse at the Missouri Botanical Garden. The methods employed were those of Goldblatt & Gentry (1979). Root tips were pretreated in 0.003 M hydroxyquinoline for about seven hours at refrigerator temperatures, then fixed in 3:1 absolute ethanol:glacial acetic acid for one minute. The roots were hydrolyzed in 10% HCl for six minutes, then squashed and heated in formic-lacto-propionic orcein.

Results

Chromosome numbers in *Zapoteca* were reported in Hernández (1986a). Counts for two additional taxa are included here (Table 11). All cytologically investigated species of *Zapoteca* have $n = 13$ (Figs. 28, 29), which is consistent with the basic numbers reported for the remaining genera of Ingeae (Goldblatt, 1981). Chromosome numbers are now known for seven of the 17 species recognized in this monograph, all of which are members of subg. *Zapoteca*. The species of the remaining subgenera remain unknown cytologically.

Systematic Treatment

Taxonomic history of *Zapoteca*

Analysis of several critical characters of the neotropical species of *Calliandra*, a large genus currently undergoing revision (Forero, 1984; Hernández, 1984), showed that *Calliandra* sensu Bentham apparently is polyphyletic. Consequently, the species of Bentham's *Calliandra* ser. *Laetevirentes* were recognized as generically distinct (Hernández, 1986a). For this natural group I proposed the name *Zapoteca*.

Mimosa portoricensis Jacq. (= *Zapoteca portoricensis*) and *M. caracasana* Jacq. (= *Z. caracasana*) were the first species to be published of what is now *Zapoteca*. They were described in 1791 on the basis of material collected by the Austrian bo-

TABLE 11. Chromosome numbers in *Zapoteca*.

Taxon	2*n*	Reference or Collection
Z. alinae	26	Mexico, Oaxaca: (Hernández, 1986a)[1]
Z. caracasana subsp. *weberbaueri*	26	Colombia, Valle: *Johnson 2494-82* (MO)
Z. formosa subsp. *formosa*	26	Mexico, Oaxaca: (Hernández, 1986a)
Z. formosa subsp. *formosa*	26	Mexico, Yucatán: (Hernández, 1986a)
Z. media	26	Mexico, Hidalgo: (Hernández, 1986a)
Z. portoricensis subsp. *flavida*	26	Mexico, Veracruz: *H-793* (MO, MEXU)
Z. portoricensis subsp. *portoricensis*	26	Mexico, Veracruz: (Hernández, 1986a)
Z. tehuana	26	Mexico, Oaxaca: (Hernández, 1986a)[2]
Z. tetragona	26	Mexico, Veracruz: (Hernández, 1986a)
Z. tetragona	26	Mexico, Veracruz: (Hernández, 1986a)
Z. tetragona	26	Costa Rica, Cartago: (Hernández, 1986a)

[1] Referred to as sp. nov. (1)
[2] Referred to as sp. nov. (2)

tanical expeditions to the West Indies and Venezuela during the second half of the eighteenth century. These species, as well as a few that have been described in *Acacia*, were treated by Bentham as *Calliandra* ser. *Laetevirentes*. Bentham (1875) recognized 12 species in ser. *Laetevirentes*, five of which he described in previous papers (Bentham, 1840, 1844). Seven of the 12 species included by Bentham in ser. *Laetevirentes* are maintained in the present treatment.

The species in Bentham's ser. *Laetevirentes* were treated by Britton & Rose (1928) as *Anneslia* group *Portoricenses* and group *Formosae*. They recognized 25 species within these groups, of which 11 were published as new. Ten of these 25 species are maintained in the present treatment, including two of the new species. Three additional species, all of them clearly recognizable as *Zapoteca*, were arbitrarily included by Britton & Rose under *Anneslia* group *Molliculae*. Britton & Rose's treatment is characterized by excessively narrow definitions of taxa, and their subdivisions are artificial. Britton & Rose studied only a fraction of the over 4,000 herbarium specimens that were available for the present study. *Calliandra* was conserved over *Anneslia* (Bunting, 1967; Hernández, 1986b) and, as a consequence, a number of names recognized by Britton & Rose required new combinations under *Calliandra* in recent regional floras. Since Britton & Rose's treatment, only five new species of *Zapoteca* have been published.

Zapoteca H. Hern., Ann. Missouri Bot. Gard. 73: 755–763. 1986. TYPE: *Zapoteca tetragona* (Willd.) H. Hern.

Ramose, erect, scandent, prostrate or subprostrate, glabrous or hairy, unarmed, shrubs, rarely small trees, rarely with spinescent stipules, the young branches terete or 4-angled. Phyllotaxy dis-

FIGURES 28, 29. Mitotic chromosomes of *Zapoteca*. 28. *Z. tehuana*, 2*n* = 26 (prometaphase) (*H. Hernández 950*).—29. *Z. tetragona*, 2*n* = 26 (metaphase) (*H. Hernández 675*). Collections at MEXU and MO. Scale bars = 5 μm.

tichous. Leaves bipinnate; petiole rarely with nectariferous glands, usually with a conspicuous adaxial channel; leaflets 1 to numerous pairs per pinna, opposite, sessile, usually membranous, rarely chartaceous or coriaceous, usually glaucous beneath, glabrous or hairy. Stipules usually conspicuous, leafy, rarely spinescent, persistent. Inflorescences capitate, pedunculate, densely flowered, axillary or organized in simple or compound pseudopanicles, with the peduncles solitary or fasciculate at distant nodes, homomorphic, heterogamic or homogamic. Flowers bracteate, sessile, actinomorphic, (4–)5(–6)-merous; calyx cup-shaped, dentate or denticulate, glabrous or hairy; corolla campanulate or infundibuliform, membranous, with the petals valvate in bud, usually revolute at anthesis; nectariferous disk present in all flowers; stamens ca. 30 60; filaments long-exserted, ca. 19–43 mm long, white, pink, red-purple, or a combination of two colors, the staminal tube included; anthers dithecal, dorsifixed, eglandular, each anther containing 8 polyads; polyads 16-grained, discoid, heteromorphic, usually with eccentric lens-shaped thickenings on the central cells; ovary 1, sessile or shortly stipitate, with ca. 10–15 ovules; style filiform, ca. 15–56 mm long in fertile pistils; stigma cup-shaped. Pods usually pendent, dry, membranous to coriaceous, linear, straight, rarely slightly curved, planocompressed, with the margins thickened, usually with constrictions in interseminal areas, the valves dehiscing elastically from apex to base. Seeds in 1 series, hard, ovoid to rhomboid, rarely ellipsoid, nonarillate, nonalate, usually with irregular or regular 90% pleurogram. Seedlings phaneroepigeal; cotyledons ephemeral, foliaceous, sessile, elliptic to elliptic-ovate; first and second eophylls opposite, the third and fourth alternate; leaflets thin, membranous. $x = 13$.

Distribution. Usually abundant in open sites derived from tropical deciduous forest, or in arid or semiarid, scrubby vegetation and wet evergreen forests, from southwestern United States and northern Mexico, from about latitude 32°30′N, southward through most of Mexico, Central America, West Indies, and part of South America, to northern Argentina at about latitude 27°30′S. Collections come from altitudes of 0 2,850 m.

Zapoteca consists of four subgenera, 17 species, and 11 subspecies. The following systematic treatment includes all the known taxa in the genus. The sequence of the taxa reflects approximate relationships.

Key to the Subgenera and Species of *Zapoteca*

1a. Pinnae 1-, rarely 2-jugate; leaflets usually larger, (1.5–) 2.2–22 cm long, chartaceous to coriaceous, 1 7 pairs per pinna, usually glabrous or ciliate; leaflet venation patterns strongly conspicuous on both surfaces.
  2a. Leaves with cup-shaped glands at the insertions of the pinnae and sometimes between the distal pairs of leaflets; leaflets grayish, olive-green or brown; polyads without lens-shaped thickenings; pods thickly membranous; Hispaniola ..... I. Subgenus *Nervosa* (1. *Z. nervosa*)
  2b. Leaves eglandular; leaflets usually green or olive-green; polyads with lens-shaped thickenings; pods coriaceous; Colombia, Ecuador, and Peru.
    3a. Stipules spinescent; leaflets 3–7 pairs per pinna, ovate-lanceolate, 1.5–6.3 cm long; capitula axillary; Ecuador ..... III. Subgenus *Aculeata* (15. *Z. aculeata*)
    3b. Stipules leafy; leaflets 1 1½ pairs per pinna, falcately lanceolate or falcately ovate-lanceolate, 7 22 cm long; capitula in simple or compound, elongate pseudopanicles; Colombia and Peru ..... IV. Subgenus *Amazonica*
      4a. Leaflets 1½ pairs per pinna, ciliate; stipules to 2 mm long; pseudopanicles simple; filaments white; erect shrubs; Colombia ..... 16. *Z. microcephala*
      4b. Leaflets 1 pair per pinna, glabrous or glabrate; stipules to 22 mm long; pseudopanicles compound; filaments white in the basal half and red-purple distally; scandent shrubs; Amazonian Peru ..... 17. *Z. amazonica*

1b. Pinnae 1 8-jugate; leaflets usually smaller, 0.4 4(5.9) cm long, membranous, rarely thinly chartaceous, 3 67 pairs per pinna, glabrous to densely pubescent; leaflet venation mostly inconspicuous (except *Z. tehuana*); *Z. filipes* and *Z. scutellifera* with somewhat conspicuous veins abaxially ..... II. Subgenus *Zapoteca*
  5a. Leaflets oblong-obovate to very widely obovate (except *Z. formosa* subsp. *gracilis* and occasionally subsp. *rosei* with elliptic to elliptic-oblong leaflets), usually 3–17 pairs per pinna.
    6a. Leaves without glands; stipules lanceolate to ovate-lanceolate, or linear-triangular, to 13 mm long; filaments white, red-purple, white in the basal half and pink distally, or white basally and red-purple distally; essentially erect shrubs; southern United States and northern Mexico to northern Argentina and West Indies ..... 12. *Z. formosa*
    6b. Leaves with scutelliform glands at the petioles, at the insertions of the pinnae, and sometimes between the distal pairs of leaflets; stipules linear-triangular, to 4 mm long; filaments white basally and pink distally; scandent shrubs; Brazil and Bolivia ..... 13. *Z. scutellifera*
  5b. Leaflets narrowly oblong to elliptic or lanceolate, oblong-ovate or oblong-lanceolate (except *Z. costaricensis* with the distal leaflets oblong-obovate), usually 5–67 pairs per pinna.

7a. Leaflets 2–2.7 cm long; stipules ovate to widely ovate, rounded to cordate at the base; Costa Rica ..... 11. *Z. costaricensis*

7b. Leaflets 0.4–2 cm long; stipules triangular to shallowly triangular, triangular-lanceolate, rarely ovate; Mexico to northern Argentina.

8a. Branchlets conspicuously 4-angled, at least in the younger parts.

9a. Filaments white; stipules triangular-linear to triangular-lanceolate, adpressed, without basal auricles, to 2.5 cm long; seeds with regular pleurograms; Mexico to Ecuador ..... 9. *Z. tetragona*

9b. Filaments white basally and red-purple distally; stipules triangular, descending or depressed, with 2 basal auricles, to 0.6 cm long; seeds with irregular pleurograms; Ecuador, Peru, and Bolivia ..... 10. *Z. andina*

8b. Branchlets terete or angled, but never as above (except some populations of *Z. portoricensis* subsp. *portoricensis*).

10a. Leaves with conspicuous, cylindrical glands on the petiole, at the points of insertion of the pinnae, and usually between the leaflets; Brazil ..... 5. *Z. filipes*

10b. Leaves without glands (except *Z. lambertiana* very rarely with minute glands between the proximal pairs of pinnae); Mexico to Brazil and Peru.

11a. Leaflets with the 1°, 2°, and 3° veins conspicuous showing the brochidodromous venation pattern, mostly thinly chartaceous; stipules to 2 mm long; southeastern Oaxaca ..... 14. *Z. tehuana*

11b. Leaflets with the venation patterns mostly inconspicuous, essentially membranous; stipules usually larger than above, to 14(–17) mm long; Mexico to Brazil and Peru.

12a. Pinnae predominantly 1–2(–3)-jugate.

13a. Filaments white basally and red-purple distally; leaves glabrous, pubescent or pilose; stems usually well branched near the base; southern Texas and northern Mexico to Puebla and Oaxaca ..... 2. *Z. media*

13b. Filaments white; leaves glabrous or nearly so; stems usually branched far above the base; Oaxaca ..... 3. *Z. alinae*

12b. Pinnae predominantly 3–7-jugate, rarely 1–2-jugate.

14a. Pods membranous, with the surface usually undulate, glabrous; filaments red-purple; northeastern to southeastern Mexico ..... 4. *Z. lambertiana*

14b. Pods usually more rigid than above (thick membranous), with the surface relatively flat, glabrous, puberulent, densely villous, canescent or pubescent; filaments white, or white basally and red-purple distally; Mexico to Peru.

15a. Filaments white basally and red-purple distally; leaflets 0.4–1.1 × 0.1–0.3 cm; capitula commonly arranged in pseudopanicles, sometimes axillary; subprostrate or prostrate shrubs ..... 8. *Z. caracasana*

15b. Filaments white; leaflets 0.4–2 × 0.1–0.6 cm; capitula commonly axillary, sometimes arranged in pseudopanicles; erect or scandent shrubs.

16a. Pods glabrous or occasionally puberulent; Mexico to South America, and West Indies ..... 6. *Z. portoricensis*

16b. Pods densely villous with long tawny hairs; Costa Rica and Panama ..... 7. *Z. mollis*

I. Zapoteca subg. **Nervosa** H. Hern., subg. nov. TYPE: *Zapoteca nervosa* (Urban) H. Hern.

Caules dense lignosi cortice fissurato. Foliorum pinnae unijugae, nectaria glabra vel sub-glabra; foliola 3–4-juga in pinna utraque, mediocria coriacea, ordinatione venarum manifeste conspicua; stipulae foliosae. Capitula axillaria. Pollinia sine tumoribus lenticularibus. Legumina crasso-membranacea glabra.

Stems densely wooded; the bark fissured. Pinnae 1-jugate, with nectaries, glabrous or nearly so; leaflets 3–4 pairs per pinna, moderately large, coriaceous, with a very conspicuous venation pattern; stipules leafy. Capitula axillary. Polyads without lens-shaped thickenings. Pods thickly membranous, glabrous.

This subgenus comprises a single species, *Z. nervosa*, which has a combination of characters unlike that of any other known species of the genus.

1. Zapoteca nervosa (Urban) H. Hern., comb. nov. *Pithecellobium nervosum* Urban, Symb. Ant. 2: 257. 1900. *Calliandra nervosa* (Urban) Urban & E. Ekman, Ark. Bot. 22A(8): 27. 1928. *Jupunba* (?) *nervosa* (Urban) Britton & Rose, N. Amer. Fl. 23: 27. 1928. TYPE:

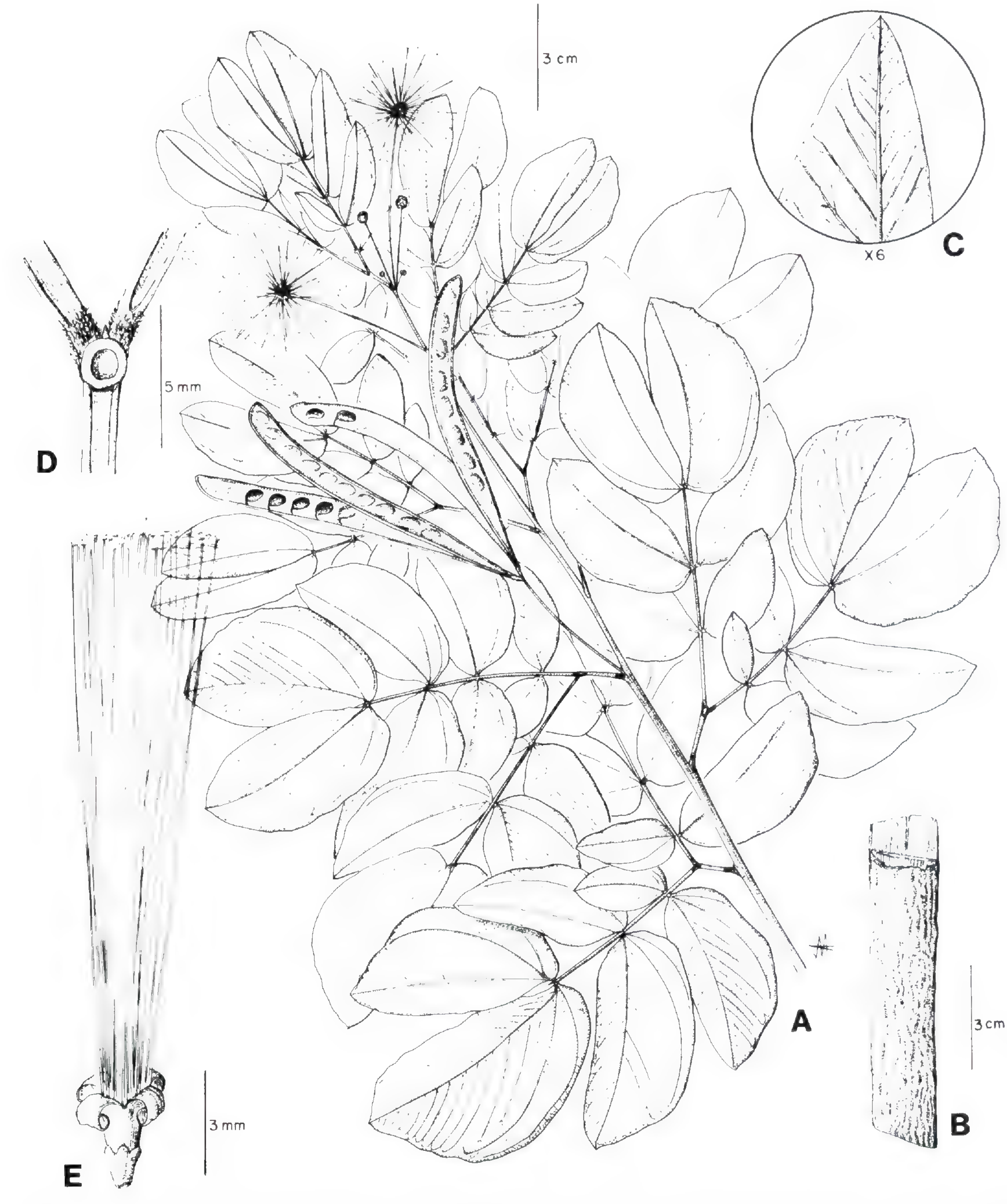


FIGURE 30. *Zapoteca nervosa*. —A. Branchlet with inflorescences at anthesis, and dehisced pods. —B. Detail of the primary stem showing fissured bark. C. Detail of leaflet venation at leaflet apex. —D. Petiolar gland. —E. Flower. (From *Ekman 8959* (US) and *Ekman 8914* (MO); stem and flowers from *Mejia et al. 35509* (MO).)

Haiti: ad Corail, 1,200 m, Dec. 1894, *Picarda 1362* (lectotype, here designated, NY (fragment)). Aside from the fragment at NY, which consists of several leaflets clearly identifiable as this species, there appear to be no additional extant duplicates of Picarda's collection in any of the herbaria where his collections are presumably deposited (B, BR, L, and S). Figure 30.

Shrubs to 3 m high, with slender stems ca. 2 cm diam., the bark fissured; branchlets terete, grayish-brown, smooth, glabrous. Pinnae consistently 1-jugate; petioles terete, with a conspicuous

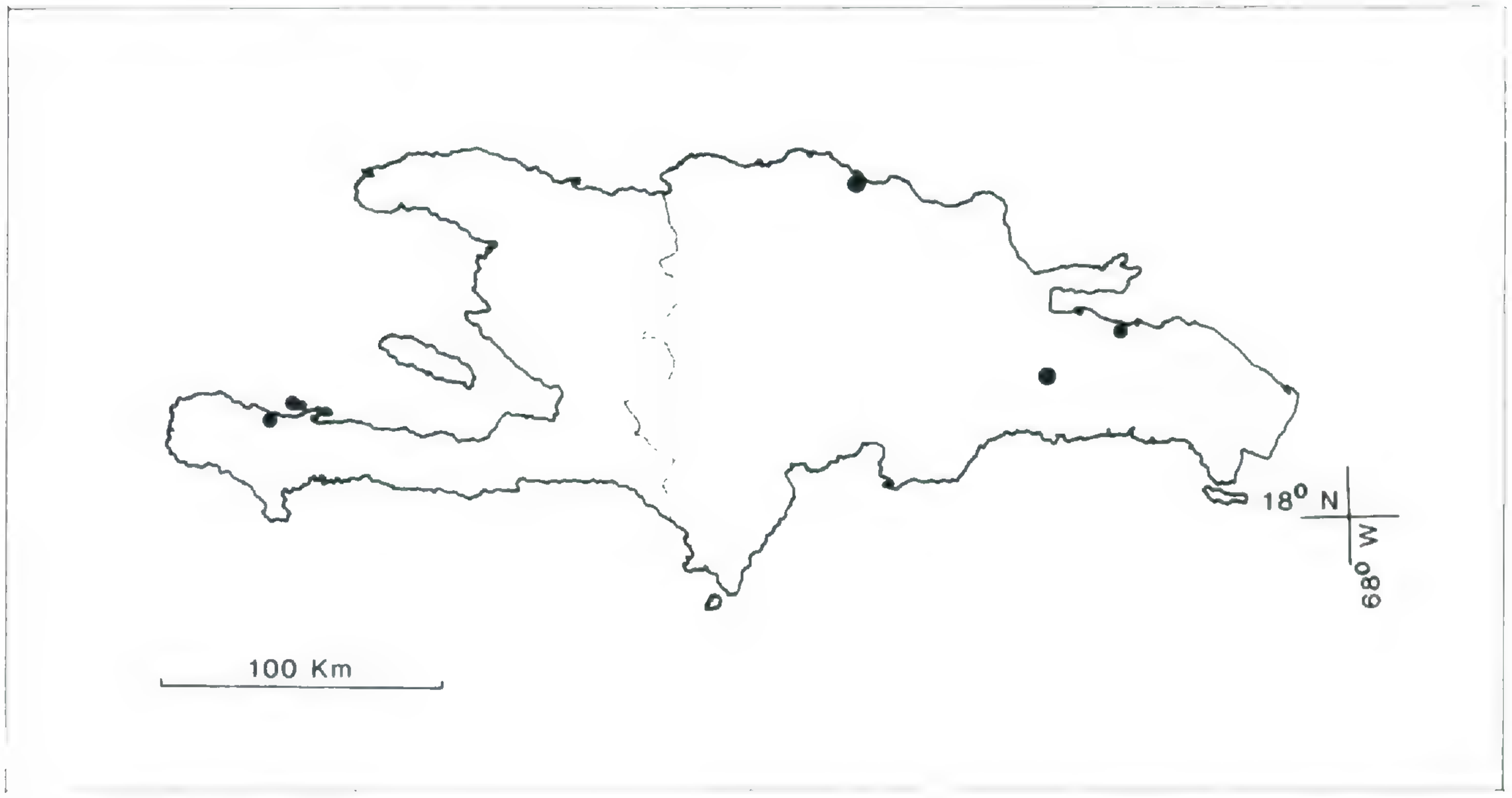


FIGURE 31. Distribution of *Zapoteca nervosa*, Hispaniola.

channel in the adaxial surface, 5–13 mm long, glabrous; rachillae 2.2–7.2 cm long, glabrous, sometimes sparsely villous in the extremes between the leaflets; extrafloral nectaries located at the insertion of the pinnae and occasionally between the distal pairs of leaflets, elevated, cup-shaped, ca. 1 mm diam. or less; leaflets 3–4 pairs per pinna, with the proximal anterior one reduced in size, ovate to lanceolate, sometimes rhombic, the base oblique, the apex obtuse to rounded, sometimes acute, rarely truncate, usually mucronulate, the distal leaflets 2.7–6.8 × 0.9–3.8 cm, the proximal ones smaller, all coriaceous, usually grayish adaxially and olive-green to brown abaxially, glabrous, occasionally floccose abaxially at the base, ciliate when developing; primary, secondary, and higher-order veins very conspicuous on both surfaces; stipules reduced to small scales, deltate, 1 mm long or less, glabrous, rarely villous. Capitula always axillary; peduncles solitary or fasciculate, filiform, (1.6–)3.7–5.5 cm long at anthesis, glabrous, occasionally sparsely pubescent. Calyx denticulate to subtruncate, 1 mm long, glabrous or sparsely pilose, the teeth very shallowly triangular, ciliate; corolla infundibuliform, 4–5 mm long, glabrous, the lobes ovate-lanceolate; filaments purple, the staminal tube ca. 2 mm long; ovary ca. 1.5 mm long, glabrous, the stipe ca. 1 mm long. Pods ca. 8.5–13.5 cm long, rounded at apex, rostellate, thickly membranous, glabrous.

Distribution (Fig. 31). Endemic to Hispaniola, where it has been collected at several scattered localities, mainly on karst limestone, including Ile Grande Cayemite, Haiti; 0–250 m.

Common name. Pti-gaiac (Haiti).

Additional specimens examined. HISPANIOLA ISLAND. HAITI: Grande Cayemite, Anse à Macon, *Ekman 8914* (MO); Grande Cayemite, Anse du Nord, *Ekman 8959* (F, GH, LL, NY, US); Grande Cayemite, *Everman 284* (A, F, GH, MO, NY, US). DOMINICAN REPUBLIC: Civ. Santo Domingo, Cordillera Central, Prov. de Samaná, Los Haitises, Boca del Infierno, *Ekman 15423* (A, GH, US); Los Haitises, near the mouth of Barracote River, S of Samaná Bay, *Liogier 14510* (NY, US); Pilancón, Bayaguana, *Liogier & Liogier 18868* (F, NY); El Choco, Cabarete, Puerto Plata, *Liogier & Liogier 26501* (MO, NY); Prov. Seibo, Parque Nacional Los Haitises, *Mejía et al. 35509* (MO).

This species, the only member of subg. *Nervosa*, is highly isolated morphologically and geographically from the rest of the genus. Its general features and the manner of dehiscence of the pods are identical to those of subg. *Zapoteca*. These characters, as well as the overall characteristics of its inflorescences and flowers, justify its inclusion within *Zapoteca*. It is readily recognized by having fissured bark, extrafloral nectaries, conspicuous eucamptodromous/brochidodromous leaflet venation patterns, large, coriaceous, grayish leaflets, and denticulate to subtruncate calyces, all of which are unique in the genus except the extrafloral nectaries. The stems of *Z. nervosa*, which are characterized by having dense hardwood, differ from those of subg. *Zapoteca*, in which the wood usually is comparatively softer and lighter. Of particular

interest, however, is the absence of the prominent lens-shaped structures in the central cells of the 16-celled polyads (Guinet, pers. comm.), which, as pointed out above, are important diagnostically in the genus. This plesiomorphic character state in *Z. nervosa*, in association with its distinctive morphology, suggests that this species has been separated from the main *Zapoteca* stock since early in the evolution of the genus.

II. Zapoteca subg. **Zapoteca.** TYPE: *Zapoteca tetragona* (Willd.) H. Hern.

Calliandra Benth. ser. *Laetevirentes* Benth., London J. Bot. 3: 97. 1844; Benth., Trans. Linn. Soc. London 30: 542. 1875.
Calliandra Benth. sect. *Eucalliandra* Griseb., Fl. Brit. W. Ind. 224. 1860; Cat. Pl. Cub. 83. 1866, pro parte.
Calliandra Benth. sect. *Pseudacacia* Griseb., Fl. Brit. W. Ind. 224. 1860.
Anneslia Salisb. "group *Formosae*" Britton & Rose, N. Amer. Fl. 23: 49. 1928.
Anneslia Salisb. "group *Molliculae*" Britton & Rose, N. Amer. Fl. 23: 49. 1928.
Anneslia Salisb. "group *Portoricenses*" Britton & Rose, N. Amer. Fl. 23: 49. 1928.

Caules plerumque molliter lignosi, cortice fere laevi. Pinnae (1)2 8-jugae, petiolo plerumque sine nectariis, glabris vel dense pubescentibus, foliolis (2)3–67-jugis in utraque pinna, saepe parvis interdum majusculis, membranaceis raro tenui-chartaceis, ordinatione venarum inconspicua; stipulae foliosae. Capitula axillaria vel in pseudopaniculis simplicibus vel compositis disposita. Pollinia tumoribus lenticularibus praedita. Legumina crasso-membranacea, glabra vel dense pubescentia. Semina pleurogramate praedita.

Stems usually with soft wood; bark essentially smooth. Leaves glabrous to densely hairy, the pinnae (1–)2–8-jugate, the leaf-stalk usually without nectaries, leaflets (2–)3–67 pairs per pinna, usually small, occasionally moderately large, membranous, rarely thinly chartaceous; venation usually inconspicuous; stipules leafy. Capitula axillary or organized in simple or compound pseudopanicles. Polyads with lens-shaped thickenings. Pods thick-membranous, glabrous to densely pubescent. Seeds with pleurogram.

This subgenus is the most diversified evolutionary line within *Zapoteca*, comprising 13 species and 11 subspecies. It ranges from the southern United States and northern Mexico to northern Argentina.

2. Zapoteca media (M. Martens & Galeotti) H. Hern., Ann. Missouri Bot. Gard. 73: 755–763. 1986. *Acacia media* M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 10: 316. 1843. *Anneslia media* (M. Martens & Galeotti) Britton & Rose, N. Amer. Fl. 23: 66. 1928. *Calliandra media* (M. Martens & Galeotti) Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 309. 1929. TYPE: Mexico. Hidalgo: Hacienda de Guadalupe près Mextitlán, 5,000 ft., June–Oct. 1840, *Galeotti 3362* pro parte (lectotype, BR; Hernández, Ann. Missouri Bot. Gard. 73: 757. 1986). There are four specimens labeled *Galeotti 3362*, but they are not duplicates of the specimen at BR and consequently are not treated as isolectotypes. The specimen at K is from "ravines de Regla," whereas the ones at G and P are from "ravines de Real del Monte"; a fragment at F lacks locality information. As McVaugh (1978) pointed out, evidence indicates that Galeotti's Mexican collections were sorted systematically and then arbitrarily numbered after they arrived in Europe. In this way, three collections made on different dates were brought together under number *3362* after they were interpreted to represent the same species.

Calliandra angelica Benth., London J. Bot. 3: 100. 1844; Benth., Trans. Linn. Soc. London 30: 544. 1875. *Feuilleea angelica* (Benth.) Kuntze, Revis. Gen. Pl. 187. 1891. TYPE: Mexico. Hidalgo: ravines de Regla, *Galeotti 3362* pro parte [lectotype here designated, K. The sheet at K, where Bentham worked, is the only sheet I have located of *Galeotti 3362* with the locality information specified by Bentham. As noted above, other sheets with this number (at BR, G, and P) have different locality data].
Calliandra coulteri S. Watson, Proc. Amer. Acad. Arts 17: 352. 1882. *Anneslia coulteri* (S. Watson) Britton & Rose, N. Amer. Fl. 23: 66. 1928. TYPE: Mexico. Coahuila: Soledad, 25 mi. southwest of Monclova, Sep. 1880, *Palmer 2129* [lectotype here designated, GH; isolectotypes K, US (fragment)].
Calliandra oaxacana Rose, Contr. U.S. Natl. Herb. 5: 193. 1899. *Anneslia oaxacana* (Rose) Britton & Rose, N. Amer. Fl. 23: 66. 1928. TYPE: Mexico. Oaxaca: granitic ledges, Tomellín Canyon, 4,000 ft., 10 July 1897, *Pringle 6734* (lectotype here designated, US no. 316706; isolectotypes, A, BM, F, GH, K, LE, MEXU, MO, NY, S, UC, US).

Shrubs 0.2–1.5(–3) m tall, the stems slender, usually branching at the base; branchlets terete, costate under magnification, glabrous to densely pubescent or pilose. Pinnae 1–2(–3)-jugate; petioles eglandular, terete, with a conspicuous channel in the adaxial surface, 0.7 4 cm long, glabrous to sparsely pubescent; rachis of 2-jugate pinnae (1) 2–12 mm long; rachilla 1 4.5(–7) cm long; leaflets

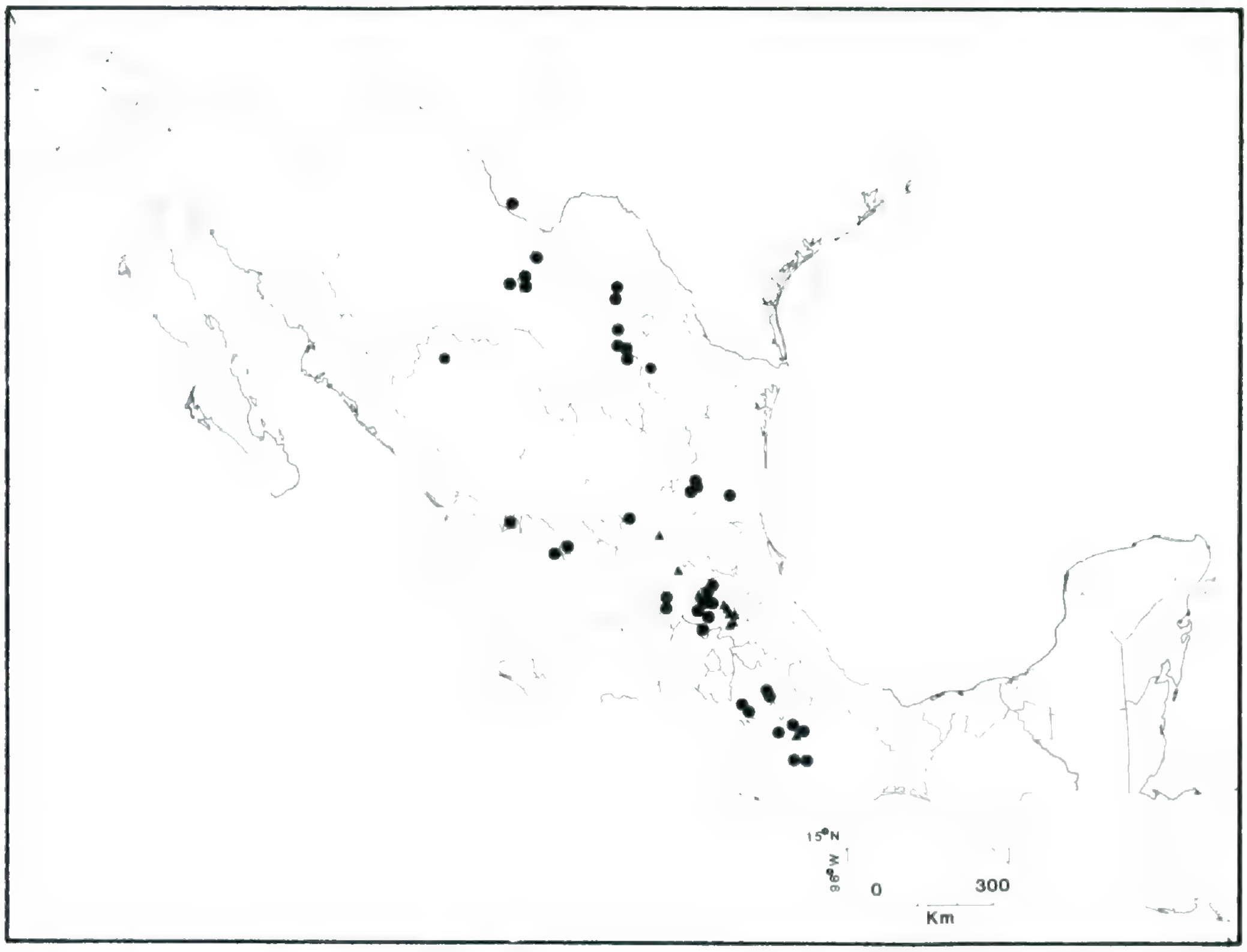


FIGURE 32. Distribution of *Zapoteca media*. Populations with essentially glabrous leaflets = dots; populations with pilose or pubescent leaflets = triangles.

(5–)7–17(–22) pairs per pinna, oblong to elliptic, oblique at the base, except the proximal pairs cuneate at base, acute to rounded at the apex, sometimes rostellate, 4–13 × 1 5.5 mm, membranous, glabrous to pubescent or pilose on both surfaces; leaflet venation usually inconspicuous; stipules leafy, lanceolate to ovate-lanceolate, rarely widely deltate, striate, (1–)2–7 mm long, glabrous to pubescent or pilose. Capitula axillary, rarely in short, terminal pseudopanicles; peduncles solitary or, more commonly, fasciculate at distant nodes, (1–)1.6–7(–10.5) cm long at anthesis, glabrous, sometimes pilose. Calyx ca. 1.5 2 mm long, glabrous or finely ciliate, rarely sparsely pilose, the teeth narrowly oblong, acute at apex; corolla campanulate, ca. 3–3.5 mm long, glabrous, the lobes narrowly elliptic, acute at apex; filaments ca. 20 mm long, white in the basal half, red-purple in the distal half, staminal tube ca. 1–1.5 mm long; ovaries ca. 1 mm long when fertile, occasionally 2 per flower, glabrous, shortly stipitate. Pods to 10 × 0.6 cm when mature, apex rounded to acute or truncate, rostellate, thickly membranous, glabrous, reticulate-veined. Seeds widely rhomboid to widely ovoid, flattened, ca. 4 × 3 mm; pleurogram irregular. Somatic chromosome number $2n = 26$.

Distribution (Fig. 32). This species occurs primarily on dry rocky calcareous slopes and along the margins of seasonal streams in thorn and tropical dry forests, and in arid scrublands. It ranges from the Chinati Mountains (Presidio County) of Texas south over the Mexican Plateau and the arid slopes of the Sierra Madre Oriental and, to a lesser extent, the Sierra Madre Occidental, where it has been collected at scattered localities. Its southern limit is in the districts of Teposcolula, Nochixtlán, and Cuicatlán of Oaxaca, about 17°30′N. Collections come from elevations of 1,000–2,150 m.

Common name. Cabellito de angel (Hidalgo).

Additional specimens examined. U.S.A. TEXAS: Presidio Co., S Chinati Mts., Mesquite Ranch, Tinaja Prieta Canyon, *Lott 64* (TEX). MEXICO. AGUASCALIENTES: 9 km NE Calvillo, sobre carretera a Aguascalientes, *Rzedowski & McVaugh 1245* (ENCB, MICH); road to Calvillo, W of Aguascalientes, near km 40, *McVaugh 18303* (MICH). CHIHUAHUA: vicinity of Fierro, 4 km SE Rancho Encinillas, *Stewart 773* (F, GH, LL, MEXU). COAHUILA: Sierra de Cruces, ca. 14 (air) mi. E Jaco, ca. 45 (air) mi. N Esmeralda (27°56′N, 103°42′W), *Henrickson 6876* (LL); Canyon of Tinaja Blanca, central mass of Sierra de las Cruces, W Sta. Elena Mines, *Johnston & Mueller 268* (GH, LL, MICH); La Favorita Ranch, N slope of Canyon Bonanza, SE Sierra Purísima, *Johnston et al.*

10300 (LL, MEXU, MO); Cañón de la Gavia, S Rancho de la Gavia, *Johnston et al. 12043* (LL, MEXU); 1.4 mi. N of Puente la Muralla, Hwy. 57 (199 mi. S of Piedras Negras), *Lewis 82* (LL); Múzquiz, Santa Ana Canyon, *Marsh 440* (F, GH, MEXU, TEX); Santa Rosa Mts., *Marsh 1457* (F, GH, TEX); Soledad, 25 mi. SW Monclova, *Palmer 2129* (GH, K, US); Cañón del Indio Felipe, ca. 28°33′N, Sierra Hechiceros, close to the Chihuahuan boundary, *Stewart 160* (GH); vicinity Rancho El Tule, 24 km N Castillón, close to the Chihuahuan boundary, *Stewart 512* (LL, GH); Sierra de la Gloria, Cañón Oscuro Chiquillo, entering C. Chilpitín from S near El Chilpitín (26°47′35″N, 101°17′50″W), *Wendt & Riskind 1699* (ENCB, LL, MEXU, MO). DURANGO: Mpio. Tepehuanes, Los Cedros, al SW de Tabahueto, camino de herradura La Hacienda-Topia, *Tenorio et al. 4207* (MEXU, MO); Mpio. de Rodeo, Mina La Amparo, 6 km NW de las Higueras, *Tenorio et al. 1268* (MEXU); Tabahueto (al Catorce), 196 km W de Tepehuanes, *Torres et al. 3553* (MEXU). GUANAJUATO: near Xichú, *Kenoyer 2254* (A). HIDALGO: Mpio. Tasquillo, 3 km N Puente Tasquillo del Río Tula, carr. a Zimapán, *Delgado et al. 1095* (ENCB, F, MEXU, NY); 3.5 km Zimapán, Ojo de Agua, *González Q. 2751* (MEXU); Paso del León, entre Atotonilco el Grande y Los Venados, *H. Hernández & Torres 129* (MEXU, MO); 12.6 km de Los Venados por carretera a Meztitlán, Barranca de Meztitlán, *H. Hernández & Torres 133* (MEXU, MO); Mpio. Zimapán, 8 km de Zimapán, en el Cañon de Tolimán, *H. Hernández & Torres 153* (MEXU, MO); Mpio. Taxquillo, cuesta de Texquedo, *R. Hernández 3644* (ENCB, MEXU); 5 km E Venados, *Medrano et al. 4160* (MEXU); Mpio. Cardonal, Cañada de La Piedra Cerrada, Barranca de Tolantongo, *Medrano et al. 9452* (MEXU, MO); Barranca de Metztitlán, *Medrano & Ortiz 10680* (ENCB, MEXU); km 275 276 on highway NE Jacala, *Moore & Wood 3986* (A, MEXU, MICH); Barranca de Tolimán, on road from Zimapán to Mina Loma del Toro, *Moore & Wood 4383* (A, MEXU, MICH); near Ixmiquilpan, *Rose et al. 8928* (GH, NY, US); cerca de Orizatlán, *Rzedowski 32210* (ENCB); Cerro del Junquillo, SW de Tasquillo, *Tenorio & Romero 505* (MEXU, MO); 15 km N Atotonilco, por carr. a Tampico, *Villaseñor et al. 128* (MEXU, TEX, WIS). NUEVO LEÓN: Huasteca Canyon, ca. 15 mi. (by road) SW Monterrey, *Ward 5724* (MICH). OAXACA: Dist. Etla, El Parián, *Conzatti 1558* (US); Distrito Nochixtlán, El Parián, *Conzatti 1929* (F); Dist. Huajuapan de León, 2 km S de Reforma, carr. Acatlán–Oaxaca, *A. García et al. 1454* (MEXU, MO); cerros SE Dominguillo, *Miranda 4747* (MEXU); Lagunas, *Orcutt 5236* (MO); Tomellín Canyon, *Pringle 6734* (ENCB, F, K, MEXU, NY, S, UC, US); Dist. Teposcolula, 5 km NE Chilapa de Díaz, *Rzedowski 34813* (ENCB); Totolapan, Río Tehuantepec, *Sousa 2686* (CAS). PUEBLA: highway 150 km 259 SE Mexico City, *Barr et al. 62* (MEXU); Mpio. Acatlán de Osorio, 3 km de Acatlán por carr. a Tehuitzingo, *H. Hernández & Torres 192* (MEXU, MO); Anicano, *Miranda 2921* (MEXU); Pollatzin, *Miranda 2948* (MEXU); San Luis Tultitlanapa, *Purpus 2667* (BM, F, GH, MO, NY, UC); Mpio. Cuicatlán, 15 km al S de Dominguillo, sobre la carretera a Oaxaca, *Rzedowski 34940* (ENCB); Tehuitzingo, El Pitayo, *Sousa 9804* (ENCB, MEXU). QUERETARO: camino a San Luis Potosí, km 10, *Arguelles 1400* (ENCB, MEXU); Mpio. Jalpan, arriba de Jalpan camino a Pinal de Amoles, *Fernández 3163* (MEXU); near Querétaro, *Rose & Rose 11160* (NY, US). SAN LUIS POTOSÍ: camino Río Verde San Ciro, *Rzedowski 4511* (MEXU). TAMAULIPAS: Sierra de San Carlos, vicinity of San Miguel, La Tamaulipeca, *Bartlett 10590* (F, MICH, US); El Madroño, 14 mi. SW Cd. Victoria along MEX 101 to Jaumave, *Dwyer et al. 42* (MO); Mpio. Jaumave, 7 km N de Magdaleno Aguilar, *Medrano et al. 9834* (MEXU); Jaumave-Nogales, *Rozynski 489* (B, F); San Lucas, *Viereck 654* (US). ZACATECAS: San Juan Capistrano, *Rose 3550* (US); 8 km NE Jalpa, *Rzedowski 14190* (ENCB); 5 mi. NE Jalpa, *McVaugh 18485* (MICH). CULTIVATED: U.S.A., Missouri, St. Louis, Missouri Botanical Garden, *H. Hernández 951* (MEXU, MO).

This morphologically plastic species is widespread in dry and semiarid regions of central and northern Mexico. It can be readily distinguished from its close relative *Z. alinae* primarily by having larger, white/purple-red filaments, usually shorter stature, and copious branching. In addition, the leaflets of *Z. media* are usually broader than those of *Z. alinae*. The relationship between these two species is discussed further under *Z. alinae*.

As shown in Figure 32, most of the known populations consist of plants with leaves glabrous or ciliate and very sparsely pilose on the rachis and rachilla. Plants with pubescent or pilose leaflets have been collected primarily in restricted areas in the southern part of its range (Oaxaca, Puebla, Hidalgo, Guanajuato, San Luis Potosí, and Tamaulipas). Most of the collections with hairy leaflets are concentrated west of Hidalgo (Fig. 32), where Galeotti collected the type. With the exception of a population from the Barranca de Tolimán, Mpio. Zimapán, Hidalgo, where plants with hairy and with glabrous leaflets have been collected (*H. Hernández & Torres 157*, *Moore 1383*), populations of plants with hairy leaflets seem to be geographically segregated from the glabrous ones.

The distributions of *Z. media* and *Z. formosa* approach one another closely in some areas of northern Oaxaca and southern Puebla, but individuals from these species are not known to grow together. There is evidence of hybridization, which results in morphological intergradation between the two. Plants collected in the area of Acatlán de Osorio and Tehuitzingo, Puebla (*H. Hernández & Torres 192*, *Miranda 2921*, *2918*, *Sousa et al. 9804*), and Cuicatlán and Nochixtlán, Oaxaca (*Conzatti 1929*, *Miranda 1717*) have characteristics (e.g., hairy leaflets, fewer pairs of leaflets per pinna, and broader leaflets) that differ from those typical of *Z. media* and tend to approximate those of *Z. formosa* subsp. *mollicula* or subsp. *rosei*.

3. Zapoteca alinae H. Hern., sp. nov. TYPE: Mexico. Oaxaca: Distrito Tlacolula, 6 km NE de Mitla por camino a Albarradas, 1,690 m, veg. matorral xerófito muy alterado, 1 Aug.

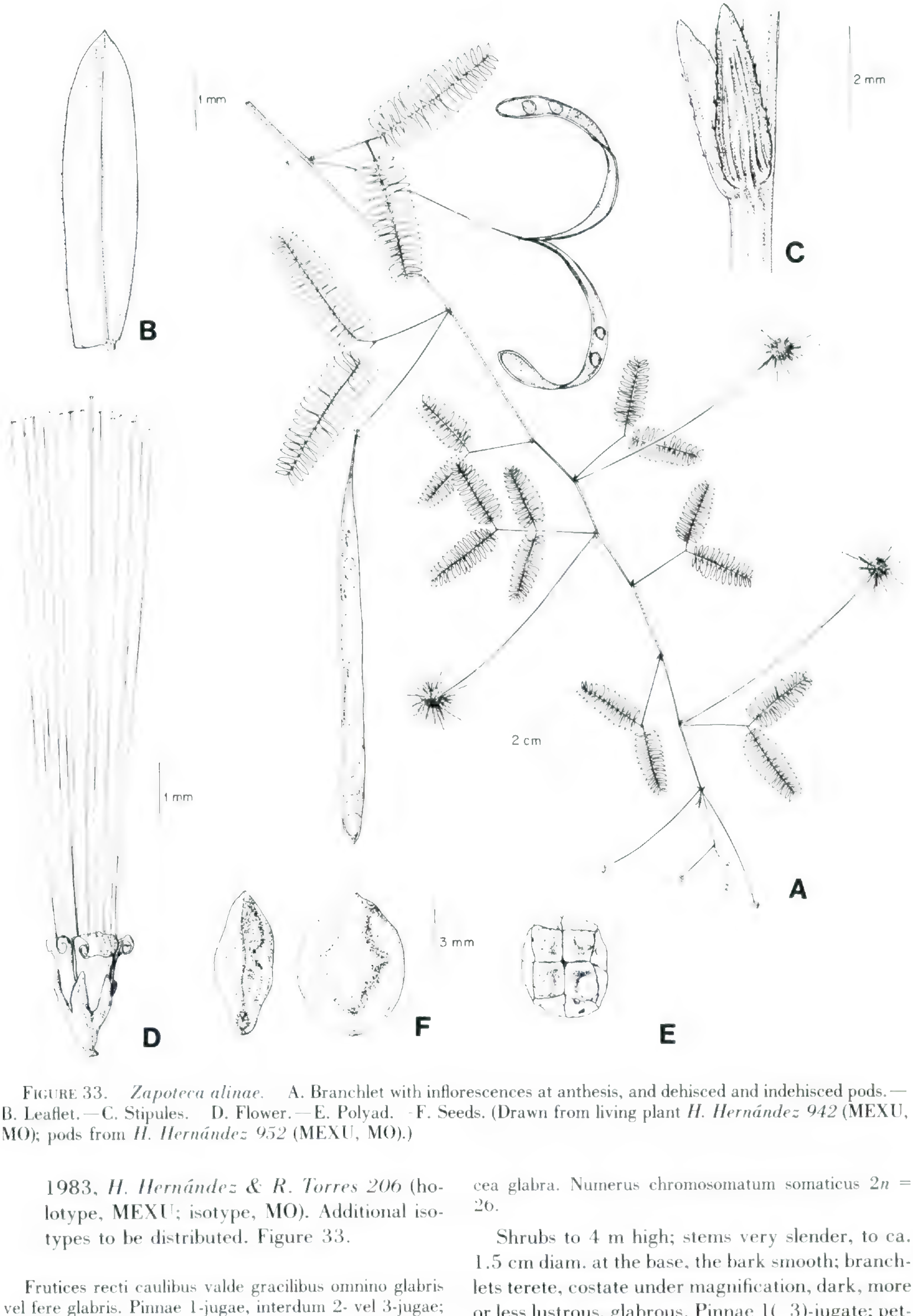


FIGURE 33. *Zapoteca alinae.* A. Branchlet with inflorescences at anthesis, and dehisced and indehisced pods.—B. Leaflet.—C. Stipules. D. Flower.—E. Polyad. -F. Seeds. (Drawn from living plant *H. Hernández 942* (MEXU, MO); pods from *H. Hernández 952* (MEXU, MO).)

1983, *H. Hernández & R. Torres 206* (holotype, MEXU; isotype, MO). Additional isotypes to be distributed. Figure 33.

Frutices recti caulibus valde gracilibus omnino glabris vel fere glabris. Pinnae 1-jugae, interdum 2- vel 3-jugae; foliola 16 19-juga in pinna utraque augusto-oblonga vel lanceolata, venatione inconspicua. Capitula axillaria raro in pseudopaniculis brevibus simplicibusque disposita. Flores filamentis albis praediti. Legumina crassa, membranacea glabra. Numerus chromosomatum somaticus $2n = 26$.

Shrubs to 4 m high; stems very slender, to ca. 1.5 cm diam. at the base, the bark smooth; branchlets terete, costate under magnification, dark, more or less lustrous, glabrous. Pinnae 1(3)-jugate; petiole eglandular, terete, 0.9–3.7 cm long, glabrous; rachis 3–10 mm long in leaves with 2 or more pairs of pinnae, glabrous; rachillae 1.7–4 cm long

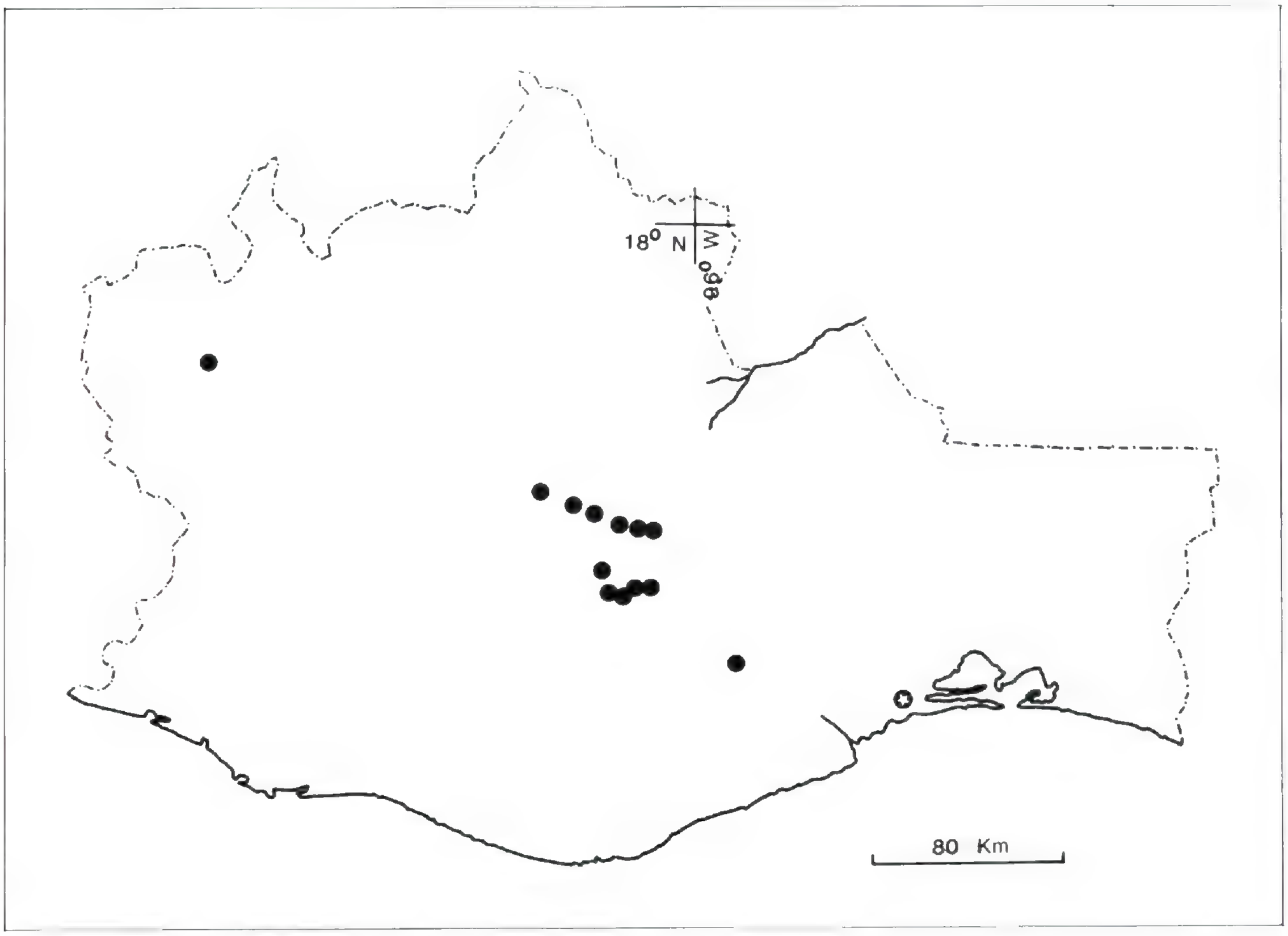


FIGURE 34. Map of Oaxaca, Mexico, showing the distribution of *Zapoteca alinae* (dots) and *Z. tehuana* (dot with star).

in well-developed leaves; leaflets 16–19 pairs per pinna, narrowly oblong to lanceolate, at base strongly oblique, at apex rounded or acute, usually mucronulate, 4 12 × 1–2.5 mm, membranous, glabrous, sometimes ciliolate; leaflet venation inconspicuous; stipules leafy, narrowly triangular to lanceolate, 2–3 mm long, glabrous. Capitula axillary, rarely also in simple pseudopanicles 1.5–4 cm long; peduncles solitary or fasciculate, filiform, 2.5–6.5 cm long at anthesis. Flowers ca. 15 25 per capitulum; the calyx ca. 2 mm long, the teeth ovate-lanceolate, acute at apex, mucronulate, glabrous; corolla campanulate, ca. 4 mm long, the lobes ovate to narrowly ovate, acute at apex, glabrous; filaments 15 20 mm long, white, the staminal tube ca. 1 mm long; ovaries ca. 1.2 mm long, on occasion 2 in a single flower, glabrous; style ca. 16 mm long. Pods to 10 × 0.8 cm when mature, at apex rounded, rostellate, thick-membranous, glabrous. Seeds widely rhomboid to widely ovoid, flattened, grayish or darker, ca. 5 × 4 mm; pleurogram irregular, usually demarcated by a dark line. Somatic chromosome number $2n = 26$.

Distribution (Fig. 34). Essentially endemic to central Oaxaca, in the districts of Tlacolula, Yautepec, Centro, Miahuatlán, and Teposcolula. *Zapoteca alinae* grows mainly on steep, rocky slopes in tropical deciduous and thorn forests and in secondary vegetation derived from these vegetation types; it has also been collected along seasonal streams. Collections come from elevations of 1,050 1,800 m.

Common name. Barba de chivo.

Additional specimens examined. MEXICO. OAXACA: Dist. del Centro, Cerro del Tule, *Conzatti 5474* (NY); 5 km SW Miahuatlán, *García 1607* (MEXU); Dist. Tlacolula, a 7 km NE de Mitla por carr. a Tamazulapan, *H. Hernández & Torres 271* (MEXU, MO); Dist. Tlacolula, 11 km E-NE de Totolapan por carr. a Tehuantepec, *H. Hernández & Torres 280* (MEXU, MO); Dist. Tlacolula, 33 km de San José de Gracia sobre carr. Tehuantepec Oaxaca, entre San José de Gracia y San Juan Guegoyache, *H. Hernández & Ramírez 939* (MEXU, MO); Dist. Tlacolula, 7 km NW de Totolapan por carr. a Oaxaca, *H. Hernández & Ramírez 942* (MEXU, MO); arroyo abajo de Cueva Blanca, cerca de Tlacolula, *Schoenwetter JSOX-2* (ENCB, US); E Totolapan, cañón Río Tehuantepec, *Sousa 2689* (CAS, GH, MEXU, US); Dist. Tlacolula, 3 km NE San Bartolo Albarradas, 19 km E-NE Mitla, *Sousa et al. 7846* (MEXU, MO); Dist. Tlacolula, 11 km E-NE Totolapan, *Sousa & Téllez 8565* (CAS, ENCB, MEXU, MICH); Dist. Yautepec, 1 km S El Laurel,

carr. Est. Microndas, *Sousa & Téllez 8611* (MEXU, MO); Dist. Teposcolula, Las Pilas, a 4 km al E de Tamazulapan, *Sousa et al. 8991* (MEXU, MO); Dist. Tlacolula, 16 km N Totolapan, *Sousa et al. 9424* (ENCB, MEXU); Dist. Tlacolula, 6 km N de Mitla, carr. a Totontepec, *Torres et al. 3947* (MEXU, MO); Dist. Yautepec, Torre de Microondas, San Cristóbal, al W de Portillo Nejapa, *Torres & Martínez 7449* (MEXU).

This endemic species, which is relatively consistent morphologically, is closely allied to *Z. media* by its 1- to 3-jugate pinnae, small, numerous leaflets, and habitat preferences. It can be readily distinguished from that species by the usually more slender stems, branchlets, and peduncles, narrower and consistently glabrous leaflets, and primarily by its flowers with shorter, white filaments. *Zapoteca alinae* is allopatric with *Z. media*. Its distribution overlaps at the east of its range (*H. Hernández & Torres 942*) near Totolapan, Dist. Tlacolula, with that of *Z. formosa* subsp. *rosei* (*H. Hernández & Torres 943*), but no evidence of hybridization was observed there.

4. Zapoteca lambertiana (G. Don) H. Hern., Ann. Missouri Bot. Gard. 73: 755–763. 1986. *Acacia lambertiana* G. Don, Edward's Bot. Reg. 9: t. 721. 1823. *Calliandra lambertiana* (G. Don) Benth., London J. Bot. 3: 100. 1844. Benth., Trans. Linn. Soc. London 30: 543. 1875. *Feuilleea lambertiana* (G. Don) Kuntze, Revis. Gen. Pl. 188. 1891. *Anneslia lambertiana* (G. Don) Britton & Rose, N. Amer. Fl. 23: 66. 1928. TYPE: Mexico: locality unknown, cultivated by George Don from material sent to him by Mr. Lambert from Boyton, where plants of this species had been raised from seeds collected in Mexico (lectotype, K; Hernández, Ann. Missouri Bot. Gard. 73: 757. 1986).

Erect shrubs to 4 m tall; stems slender; branchlets terete, costate under magnification, glabrous to villous or pilose. Pinnae (1–)2–4-jugate, rachis usually eglandular, rarely with small (ca. 0.3 mm diam.), cup-shaped, slightly elevated glands between the basal pairs of pinnae, the proximal pairs of pinnae rarely alternate; petiole terete, with a conspicuous adaxial channel, (1.2–)1.5–4.6 cm long, glabrous, rarely villous or pilose; rachis of 2-jugate pinnae (0.2–)0.4–1.8 cm, much longer when 3- or 4-jugate, glabrous to villous; rachillae 2.4–6.4(–7.5) cm long; leaflets (6–)7–17(–22) pairs per pinna, narrowly oblong to oblong or oblong-ovate, occasionally lanceolate, at base oblique, at apex acute, the median ones 8–14(16) × 2.5 4(–5) mm, the proximal ones smaller, membranous, all glabrous to villous or puberulent on both surfaces, occasionally hairy only abaxially, sometimes ciliate; leaflet venation visible superficially; stipules leafy, triangular-lanceolate to ovate, acute at apex, striate, 2–8 mm long, glabrous to sparsely villous. Capitula axillary, or more commonly arranged in compound or most commonly simple pseudopanicles 3.5–9.5 cm long; peduncles fasciculate at distant nodes, (0.5)1.5–6.5 cm long at anthesis, glabrous. Calyx ca. 2 mm long, glabrous, sometimes ciliolate, the teeth narrowly oblong or triangular, acute at apex; corolla campanulate, 3–4 mm long, glabrous, the lobes narrowly elliptic, acute at apex; filaments ca. 2.5 cm long, red-purple, the staminal tube 1–1.5 mm long; ovary sessile, glabrous. Pods to 9 × 1 cm when mature, rounded, retuse or acute at apex, rostellate, membranous, glabrous. Seeds quadrate-rhomboid to very widely ovoid, 3.5–4 × 3–3.5 mm, dark brown, the areola lighter; pleurogram irregular.

Distribution (Fig. 35). *Zapoteca lambertiana* has been collected primarily in tropical dry forests and less commonly in tropical thorn, tropical subdeciduous, or tropical evergreen forests, where it usually is associated with secondary vegetation. It is distributed discontinuously from northeastern to southeastern Mexico, where a series of disjunctions occur. Most collections have been made in the following regions: 1) Sierra de Tamaulipas, Tamaulipas; 2) Region of Villa Juárez and Huasteca, San Luis Potosí; 3) Coastal Plain of the Gulf of Mexico, east and northeast of Xalapa, Veracruz; 4) Region of Los Tuxtlas, Veracruz; and 5) Slopes of the Central Depression of Chiapas. Collections come from altitudes of 190 900 m.

Common names. Barba de chivo (Tamaulipas), t'sak xiixit (Huasteca).

Additional specimens examined. MEXICO. CHIAPAS: Mpio. Cintalapa, Rizo de Oro, *Breedlove 36732* (DS, MEXU, MICH, NY); Mpio. Chicoasén, above Chicoasén, *Breedlove 37255* (DS, MEXU, TEX); Mpio. Acalá, 45 km from Tuxtla, Presa La Angostura, *Breedlove 37412* (DS, MEXU); Mpio. Chiapa de Corzo, El Chorreadero, *Breedlove 39694* (DS, MEXU, NY); same locality, *Hernández & Ramírez 891* (MEXU, MO); Encañada Chacona–S. Fernando (NW Tuxtla Gutiérrez), *Miranda 6462* (MEXU); 5.6 mi. SE de Chiapa de Corzo, El Chorreadero, *Ton 2942* (DS, ENCB, LL, MO, NY, US); Mpio. Venustiano Carranza, above Finca Carmen, along the road from Acalá to Pujiltik, *Ton 3042* (DS, MO, NY, US). SAN LUIS POTOSÍ: S of Villa Juárez, *Clark 7418* (MO); Mpio. San Antonio, Lejem, *Alcorn 1756* (MEXU). TAMAULIPAS: Mpio. Aldama, región of Rancho Las Yucas, 40 km NNW of Aldama, Los Cerritos to Sierra La Borrada (23°14′N, 98°10′W), *Dressler 2006* (GH, MO); Mpio. Aldama, 17.2

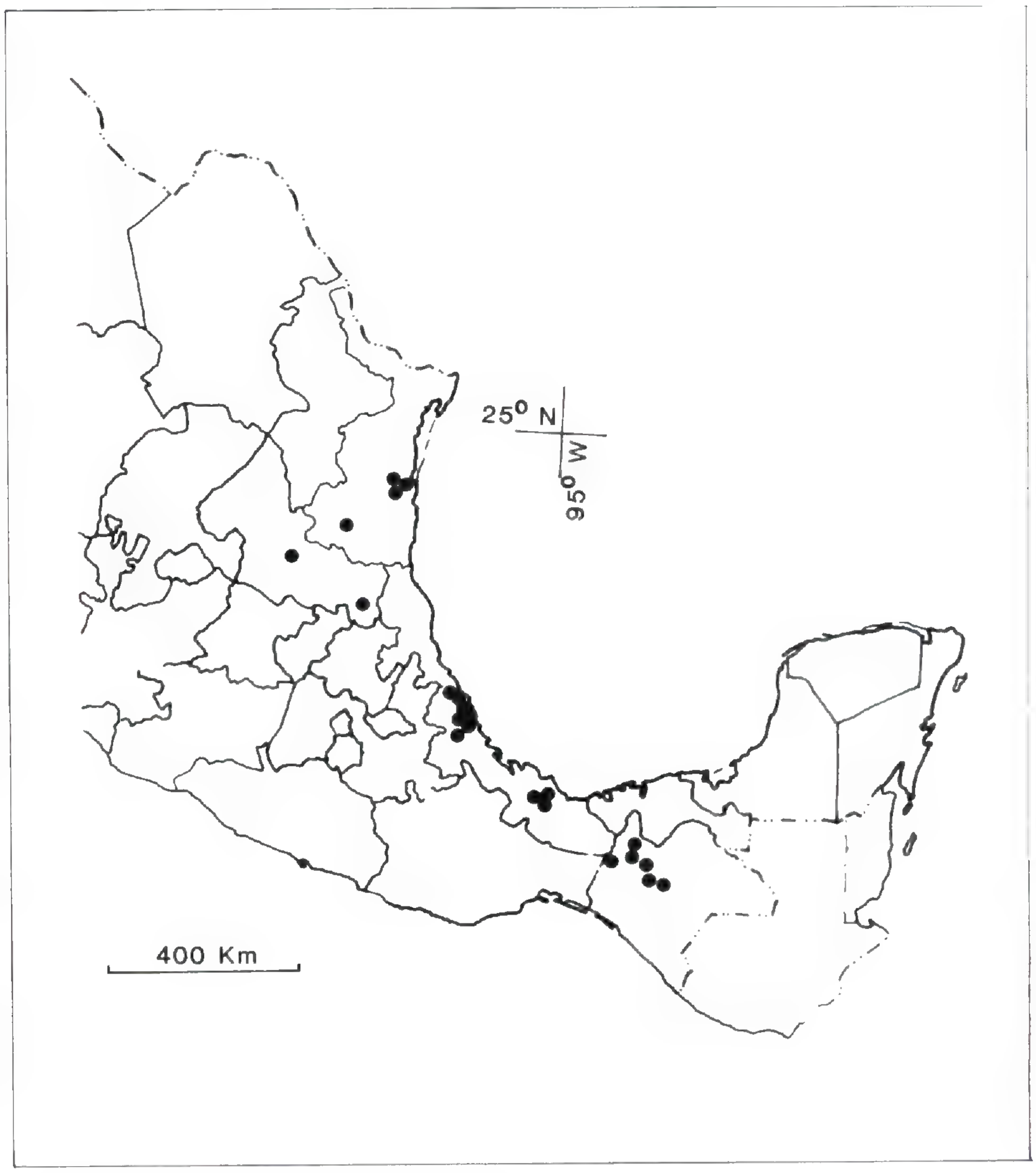


FIGURE 35. Distribution of *Zapoteca lambertiana*.

km W de la carr. Aldama Soto la Marina, por camino a Rancho Las Yucas, 38 km NW de Aldama, *H. Hernández & Torres 147* (MEXU, MO); Chamal, Ocampo rd., *Kenoyer & Crum 3596* (A, MICH); Rancho Los Alados, Cerro de Metate, *Martínez O. 284* (MEXU, MO). VERACRUZ: Mpio. Actopan, Sierra de Manuel Díaz, *Acosta 134* (XAL, MO); Mpio. Vega de Alatorre, Cañada de Mesillas, entrada por Santa Ana, *Calzada 7724* (XAL); Cerro Gordo, 3 km de Plan del Río, carr. Xalapa Veracruz (19°25'N, 96°39'W), *Castillo & Tapia 1223* (XAL); Mpio. Vega de Alatorre, El Centenario, a 20 km de Santa Gertrudis, *Castillo & Venavides 2003* (XAL); region of San Andrés Tuxtla, along river draining Laguna de Catemaco, *Dressler & Jones 226* (BM, GH, MEXU, MICH, MO, NY, UC); Mpio. San Andrés Tuxtla, Salto de Eyipantla, *H. Hernández & Torres 780* (MEXU, MO); rim of the Barranca Zacuapán, *Purpus 10770* (US); Rancho Remudadero, *Purpus 11292* (A); entre El Carrizal y Los Baños, *Ramos 322* (MEXU); S de la Laguna Nixtamalapan, *Sousa 2201* (MEXU); orilla W del Lago Catemaco, *Sousa 2898* (CAS, GH, MEXU); Mpio. Zapata, La Laja, entre Corral Falso y Pinotepec, a 900 m de carr. Jalapa–Veracruz, desviación 16 km SE Jalapa, *Sousa & Ramos 4757* (MEXU); Dos Ríos, Plan del Río, *Ventura 4197* (ENCB, MEXU); Mpio. Dos Ríos, Coral Falso, *Ventura 5807* (ENCB, MEXU, MICH); Dos Ríos, Plan del Río, *Ventura 10594* (CAS, ENCB, MEXU).

Zapoteca lambertiana can be readily distinguished from other species of subg. *Zapoteca* primarily by its much thinner pods with undulate surfaces and thinner margins, and specifically from *Z. portoricensis* by its red-purple filaments. Extrafloral nectaries between the pinnae in a single specimen (*Dressler 2006*, GH) and presumed similarities in the texture of the pods suggest a possible close relationship between this species and *Z. filipes*. Leaf indument is very variable in *Z. lambertiana*; it varies at both intra- and interpopulation levels and does not seem to follow a geographical pattern.

There is no morphological differentiation among the disjunct populations that occur over the extensive geographical range of *Z. lambertiana*. It is likely that such discontinuities are of recent origin. Perhaps they resulted from tropical dry

forest fragmentations that occurred in the tropics subsequent to the Pleistocene glaciation, after the present wetter conditions originated disjunctions in the formerly extensive and continuous areas covered by tropical dry forests.

5. Zapoteca filipes (Benth.) H. Hern., comb. nov. *Calliandra filipes* Benth., J. Bot. (Hooker) 2: 139. 1840; Benth., Lond. J. Bot. 3: 99. 1844; Benth., Trans. Linn. Soc. London 30: 542. 1875; Benth. in C. Martius, Fl. Bras. 15(2): 412. 1876; J. F. Macbr., Field Mus. Nat. Hist., Ser. Bot. 13: 71. 1943; L. Cárdenas, Revista Fac. Agron. (Maracay) 7: 131. 1974. *Feuilleea dimidiata* Kuntze, Revis. Gen. Pl. 185. 1891. (This was published as a nomen novum because the name *F. filipes* was preoccupied by a species based on *Inga felipes*.) TYPE: Brazil: *Pohl 1458* (lectotype, K, here designated; isolectotype, K).

Erect shrubs to 2 m tall; branchlets terete, costate under magnification, sparsely villous, becoming glabrous. Pinnae 4–5-jugate; petioles terete to subtetragonal, with a conspicuous adaxial channel, 2–3.5 cm long, glabrous to sparsely villous; rachis 2.5–4.5(–7.5) cm long; rachillae 2.5–5.5(–7) cm long; with glands near the base of the petiole, at the insertions of the pinnae, and usually at the insertions of the leaflets, these cylindrical, concave at apex, to ca. 1 cm long but usually smaller; leaflets (9–)11–16 pairs per pinna, mostly falcately oblong-lanceolate, oblique at the base, at apex rounded to acute, mucronulate, 8–14 × 2.5–5 mm, membranous, glabrous or at most sparsely ciliate; primary and secondary leaflet veins conspicuous, especially abaxially; stipules leafy, lanceolate, parallel-veined, usually 3–5 mm long, glabrous. Capitula axillary; peduncles fasciculate, (3.5–)4.5–8 cm long at anthesis, glabrous. Flowers basically pentamerous but the number of flower parts variable; calyx ca. 2 mm long, glabrous, the teeth irregular, triangular or narrowly oblong, acute at apex; corolla campanulate, ca. 4 mm long, glabrous, the lobes lanceolate; filaments white in the basal half and red-purple in the distal half, the staminal tube ca. 2 mm long; ovary 1.5–2 mm long, sessile, glabrous. Pods ca. 7.5 × 0.7 cm when mature, at apex truncate, rostellate, membranous, glabrous.

Distribution. This species has been collected at a few localities in the Brazilian states of Goiás and Minas Gerais, where it is commonly associated with cerrado vegetation at 950 m elevation. It was incorrectly reported by Macbride (1943) from Peru and by Cárdenas (1974) from Venezuela.

Additional specimens examined. BRAZIL. MINAS GERAIS: Sierra do Espinhaço, ca. 5 km NE Francisco Sá, road to Salinas, *Irwin et al. 23205* (K); BR-4 entre km 810 811, *Pabst & Pereira 9414* (NY). GOIÁS: Salgado, *Pohl 3492* (F, NY).

Zapoteca filipes is probably closely related to *Z. lambertiana* as judged by the vegetative characteristics of these species, especially by the common possession of membranous pods. Extrafloral nectaries, universal in *Z. filipes*, are occasional in *Z. lambertiana*. *Zapoteca filipes* can be readily distinguished from the remaining species of subg. *Zapoteca* by the cylindrical glands on the petiole, rachis, and rachillae.

6. Zapoteca portoricensis (Jacq.) H. Hern., Ann. Missouri Bot. Gard. 73: 755–763. 1986. *Mimosa portoricensis* Jacq., Collectanea 4: 143. 1791; Jacq., Icon. Pl. Rar. 3: 20, t. 633. 1793. *Acacia portoricensis* (Jacq.) Willd., Spec. 4: 1069. 1806; DC., Prodr. 2: 467. 1825; Schldl. & Cham., Linnaea 5: 595. 1830; G. Don, Gen. Hist. 2: 419. 1832; Schldl., Linnaea 12: 566. 1838. *Calliandra portoricensis* (Jacq.) Benth., London J. Bot. 3: 99. 1844; Benth., London J. Bot. 5: 102. 1846; Griseb., Fl. Brit. W. Ind. 224. 1860; Benth., Trans. Linn. Soc. London 30: 543. 1875; Benth. in C. Martius, Fl. Bras. 15: 411. 1876; Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 492. 1937; Standley & Calderón, Fl. Salvadoreña 125. 1941; J. F. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13: 72. 1943, pro parte; Standley & Steyerm., Fieldiana, Bot. 24: 25. 1946; L. Cárdenas, Revista Fac. Agron. (Maracay) 7: 131. 1974. *Feuilleea portoricensis* (Jacq.) Kuntze, Revis. Gen. Pl. 184. 1891. *Anneslia portoricensis* (Jacq.) J. D. Smith, Enum. Pl. Guat. 2: 18. 1891. TYPE: Puerto Rico: *Bredemayer 16* (neotype, B-W, here designated, seen on microfiche). Although there is no direct evidence, it is likely that the Bredemayer specimen collected in Puerto Rico, and here designated as the neotype was used by Jacquin as a basis for his description of *Mimosa portoricensis*. Bredemayer participated in two of the Austrian botanical expeditions to the West Indies in 1783–1785 and 1785–1788, which provided materials for Jacquin to use in his *Collectanea* and other works. In connection with this, D'Arcy (1970) pointed out that "it is likely that Jacquin based many of his descriptions of new species on plants brought in by the official Austrian bo-

tanical expeditions and grown in Austrian gardens."

Erect or scandent shrubs usually to 3(7) m tall; stems slender, sometimes to 12 cm diam. at base; branchlets terete, occasionally 4-angled or nearly so, glabrous to very densely villous with white or tawny hairs, usually becoming glabrate. Pinnae (1)3 6(–8)-jugate; petioles eglandular, usually angulate or 4-angled, (1–)2–5 cm long, villous to densely villous, rarely glabrous; rachis 0.9 5.5(–10) cm long; rachilla (2)3–9.5(11) cm long; leaflets (8–)15 67 pairs per pinna, narrowly oblong to lanceolate or oblong to oblong-obovate, occasionally subfalcate, oblique at base, acute to rounded at apex, usually mucronulate, the median leaflets 4–20 × 1 6 mm, membranous, either glabrous, villous, puberulent, or sericeous on both surfaces, usually ciliate; leaflet venation inconspicuous; stipules leafy, adpressed, triangular to triangular-lanceolate, occasionally linear-triangular, sometimes slightly curved, to 11(17) mm long, glabrous to densely villous. Capitula usually axillary, occasionally arranged in pseudopanicles to 20 cm long; peduncles fasciculate, (1.3–)3–12(–15) cm long at anthesis. Flowers pentamerous, rarely tetramerous; calyx cup-shaped, 1 3(3.5) mm long, glabrous to ciliate or densely villous around the teeth, these usually triangular to deltate, sometimes lanceolate to linear-lanceolate or narrowly oblong, acute; corolla campanulate, 3 8(10) mm long, glabrous, occasionally villous apically, the lobes lanceolate; filaments ca. 2.5 cm long, white, the staminal tube ca. 2 mm long; ovary ca. 1.5 mm long when fertile, glabrous, sessile. Pods linear, rarely slightly curved, the apex rounded to truncate, rostellate, to 16.5 cm long when mature, thickly membranous, glabrous or puberulent. Seeds widely rhomboid to very widely ovoid, 5–7 × 3–5 mm, brown, dark brown, or black, the areola sometimes mottled; pleurogram irregular, sometimes regular. Somatic chromosome number $2n = 26$.

Distribution (Fig. 36). Frequent in open sites such as forest clearings, forest edges, roadsides, river banks, and wet thickets; in general in secondary habitats derived from a variety of vegetation types. Collections come from elevations of 0–2,100 m. Standley (1930) incorrectly included this species in the *Flora of Yucatán*.

Zapoteca portoricensis as circumscribed here, consists of three rather variable subspecies: *portoricensis*, *pubicarpa*, and *flavida*. Each has a few distinguishing, variable characters (Table 12), although they intergrade and overlap. Consequently, these subspecies are defined on the basis of combinations of characters. Viewed in a local context, each subspecies might be accorded specific rank; however, a synthetic analysis of all available material reflects the absence of strong morphological discontinuities distinguishing them.

The three subspecies of *Z. portoricensis* have distinct habitat preferences: subsp. *portoricensis* occurs primarily in relatively wet, mid- to high-altitude habitats; subsp. *flavida* is found in wet, lowland areas; and subsp. *pubicarpa* occurs in dry, mid-altitude areas. However, in the West Indies, subsp. *portoricensis* usually occurs in much drier, low, sometimes coastal, habitats.

KEY TO THE SUBSPECIES OF *ZAPOTECA PORTORICENSIS*

1a. Shrubs scandent; leaflets 7 20 × 2 6 mm; corolla 3–4 mm long; mature pods to 16.5 cm long ..... 6c. subsp. *flavida*

1b. Shrubs erect; leaflets 4–12(–15) × 1–3 mm; corolla 4–8(–10) mm long; mature pods to 12 (14.5) cm long.

2a. Pods glabrous, rarely hairy; peduncles (1.8)3.5–12(–15) cm long at anthesis; calyx glabrous to ciliate, the teeth rarely sparsely villous; corolla 4–8 mm long ..... 6a. subsp. *portoricensis*

2b. Pods puberulent; peduncles 1.3–3.5(6) cm long at anthesis; calyx teeth consistently villous; corolla 7–8(–10) mm long ..... 6b. subsp. *pubicarpa*

6a. Zapoteca portoricensis (Jacq.) H. Hern. subsp. **portoricensis.**

Mimosa guineensis Schum. & Thonn., Beskr. Guin. Pl. 323. 1827.

Acacia linearis Desv. ex Ham., Prodr. Pl. Ind. Occid. 59. 1825.

A. hamiltonii Desv. ex Ham., Prodr. Pl. Ind. Occid. 59. 1825.

A. alba Colla, Hort. Ripul. Appendix 2: 339. 1826.

A. colleana K. Presl. Repert. Bot. Syst. 183. 1833.

A. vespertina Macfad., Fl. Jam. 1: 318. 1837.

A. ungulata Desv., J. Bot. Agric. 3: 68. 1854.

Lysiloma marchiana Griseb., Fl. Brit. W.I. 223. 1860. TYPE: Jamaica, *March s.n.* (holotype, GOET (not seen); isotypes, GH, NY).

Calliandra nicaraguensis Taub. & Loes. ex Loes., Bot. Jahrb. Syst. 23: 124. 1897. *Anneslia nicaraguensis* (Taub. & Loes. ex Loes.) Britton & Rose, N. Amer. Fl. 23: 63. 1928. TYPE: Nicaragua. Matagalpa: Cañada Yasica, 1,000 m, 4 Aug. 1843, *Rothschuh 204* (lectotype, US no. 1266103 (fragment and photo), here designated; isolectotype, NY (fragment)). The holotype, which was at B, was destroyed in 1943 (P. Hiepko, pers. comm., 1986); photos of this specimen are at F, MEXU, MO, NY, TEX, US.

Calliandra portoricensis var. *major* Sprague, Bot. Mag. 133: t. 8129. 1907. TYPE: Cult. in Hort. Bot. Reg. Kew, Aug. 1906 (lectotype here designated, K), this specimen was presumably collected by Sprague.

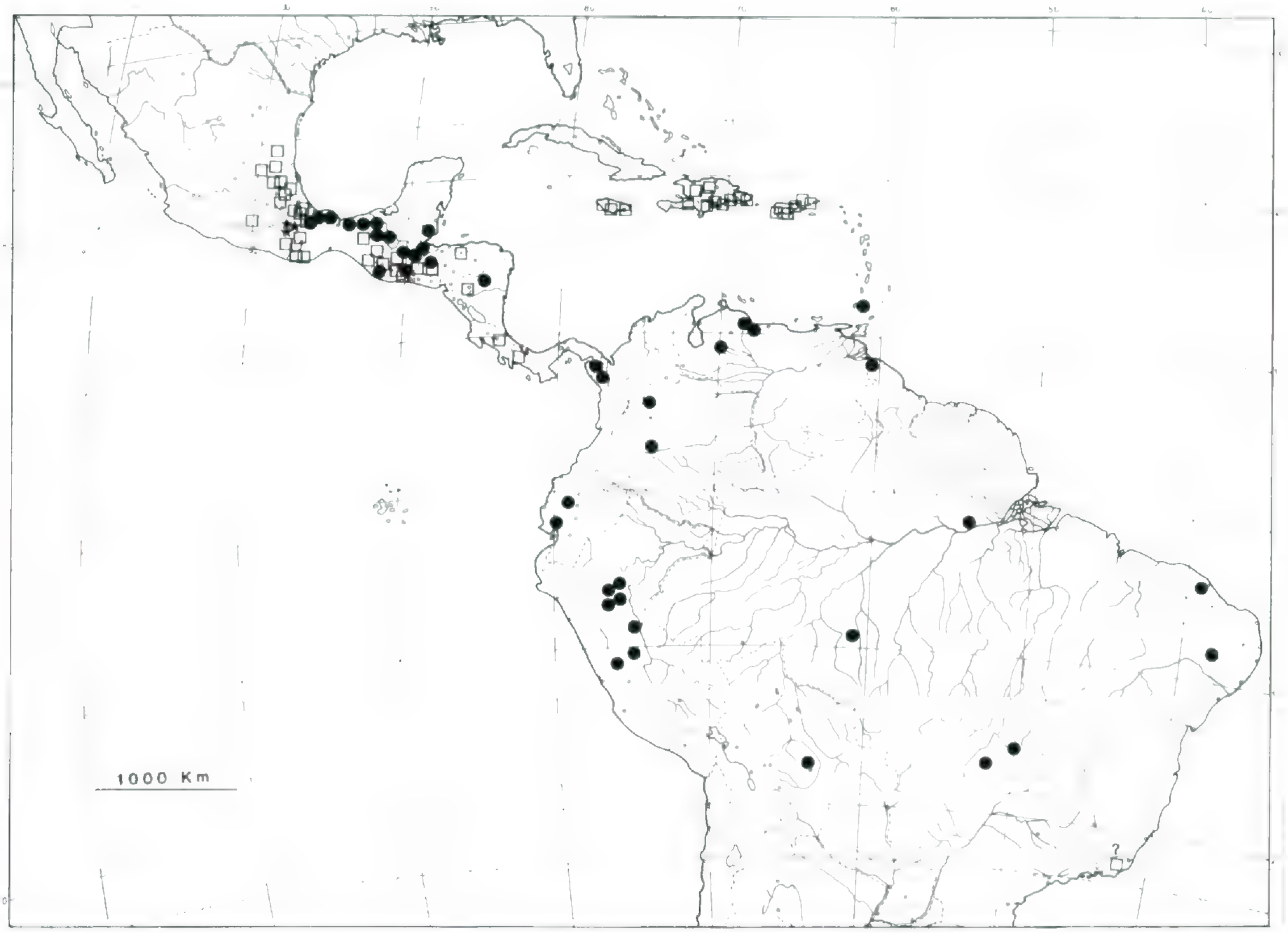


FIGURE 36. Distribution of *Zapoteca portoricensis* subsp. *portoricensis* (open squares), *Z. portoricensis* subsp. *pubicarpa* (stars), and *Z. portoricensis* subsp. *flavida* (dots).

Sprague mentioned in his discussion that "the Kew plants were purchased in 1906 from a nursery-man in Hyères as 'Inga alba' and flowered in the Temperate House in June and July of that year."

Anneslia spraguei Britton & Rose, N. Amer. Fl. 23: 66. 1928. *Calliandra spraguei* (Britton & Rose) Lundell, Lloydia 2: 89. 1939. TYPE: Mexico. Veracruz: Xalapa, *Schiede 690* (lectotype here designated, NY; isolectotypes, BM, CAS, CGE, G, GH, K, LE, MEXU, MO, UC, US—fragment). The specimens at NY and K are the only ones labeled as collections made by "*Schiede 690*," whereas the specimens at LE and MO are labeled "*Schiede and Deppe 690.*" The specimens from BM and G are labeled "*Schiede*

TABLE 12. Comparison of the subspecies of *Zapoteca portoricensis*.

	Subspecies *portoricensis*	Subspecies *pubicarpa*	Subspecies *flavida*
Habit	erect shrubs	erect shrubs	scandent
Pairs of pinnae	(1)2 7(8)	2 4	(2)3–5(7)
Leaflet			
Shape	narrowly oblong to lanceolate	narrowly oblong to lanceolate	oblong to oblong-lanceolate
l × w	5–15 × 1 3 mm	4–7 × 1–2 mm	7 20 × 2 6 mm
Pairs pinna	(12–)16–67	15 30	(8)18 36
Stipule length	10(17) mm	11 mm	11(13) mm
Peduncle length	(1.8)3.5 12(–15) cm	1.3–3.5(6) cm	3 7.5 cm
Calyx			
Length	1 3 mm	2–3(–3.5) mm	1 2 mm
Indument	glabrous to ciliate	villous to densely villous	glabrous
Corolla length	4–8 mm	7–8(10) mm	3 4 mm
Pod			
Length	12(–14.5) cm	6–7 cm	16.5 cm
Indument	glabrous	puberulent	glabrous

and Deppe" (*s.n.*), and the one at UC is labeled "*Schiede*" (*s.n.*). The specimens at CAS, CGE, GH, and MEXU do not have any reference to collector, although records from the last herbarium make reference to this specimen as collected by Schiede. With the exception of three (BM, MEXU, and UC), all the collections are hand annotated as "*Acacia portoricensis* Willd.," and judging from the handwriting, the other data provided, and the aspect of the plants, all these specimens almost certainly are duplicates of the same *Schiede 690* collection. The specimens at G, GH, and NY have a mark, presumably made *a posteriori*, with the name "Schlech."; nevertheless, it is well known that Schlechtendal never traveled outside Western Europe, although a number of collections from Mexico have mistakenly been attributed to him. According to R. Barneby (pers. comm.), Schlechtendal distributed Schiede's plants.

Calliandra nogalensis Lundell, Lloydia 2: 88. 1939. TYPE: México. Veracruz: Nogales, *E. Matuda 1153*, 2 May 1937 (holotype, MICH; isotypes, F, MEXU, NY).

Calliandra siltepensis Lundell, Phytologia 2: 1. 1941. TYPE: Mexico. Chiapas: Barranca Honda, Siltepec, Oct.–Nov. 1940, *E. Matuda 4040* (holotype, MICH; isotypes, A, F, MEXU, NY).

Erect shrubs, 2–3(6) m tall; stems slender, sometimes to 12 cm diam. at the base; branchlets terete, sometimes 4-angled, glabrous to densely villous with tawny hairs, often glabrate. Pinnae (1)3–7(–8)-jugate; leaflets (12–)16 67 pairs per pinna, narrowly oblong to lanceolate, rarely oblanceolate, oblique at the base, acute to rounded at the apex, usually mucronulate, 5 15 × 1–3 mm, glabrous to villous, puberulent, or sericeous on both surfaces, usually ciliate; stipules triangular to narrowly triangular, sometimes slightly curved, 10 (–17) mm long, glabrous to villous. Capitula axillary; peduncles (1.8 -)3.5–12(15) cm long at anthesis, glabrous to densely villous. Calyx 1–3 mm long, the teeth usually triangular, sometimes lanceolate to linear-lanceolate, usually glabrous or ciliate, sometimes with a few hairs in the area of the teeth; corolla 4–8 mm long, glabrous. Pods to 12(–14.5) × 1(–1.2) cm, straight or slightly curved, glabrous. Seeds widely rhomboid to ovoid, 5–7 × 3–5 mm, brown to black, the areola sometimes mottled; pleurogram usually irregular, sometimes regular. Somatic chromosome number $2n = 26$.

Distribution (Fig. 36). This widespread subspecies has been collected in several relatively localized areas: 1) Atlantic slopes of the Sierra Madre Oriental, in the states of Hidalgo, Puebla, and San Luis Potosí, and the eastern portion of the Transverse Volcanic Belt in Veracruz; 2) Sierra Madre del Sur, including parts of the Mixteca Region in Oaxaca; 3) Sierra Madre of Chiapas, and the Chiapas and Guatemala Highlands; and 4) West Indies, in Jamaica, Hispaniola, and Puerto Rico (including some of the Virgin Islands). Disjunctions occur in the Sierra de Tamaulipas, Tamaulipas; Temascaltepec, State of México; and in Honduras, Nicaragua, Costa Rica, and Panamá. There is a collection from Nova Friburgo, Rio de Janeiro, Brazil (*Curran 655*), which was probably obtained from cultivated plants. This subspecies has usually been collected in mountain areas of moderate to relatively high altitude (800–2,100 m), in plant communities such as oak, pine, pine–oak, temperate deciduous, wet montane cloud, and montane rain forests, especially in secondary habitats. Nevertheless, in some areas such as the Huasteca in the states of Hidalgo and San Luis Potosí, Mexico, populations usually occur at lower elevations, reaching as low as 165 m. Similarly, plants from the West Indies usually inhabit low elevation areas, down to sea level, with a much drier climate.

Common names. Barba de chivo (Nicaragua), carboncillo blanco (Costa Rica), granolino (Dominican Republic), guacamaya montés (El Salvador), guaje cimarrón (Veracruz), guajillo (Veracruz), guajillo blanco (Veracruz), night-flowering acacia (Jamaica), pelo de angel (Puebla, San Luis Potosí), tamarindo de monte (Guatemala), timbrillo (Veracruz), white tamarind (Guatemala, Jamaica).

Additional specimens examined. MEXICO. CHIAPAS: 21 km al este de las Lagunas de Monte Bello, *Cabrera 3690* (MEXU, MO); El Chorreadero, 5.6 mi. east of Chiapa de Corzo, *Breedlove 11889* (CAS, LL, MICH, MO, US); Mpio. of Motozintla de Mendoza, SW side of Cerro Mozotal, *Breedlove 25917* (CAS, MEXU, MICH, MO, NY); Mpio. of Zinacantán, Paraje Granadilla, *Laughlin 1069* (CAS, MICH, US); Ovando, *Matuda 17923* (F, MEXU, NY); Escuintla, El Triunfo, *Matuda 18098* (CAS, MEXU, NY); Siltepec, Cascada, *Matuda 18666* (CAS, MEXU, NY). HIDALGO: Mpio. de Tlanchinol, a 0.5 km ESE de Tlanchinol, *Flores 233* (CAS, MEXU, MICH, NY); Rancho Viejo, Jacala, *Fisher 46126* (CAS, F); 13 km al sur de Tepemaxac, *Grether 591* (MEXU); Mpio. de Tenango de Doria, 10 km NE of Tenango de Doria, *H. Hernández & Torres 122* (MEXU, MO); Mpio. Meztitlán, 1 km de la desviación a Santa Mónica, *H. Hernández & Torres 134* (MEXU, MO); Mpio. de Tianguistengo, 5 km NW Tianguistengo por carretera a Molango, *H. Hernández & Torres 135* (MEXU, MO); Mpio. de Xochicoatlán, 16 km NW de Tianguistengo, *H. Hernández & Torres 136* (MEXU, MO); Mpio. Molango, 1 km N de Molango, *H. Hernández & Torres 138* (MEXU, MO); Mpio. de Chapulhuacán, 5 km S de la frontera SLP–Hgo., *H. Hernández & Torres 149* (MEXU, MO); Mpio. Chapulhuacán, 9.6 km SW de Chapulhuacán por carr. a Jacala, *H. Hernández & Torres 150* (MEXU, MO); 29 km SW Chapulhuacán por carretera a Jacala, *H. Hernández & Torres 151* (MEXU, MO); Mpio. de Tianguistengo, 4 km al E de Tianguistengo, *R. Hernández 3963* (GH, MEXU, WIS); Mpio. de Tlanchinol, 2

km al S de Tlanchinol, hacia Apantlaso, *R. Hernández 5372* (MEXU); Mpio. de Molango, Ismolintla, 2 km al N de Molango, *R. Hernández 5886* (MEXU, MO); Mpio. de Juárez, Itztacoyotla, 15 km al N de Juárez, *R. Hernández 6105* (MEXU, MO); km 301 on highway between Jacala and Santa Ana, *Moore 2680* (GH); camino entre Metepec y Tenango de Doria, entre 16 y 31.5 km al NNE de Tulancingo, *Koch 7444* (MEXU); El Capulín 6 km, del entronque de la brecha a Pisaflores con la carretera Jacala Tamazunchale, *Tenorio & Romero 2381* (MO); 42 mi. N of Puerto Ignacio Isidro Díaz, N of Zimapán, *Wunderlin et al. 1119* (MO). MÉXICO: Distr. Temascaltepec, Bejucos, *Hinton 2019* (A, F, G, MEXU, NY, US). OAXACA: Pochutla, Cerro Espino, *Conzatti 3184* (US); 5 km al NW de La Galera, carr. Pochutla–Oax. Sierra de Miahuatlán, *Sousa et al. 5610* (CAS, MEXU); Distr. de Juxtlahuaca, a 2 km al SE de Copala, *Sousa et al. 6979* (MEXU, TEX); Distr. de Putla, a 22 km al NE de Putla de Guerrero, *Sousa et al. 7688* (MEXU); sur del Distr. Cuicatlán, a 9 km N de Nacatepec, *Sousa et al. 10446* (BM, MEXU, MO); Distr. de Juquila, 3 km al W de Pueblo Viejo y a 10 de San Juan Lachão, *Sousa et al. 12603* (MO); 6.1 km al N de San Gabriel Mixtepec, carr. Puerto Escondido–Sola de Vega, *Torres & Martínez 6612* (MO). PUEBLA: 7 km al NE de Huauchinango, *Basurto & Durán 91* (CAS, ENCB); 8 km al SW de Pahuatlán, *Basurto & Durán 107* (CAS, MO); 8 km al NE de Honey, *Basurto & Durán 324* (BM, MEXU); Mpio. de Venustiano Carranza, 3 km al W de Villa Lázaro Cárdenas, *Basurto & Durán 386* (MEXU, MO); 2 km al W de Chiconcuautla, *Basurto & Durán 483* (CAS, MEXU, MO); Puente Apulco, *Boege 750* (MEXU); alrededores de Xicotepec de Juárez (Villa Juárez), *Quintero 763* (CAS, MICH, TEX); Zoactepan, *Ibarra et al. 75* (ENCB, MO). SAN LUIS POTOSÍ: Mpio. Huehutlan, Tzineja, *Alcorn 2868* (MEXU); 21 mi. N of Morelos, *Kenoyer & Crum 4089* (A); near Tancanhuitz, *Nelson 4367* (GH, NY, US); Las Canóas, *Pringle 3752* (BM, BR, F, G, GH, MEXU, MO, NY, UC, US); Tamasopo Canyon, *Pringle 3722* (A, BM, BR, F, G, GH, MEXU, MO, US); Mpio. de Xilitla, 3 km al NE de Ejido de Xilitlilla, *Rzedowski 10506* (MEXU, MICH, TEX); 2 km al SE de Ahuacatlán, *Rzedowski 10933* (CAS, TEX); Mpio. de Valles, alrededores de Cd. Valles, *Torres s.n.* (MEXU); along hwy. 85, 7.4 mi. N of Tamazunchale, 3.7 mi. S of Matlapa, *Dziekanowski et al. 3500* (ENCB, NY). TAMAULIPAS: Mpio. Gómez Farías, 1 km SE Rancho del Cielo, *H. Hernández & Torres 146* (MEXU, MO); Sierra de Guatemala, *Sullivan 471* (ENCB, NY, TEX). VERACRUZ: Mpio. Tonayán, Congregación de Ixtepan, *Calzada 2113* (MEXU); Mpio. Tantima, Sierra de Tantima, *Calzada 5539* (MEXU); Mpio. Huiloapan, Cerro de San Cristobal, *Calzada 8622* (WIS); Mpio. Yecuatla, Barranca del Cedral, *Cházaro & Gutiérrez 3665* (WIS); Texolo 3 km al SW de Xico, *Dorantes 85* (F); 2 km después de Col. El Recreo, Rumbo a Palma Sola, *Dorantes et al. 717* (F, MEXU); Cerro del lado este de Zongolica, *Galicia s.n.* (TEX); Tlaltetela, camino Cosautlán–Ixhuacán de los Reyes, Ixhuacán de los Reyes, *C. Hernández et al. 136* (ENCB, MEXU); 6.8 km N de Xalapa por carr. a Naolinco, *H. Hernández & Torres 154* (MEXU, MO); Mpio. Naolinco, 1.8 km de Naolinco por carr. a Misantla, *H. Hernández & Torres 155* (MEXU, MO); Mpio. Río Blanco, N de Río Blanco, por camino a Tenango, *H. Hernández & Torres 165* (MEXU, MO); Mpio. Río Blanco, a 1 km de Río Blanco por camino al Cerro del Cristo, *H. Hernández & Chacón 465* (MEXU, MO); ca. 5 mi. E of Huatusco along road to Cardel, *Higgins 2578* (ENCB, MICH); Mpio. Ixhuacán, El Chorro, *Luna et al. 141* (MEXU); Pastizal de Olmo, Chalatla, *Luna et al. 279* (MEXU); Tierra Colorada, arriba de Andrés Tenexapa, *Medrano 1593* (MEXU); Mpio. Chocamán, 8.5 km by road W of Chocamán, *Nee 23257* (MEXU); Al E de Plan de Las Hayas, *Nevling & Gómez-Pompa 1005* (GH, MEXU); Cerro San Miguel, 2 km al W de Orizaba, *Nevling & Gómez-Pompa 2256* (CAS, F, GH, NY); Xalapa, *Pringle 8091* (G, GH, LL, MEXU, MO, NY, UC, US); orillas del Río Matzinga, near Orizaba, *Ramos 301* (CAS, MEXU, NY); El Esquilón, cerca de Xilotepec, *Ramos 348* (CAS, MEXU, US, WIS); El Naranjito, carretera Orizaba–Zongolica, *Rosas 1460* (A, CAS, F, MEXU, US); Mpio. Zozocolo, 2.5 km N de Zozocolo, *Tenorio et al. 8591* (MEXU); Mpio. Magdalena, Magdalena, *Licea 110* (F); Mpio. Nogales, Nogales, *Licea 158* (F); Mpio. Chocamán, Chocamán, *Licea 192* (F); Mpio. de Xico, Temimi, *Ventura 862* (CAS, MICH, WIS); Mpio. de Tlacuilán, Tlacuilán, *Ventura 8857* (MEXU); Mpio. de Banderilla, Banderilla, *Ventura 9949* (LL, MICH); Mpio. de Xalapa, La Mesa de Chiveras, *Ventura 10339* (MEXU); Mpio. de Xilotepec, San Martín, *Ventura 13931* (MEXU). GUATEMALA. ALTA VERAPAZ: entre San Pedro Carchá y Sacoyoú, *Molina & Molina 12100* (F, LL, NY); carretera San Juan Chamelco, *Molina & Molina 12287* (CAS, F, LL, NY); 5 km N of San Pedro Carchá (15°32′N, 90°15′W), *Williams et al. 40226* (F, MICH, US). CHIQUIMULA: Montaña Nonojá, 3 5 mi. E of Camotán, *Steyermark 31680* (F, US); Cuilapa, *Johnston 1033* (F); Pacaya, *Johnston 1331* (F). ESCUINTLA: between San Vicente Pacayas and Calderas, *Molina & Molina 27668* (BM, F, MICH, US). GUATEMALA: Arrazola, *Heyde & Lux s.n.* (GH, K, US); 7 mi. E of Guatemala City, *Harmon 2346* (MO). HUEHUETENANGO: between Ixcán and Finca San Rafael, Sierra de los Cuchumatanes, *Steyermark 49476* (F). JUTIAPA: vicinity of Jutiapa, *Standley 76311* (F, US). QUEZALTENANGO: along old road between Finca Pirineos and Patzulín, *Standley 86574* (F); vicinity of Santa María de Jesús, *Steyermark 34256* (F); Cotzal, Finca San Francisco, *Skutch 1849* (A, F, NY, US). SANTA ROSA: Cocan Jumaytepeque, *Heyde & Lux 4463* (G, GH, NY, US). HONDURAS. LEMPIRA: Montaña Puca, entre Guatán y Cuábanos, *Molina 12942* (F, LL, NY, US). YORO: ca. 16 km from Yarucha on Quebrada de Oro to Cerro Búfalo, *Holmes 4386* (NY). EL SALVADOR. SAN SALVADOR: Volcán de San Salvador, *Standley 22958* (GH, NY, US). SANTA ANA: Cerro Monte Cristo, ca. 14 mi. NE of Metapan along road to Punta Trifinio, *Croat 12340* (MO); La Majada between Hacienda Montecristo and Los Planes, *Molina et al. 16966* (F, NY, US). NICARAGUA. ESTELÍ: Las Cruces, *Laguna 333* (MO); Laguna de Miraflores (13°16′N, 86°16′W), *Moreno 8272* (MO); La Guayabita (13°14′N, 86°14′W), *Moreno 17549* (MO); La Cabaña (13°13′N, 86°13′W), *Moreno 17569* (MO). JINOTEGA: Santa Lastenia, between Matagalpa and Jinotega, *Stevens 22582* (MO); Cordillera Central de Nicaragua E of Jinotega, *Williams et al. 24730* (F, G, NY). MATAGALPA: Cerro Apante en las afueras al E de Matagalpa, *Téllez et al. 4775* (MEXU, MO). COSTA RICA. CARTAGO: Cerro de la Carpintera, *Standley 34482* (US); between Cartago and Tierra Blanca, *Rowlee & Stork 910* (NY, US). PANAMA. CHIRIQUÍ: above Boquete on road to Cerro Horqueta, *Croat 27029* (MO, US, WIS); 3 mi. N of El Volcán, *Maxwell 5739* (MO); valley of the upper Río Chiriquí Viejo, *White 342* (MO, US). DOMINICAN REPUBLIC. SANTIAGO: Navarrete, *Abbott 1088* (GH, US);

Ciudad Trujillo, *Allard 13564* (NY, US). AZUA: Hispaniola, Valle de San Juan, on road to El Cercado, *Ekman 13376* (A, F, GH, US); Santiago, Cordillera Septentrional, Las Lagunas, at Arroyo Harenquillo, *Ekman 16086* (G, GH, LL, NY, US). BARAHONA: El Hoyo, *Fuertes 1040* (A, F, G, GH, K, NY, US); Boca Chica, *Lavastre 1623* (NY); Guayacanes, *Lavastre 1858* (A, NY); San Cristóbal; cerca de Najayo, *Liogier & Jiménez 6221* (NY); Santo Domingo City, near Los Tres Brazos, *Liogier 11823* (NY, US); E of Higuey, near Boca de Yuma, *Liogier 12263* (F, GH, NY, US); Jina Jaragua, Higuey, *Liogier 12349* (F, MEXU, NY, US); 20 mi. W of Santiago, Jaiquí Picado, *Liogier 15168* (NY, US); 40 mi. E of Santo Domingo City, Guayacanes, *Liogier 15642* (NY, US); near Las Mercedes, Pedernales, *Liogier 16678* (F, GH, NY, US); farallón de Cumayasa, *Liogier 19163* (NY); Seibo, Bayajibe, *Taylor 488* (F, NY). HAITI. DEPT. DU NORD: St. Michel de l'Atalaye, *Leonard 8026* (F, NY, UC, US); Leogane, *Pride 370* (WIS). JAMAICA. Kingston, Constant Spring, *Britton 938* (NY); St. Andrew Parish, *Barkley 38491* (GH); Gordon Town, *Hart 1316* (US); Blue Mountains, *Hitchcock s.n.* (MO); W of Malvern, *Howard & Proctor 13681* (A); S of Gutters, *Howard & Proctor 13865* (A); Mount Diablo, *Maxon & Killip 461* (A, F, GH, NY, US); near Green River, between Cinchona and Whitfield Hall, *Maxon & Killip 1350* (A, F, GH, NY, US); Port Royal Mountains, Flamstead, *Maxon 8728* (GH, US); Hollymount, *Maxon 10464* (NY, US); Balaclaya, *Orcutt 1469* (MO, UC); Troy, *Perkins 1347* (G, GH); Christiana, Holmwood, *Proctor 10265* (A, NY, US); St. Andrew Parish, Craig Hill, Port Royal Mountains, *Proctor 23828* (A, F, LL, MICH, NY, US); Portland Parish, Stony River Gorge, near Macungo River junction, *Proctor 28384* (LL). PUERTO RICO. Island of Culebra, *Britton & Wheeler 8* (F, NY, US); between Aibonito and Coamo, *Britton et al. 5891* (NY); Ceiba, *Britton & Britton 7811* (NY); Loiza, *Britton et al. 8920* (G, NY, US); Puente Alfonzo, *Goll et al. 481* (NY, US); near Laguna de Tortuguero, *Liogier 10150* (GH, NY, US); Inter Fajardo et Cabeza de San Juan, *Sintenis 1642* (US); Cayey, Monte Cedro, *Sintenis 2090* (F, NY); Guanica, *Sintenis 3544* (G, GH, US); Peñuelas, *Sintenis 4848* (US); Maunabo in Montis Malapascua, *Sintenis 5234* (G, GH); Lares, Barrio Piletas, *Sintenis 6021* (G, MO, NY, US); Yanco, *Underwood & Griggs 634* (NY, US). VIRGIN ISLANDS. SAINT THOMAS: *Eggers 210* (GH, NY). TORTOLA: Long Look, *D'Arcy 448* (A); Edney's, *Fishlock 481* (NY); road to High Bush, *Britton & Shafer 717* (F, NY, US). CULTIVATED: U.S.A. MISSOURI: Saint Louis, Missouri Botanical Garden, *H. Hernández 948* (MEXU, MO). CALIFORNIA: Santa Barbara, *Hall 8132* (UC). MEXICO. DISTRITO FEDERAL: Ciudad Universitaria Facultad de Ciencias, *Rico 245* (MEXU). MORELOS: Cuernavaca (GH). BRAZIL. Rio de Janeiro, Nova Friburgo, *Curran 655* (F, GH, US). DOMINICAN REPUBLIC. Santo Domingo, *Melo 49* (NY). FRANCE. Paris (GH). JAVA. Horto Botanico Bogoriensi, *Warburg 2109* (NY).

As shown above, there are several names that have been included among the list of synonyms of *Z. portoricensis* (e.g., Bentham, 1875; Britton & Rose, 1928). However, I have been unable to associate any relevant specimens with these epithets. *Acacia venusta* Willd. (Enum. Hort. Berol. 1052. 1809) has been traditionally included in synonymy under *Z.* (*Calliandra*) *portoricensis*, which is probably incorrect. The only material I have been able to relate to this name is a specimen at the Willdenow Herbarium (Cat. No. 19143), which comes from "Hort. Bot. Berol. W.," as indicated by a handwritten note in the lower right margin. The brief description provided in the original publication of this species is a replica of the specimen label, which probably was handwritten by Willdenow himself, judging by the style of handwriting (Burdet, 1979). This specimen consists of two leaves, with the pinnae widely separate from each other, and rather few pairs of leaflets per pinnae. Because of the lack of flowers or pods, it is not possible to relate this specimen to *Z. portoricensis*.

Zapoteca portoricensis subsp. *portoricensis*, as delimited here, is an extremely variable, broadly defined subspecies, the most variable within the species. It can be distinguished from closely related subsp. *pubicarpa* by its glabrous pods, usually smaller flowers, glabrous to ciliate calyx teeth, and usually longer peduncles (Table 12). It differs from subsp. *flavida* by its erect habit, usually smaller and more numerous leaflets, usually larger flower parts, and smaller pods (Table 12).

Perhaps the most highly variable character in subsp. *portoricensis* is the degree of pubescence of its vegetative structures. Plants range from entirely glabrous or glabrate to having branchlets and leaf parts densely villous with long tawny hairs. This type of variation occurs at both inter- and intrapopulational levels, and, consequently, is of little taxonomic value. There are geographical patterns in the expression of this character. One extreme occurs in Veracruz, and to a lesser extent in Hidalgo and Chiapas, where there is a prevalence of collections with densely villous branchlets and leaves. The other extreme occurs in San Luis Potosí, Tamaulipas, and Central America, where glabrous or sparsely villous leaves and stems predominate. In the West Indian plants, the leaflets are consistently glabrous, but the branchlets may be villous or glabrous.

Other variable characters in *Z. portoricensis* subsp. *portoricensis* are the size and number of pairs of leaflets per pinna. Most plants from the Sierra Mixteca, Sierra Madre del Sur, and Sierra Madre de Chiapas, in the states of Oaxaca and Chiapas, Mexico, are characterized by pinnae with smaller, more numerous (to 67) pairs of leaflets usually densely distributed along the rachilla, giving the pinnae a feathery aspect. Plants with small, numerous pairs of leaflets per pinna are also found in Central America. In Oaxaca, plants with leaves

of this sort also tend to have larger flowers and usually larger stipules. However, these characters have been found in numerous collections from different regions (e.g., Veracruz, Puebla, Hidalgo), where they occur in plants that do not have feathery leaves like the ones in Oaxaca, so that there is no definite geographical pattern and no basis for recognizing additional infraspecific taxa. In contrast, many of the plants from the West Indies have larger and less numerous leaflets, thereby resembling subsp. *flavida*.

The vast majority of collections of *Z. portoricensis* subsp. *portoricensis* have terete branchlets; however, plants with four-angled branchlets, a characteristic diagnostic for *Z. tetragona*, are not uncommon in some regions. Some of these plants may be the result of hybridization between subsp. *portoricensis* and *Z. tetragona*. These two taxa are generally ecologically isolated in Central America and southern Mexico, where their geographical ranges overlap. In these regions, populations of subsp. *portoricensis* are found primarily in montane cloud forest or similar habitats, whereas those of *Z. tetragona* occur in warmer lowland habitats. Populations with four-angled branchlets are most frequent in Guatemala, where these two taxa come into close proximity and in some cases are probably strict sympatric. A number of Guatemalan collections of subsp. *portoricensis* have four-angled branchlets, although sometimes this characteristic is expressed only distally, or is less marked than in typical *Z. tetragona* (e.g., *Molina & Molina 12287*, *Standley 86574*, *87132*, *Steyermark 34256*, *Williams et al. 12100*, and others). Significantly, these plants are derived from areas where *Z. portoricensis* subsp. *portoricensis* and *Z. tetragona* approach each other, as for example, in the areas of San Juan Chamelco–Cobán–San Pedro Corchá, Departamento de Alta Verapaz; Colomba Santa María de Jesús, Departamento de Quetzaltenango; Ipala–Comatán, Departamento de Chiquimula; and Escuintla–San Vicente Pacayas, Departamento de Escuintla. Individuals with four-angled branchlets also occur in some other regions (e.g., Orizaba Cordoba, Veracruz, Chiapas), and even in areas where *Z. tetragona* does not occur, such as Haiti.

West Indian populations often differ from those on the mainland in some characters, possibly the result of the smaller gene pools in insular populations and the selective effects of local climates. In many of the plants collected in the West Indies, the leaflets are comparatively larger, approximating those of *Z. portoricensis* subsp. *flavida*. Jamaican specimens are characterized by smaller (4.5–6 cm long) pods and by usually smaller, black seeds with regular pleurograms, as compared with the mainland populations. In addition, some of the plants from this island have 1–2-jugate pinnae with fewer pairs of leaflets.

Zapoteca portoricensis subsp. *portoricensis* and its close relative *Z. caracasana* subsp. *caracasana* co-occur on Hispaniola, although it is unclear whether they really grow together. Here, as elsewhere in the West Indies, most plants of subsp. *portoricensis* differ from mainland populations in having calyces with the teeth lanceolate to linear lanceolate, a characteristic of *Z. caracasana*. In some cases, the identification of herbarium specimens is troublesome if information concerning habit and filament color is not provided. However, there are several diagnostic characters for each taxon (Table 13, while comparing the two species, applies to the two subspecies discussed here). *Zapoteca caracasana* subsp. *caracasana* differs from *Z. portoricensis* subsp. *portoricensis* in its prostrate/scandent habit, smaller flowers, white/red-purple filaments, and by the frequent occurrence of pseudopaniculate inflorescences with more slender peduncles. The relationships between these two taxa are discussed further under *Z. caracasana*.

6b. Zapoteca portoricensis subsp. **pubicarpa** H. Hern., subsp. nov. TYPE: Mexico. Oaxaca: Dist. Huajuapan de León, a 6 km NW de San Jerónimo Silacayoapilla, casi en la desviación a Ciénega Zahuatlán, veg. alterada de *Bursera* con *Lysiloma*, 1,900 m, 4 Dec. 1978, *Sousa & Zárate 9822* (holotype, MEXU; isotype, CAS).

Pinnae 2–4-juga; foliola 15–30-juga in pinna utraque angusto-oblonga vel lanceolata. Calyx 2–3(–3.5) mm longus, dentibus villosis saepe forte villosis; corolla 7–8(–10) mm longa saepe apice villosa. Legumina puberula.

Erect shrubs, to 3 m tall; branchlets villous to densely villous with white-gray hairs. Pinnae 2–4-jugate; leaflets 15–30 pairs per pinna, narrowly oblong to lanceolate, oblique at base, acute at apex, mucronulate, the median ones 4–7 × 1–2 mm, ciliate, rarely sparsely villous; stipules narrowly triangular, to 11 mm long, usually densely villous. Capitula axillary; peduncles costate, 1.3–3.5(–6) cm long at anthesis, glabrous to densely villous. Calyx 2–3(–3.5) mm long, the teeth triangular, the area of the teeth villous to densely villous; corolla 7–8(–10) mm long, usually villous apically; ovary glabrous. Pods ca. 6–7 cm long, brown, puberulent.

Distribution (Fig. 36). Endemic to a restricted area in southern Puebla and northern Oaxaca, where it has been collected in disturbed places in the transition zone between oak and tropical deciduous forests and in thorn forests. Collections come from 1,850–2,120 m. Plants of this subspecies grow in a generally drier environment than other mainland populations of the species.

Additional specimens examined. MEXICO. PUEBLA: 259 km SE of Mexico City, *Barr et al. 62-709* (MEXU); vicinity of San Luis, Barranca de Tlacuilosto, *Purpus s.n.* (BM, F, GH, MO, NY, UC, US); Cerro de la Yerba, San Luis Tultitlanapa, Sierra Mixteca, *Purpus 2668* (G, UC); 4.4. mi. SW of Acatepec, *Schaffner et al. 74-64b* (US); a 7 km al SW de Acatepec, *Sousa 7740* (MO); Mpio. de Zapotitlán de las Salinas, a 8 km al SW de Acatepec, *Sousa & Rico 10322* (MO); El Coro, 10 km NW de Caltepec, o 6 km SE de Acatepec, *Tenorio 6859* (MEXU); Mpio. Caltepec, Rincón de la Hierba, Mesa Chica al W de Caltepec, *Tenorio & Romero 7604* (MEXU).

Zapoteca portoricensis subsp. *pubicarpa* is closely related to subsp. *portoricensis*, from which it can be distinguished primarily by having puberulent pods, villous calyx teeth, larger flowers, and usually shorter peduncles (see Table 12). The ovaries are glabrous, but pubescence becomes evident soon after the pods start to develop. The characteristics used to define this subspecies are not discontinuous with those of subsp. *portoricensis*. However, the particular combination of morphological characters defining subsp. *pubicarpa* is distinctive and appears to be relatively constant throughout its range. This and its biogeographic consistency justify its recognition as a separate subspecies.

The pubescence of the pods is the main diagnostic character for this subspecies. Nevertheless, hairy pods have been found in two collections of *Z. portoricensis* subsp. *portoricensis* from Nicaragua (*Laguna 333*, *Moreno 8272*). These plants, however, have smaller flowers and longer peduncles than are characteristic of subsp. *pubicarpa*; they clearly fall within the limits of subsp. *portoricensis*. Flower size is variable in subsp. *portoricensis*, with large (calyx = 2–3 mm long, corolla = 6–8 mm long) flowers found in plants throughout the range of this subspecies; such flowers, however, are rarely as large as those of *Z. portoricensis* subsp. *pubicarpa*, and the plants on which they occur never have the hairy pods or short peduncles characteristic of subsp. *pubicarpa*.

6c. Zapoteca portoricensis subsp. **flavida** (Urban) H. Hern., comb. et stat. nov. *Calliandra flavida* Urban, Ark. Bot. 24A: 4. 1931; Britton & Killip, Ann. New York Acad. Sci. 35: 137. 1936. TYPE: Grenada, ad Belvedere, 1,600 ft., Dec. 1889, *Eggers 6226* (lectotype, US 938738, here designated; isolectotype, GH).

Scandent shrubs, 2–3(–7) m tall; stems slender; branchlets terete, usually spreading and descending, glabrous to sparsely villous, sometimes densely villous in the younger parts. Pinnae (2–)3–5(–7)-jugate; leaflets 8–18(–36) pairs per pinna, the median ones oblong to oblong-obovate, sometimes subfalcate, oblique at base, rounded to acute at apex, mucronulate, 7–20 × 2–6 mm, finely villous on both surfaces; stipules triangular-lanceolate, occasionally linear-triangular, to 11(–13) mm long, glabrous, ciliate. Capitula commonly axillary, occasionally in pseudopanicles to 20 cm long; peduncles slender, 3–7.5 cm long at anthesis. Calyx 1–2 mm long, glabrous, the teeth triangular to deltate, rarely narrowly oblong, acute, occasionally irregular; corolla 3–4 mm long. Pods to 16.5 × 1.2 cm at maturity, thickly membranous, usually black at maturity. Seeds ovoid to very widely ovoid, ca. 6 × 4–5 mm, brown to dark brown, the areola usually mottled, pleurogram irregular. Somatic chromosome number $2n = 26$.

Distribution (Fig. 36). *Zapoteca portoricensis* subsp. *flavida* primarily occurs in lowland tropical forests, where it is commonly found along river banks, in inundated areas, and in wet thickets. Its range extends from southeastern Veracruz and northern Oaxaca, Mexico to Venezuela and Peru, where it has been collected in several disjunct populations. Additional collections have been made in Grenada (Lesser Antilles), Guyana, in the states of Pará, Ceará, Pernambuco, Goiás, Mato Grosso, Brazil, and in the department of Santa Cruz, Bolivia. In Mexico and Central America it is primarily a lowland subspecies, extending altitudinally from 0 to 670 m elevation; in Venezuela it reaches 1,100 m. This subspecies has been introduced to Africa, where it has been collected from naturalized populations in Ghana (*Enti 275*, *Vigne 1011*) and from cultivated individuals in Nigeria (*Guile 701*).

Additional specimens examined. MEXICO. CHIAPAS: Mpio. Palenque, a 6 km W del entronque a Palenque, *H. Hernández & Torres 805* (MEXU, MO); Bonampak, *Hoover 283* (GH, MO, US); Mpio. Ococingo, 5 km S Frontera Echeverría, *Martínez 9120* (MEXU); Mpio. Ococingo, 2 km W Crucero Corozal, camino Palenque Boca Lacantun, *Martínez 10156* (MEXU); Mpio. Ococingo, 4 km S Ejido Benemérito de las Americas, camino a Flor de Cacao, *Martínez 10779* (MEXU); Mpio. de Palenque, a 5 km al W de Catazajá, *Sousa et al. 12277* (BM, MEXU); Mpio. de Ocosingo, ca. Bonfil, *Valdivia*

2291 (XAL). OAXACA: Chiltepec, *Martínez A. 93* (XAL); Tuxtepec, Chitepec, *Martínez-Calderón 304* (A, LL, MEXU, UC, US). TABASCO: Tacotalpa, Río Tacotalpa, *Cowan 2731* (LL, MEXU); Majito, *Rovirosa 652* (K, US); Huimanguillo, San Miguel, 41 km al W de Cárdenas, *Sousa et al. 12288* (BM, MEXU). VERACRUZ: Chacaltianhuis, La Isleta, *López s.n.* (XAL); Mpio. Catemaco, Río Coxcoapa que desemboca en Laguna Sontecomapan, *H. Hernández & Torres 793* (MEXU, MO); Minatitlán, *Mell s.n.* (NY, US); Laguna de Sontecomapan, sobre la ribera del Río Coscoapan, Catemaco, *Menéndez 131* (F, MEXU, MO). GUATEMALA. ALTA VERAPAZ: Laguna Sapalá, 1 mi. SW of Sibicté, *Steyermark 44929* (F); Cubilquitz, *Tuerckheim 7737* (GH, K, MEXU, NY, US). IZABAL: Jocoló, *H. Johnson 1075* (F, US); between Dartmouth and Morales towards Lago Izabal, Montaña del Mico, *Steyermark 39103* (F, G); Lago Izabal, opposite San Felipe, between San Felipe and mouth of Río Juan Vicente, *Steyermark 39685* (F). PETÉN: Lacandón, on El Caribal, about 6 km SSW, *Contreras 3537* (F, LL, MEXU); San Pedro, Cadenas Road, *Contreras 9480* (F, LL, MEXU). RETALHULEU: Retalhuleu, *Bernoulli & Cario 1257* (K). BELIZE: Moho River, *Peck 752* (GH); Río Grande, *Schipp 1106* (A, BM, F, G, GH, K, MICH, MO, NY, UC); Jacinto Creek, *Schipp 1216* (A, BM, F, G, GH, MICH, MO, NY, UC). HONDURAS. SANTA BÁRBARA: Limones, *Standley & Lindelie 7540* (F). NICARAGUA. ZELAYA: Cerro La Gloria (13°40′10″N, 84°56′25″W), *Ortiz 1131* (MO). PANAMA: DARIÉN: Río Areti, *Duke & Nickerson 14906* (MO). VENEZUELA. DELTA AMACURO: region of Morón and Temiche to mouth of Río Cuyubini, *Steyermark 87702* (F, MICH, NY). CARABOBO: between Puerto Cabello and San Felipe, *Pittier 9133* (GH). YARACUY: Los Cañizos, *Pittier 8759* (GH, NY, US). COLOMBIA. CHOCÓ: Río Truandó, between Río Sucio and La Nueva, *Duke 9815* (NY). META: Sierra de la Macarena, Plaza Bonita, *Philipson et al. 1418* (US). SANTANDER: Carare, *André 294* (F, GH, K, NY, US). ECUADOR. GUAYAS: Capeira, between Guayaquil and Daule, *Dodson & Gentry 12579* (MO). LOS RÍOS: between Quevedo and Santo Domingo, *Dodson & Gentry 6293* (MO). PERU. HUANUCO: Pachitea, *Schunke 2571* (F, G, US). JUNÍN: Río Paucartambo Valley, *Killip & Smith 25272* (NY, US); Puerto Yessup, *Killip & Smith, 26320* (NY, US); Puerto Bermúdez, *Killip & Smith, 26435* (NY, US). LORETO: Yurimaguas, *Ule 6725* (F, G, K). SAN MARTÍN: Chazuta, Río Huallaga, *Klug 4014* (BM, CAS, F, GH, MO, NY, UC, US); Juan Jui, Alto Río Huallaga, *Klug 4298* (A, BM, F, MO, NY, UC, US); Mariscal Cáceres, Tocache Nuevo, *Schunke 4758* (CAS, F, G, GH, MICH, MO, NY, US, WIS). BRAZIL. CEARÁ: Serra Pacoti, *Guedes 378* (US). GOIÁS: Maurilândia, Rio dos Bois, *Hatschbach 34270* (NY); Serra do Caiapó, 30 km S of Caiapônia, *Irwin et al. 17993* (NY). MATO GROSSO: Aripuana, Projoto Juína, *Silva & Rosário 4811* (F). PARÁ: Serra de Baterrité, *Ducke 1517* (BM, US); Monte Alegre, Colonia Itahuajury, *Ducke 16051* (BM, US); Monte Alegre, Serro do Luna, *Fróes 30295* (US). PERNAMBUCO: Tapéra, *Bento 2430* (F, GH, MICH, US, WIS); Vicencia, Mata do Eng. Jundiá, Pedra da Negra, *Tavares 754* (NY). BOLIVIA. SANTA CRUZ: Prov. Ichilo, Buena Vista, *Steinbach 822* (F, GH, MO, NY, US, WIS); Prov. Del Sará, Cuenca del Surutú, Cantón Buenavista, *Steinbach 2460* (A).

This subspecies can be easily distinguished from subsp. *portoricensis* and *pubicarpa* by its scandent habit, larger, usually less numerous leaflets, and usually larger pods. In addition, subsp. *flavida* primarily grows in habitats associated with lowland tropical forests, whereas the two other subspecies have been collected chiefly in subtropical, mid- to relatively high-altitude habitats. *Zapoteca portoricensis* subsp. *flavida* can be distinguished from *Z. caracasana* by having larger leaflets, flower buds constantly glabrous, deltate-triangular calyx teeth, white filaments, and larger pods. The capitula are arranged in pseudopanicles only occasionally in *Z. portoricensis* subsp. *flavida*; this is a very common condition in *Z. caracasana*.

Zapoteca portoricensis subsp. *flavida* is relatively constant morphologically throughout its wide range; however, a number of collections from South America have a combination of characters that differ from those of the Mexican and Central American plants. Characteristics of a collection from Colombia (*Philipson et al. 1418*) suggest morphological intergradation between *Z. portoricensis* subsp. *flavida* and *Z. caracasana*: narrowly triangular to linear-triangular stipules, leaflets 8 × 2 mm, numerous (to 36) pairs of leaflets per pinna, capitula arranged in elongate pseudopanicles, calyx with linear-lanceolate teeth, and white filaments. An almost identical situation is displayed by most of the Brazilian collections of *Z. portoricensis* subsp. *flavida* (*Andrade-Lima 70-5777, Ducke 1517, 16051, Fróes 30295, Guedes 378, Hatschbach 34270, Pickel 2430, Tavares 754*). Here, several of the vegetative and reproductive characters diagnostic of either *Z. portoricensis* subsp. *flavida* or *Z. caracasana* intergrade in particular populations.

Although it is not known whether *Z. portoricensis* subsp. *flavida* and *Z. caracasana* ever actually grow together in specific habitats, they have been collected in comparable microhabitats (e.g., river banks, shady sites, and thickets), which raises the possibility of hybridization. Populations of *Z. caracasana*, however, occur more commonly in drier habitats than do those of *Z. portoricensis* subsp. *flavida*. The distributions of these two taxa overlap only in the area of the Andes, where there is much local microhabitat differentiation.

Collections from Bolivia have some characters that do not correspond with those commonly found in individuals of *Z. portoricensis* subsp. *flavida*. For instance, the filaments are reported to be white-pink, instead of white, in *Steinbach 822*. The calyx in almost all the Bolivian collections has lanceolate teeth (*Steinbach 5412, Weddell 4237, Williams 267*). In addition, the mature pods are always smaller than typical for this entity (to 10 cm long)

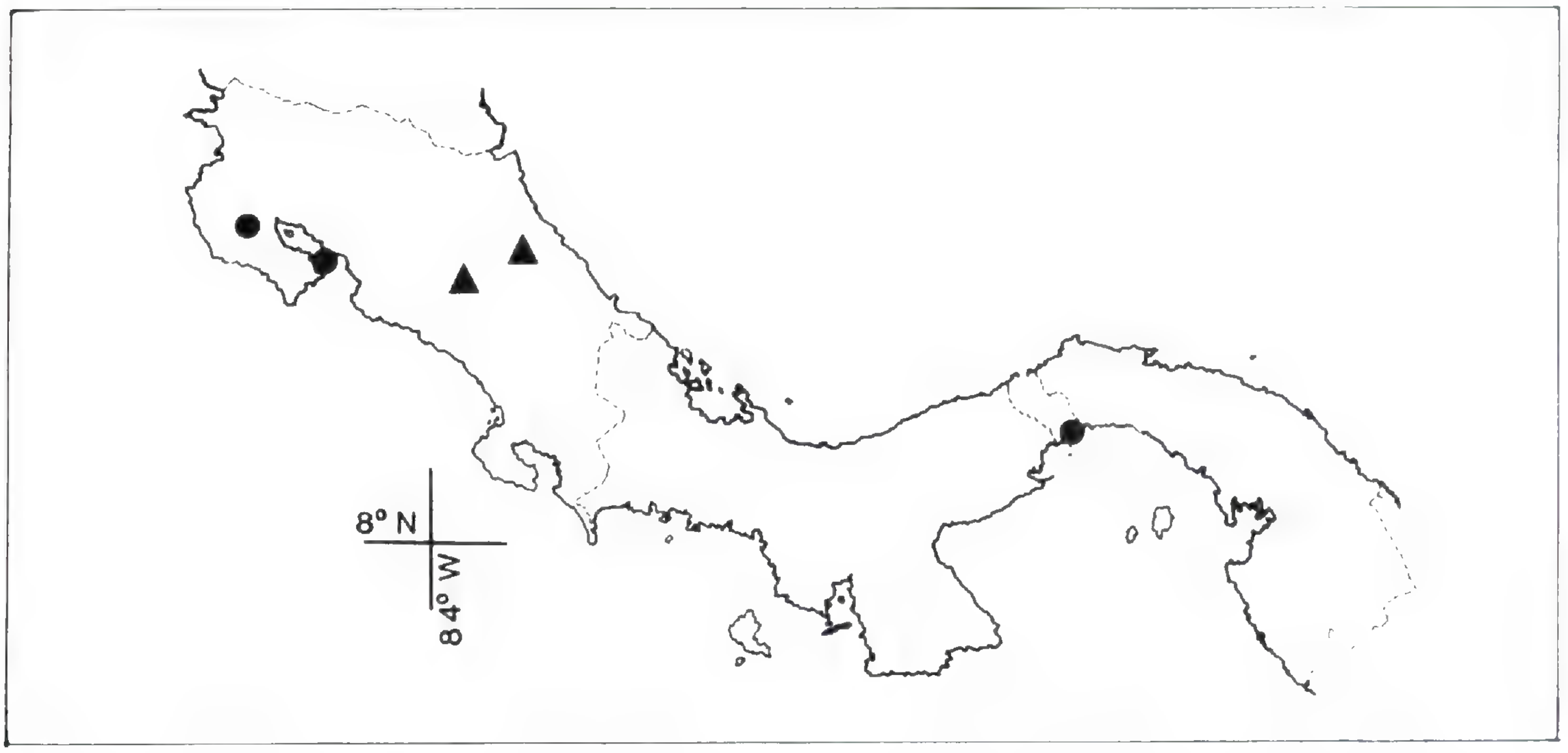


FIGURE 37. Distribution of *Zapoteca mollis* (dots) and *Z. costaricensis* (triangles), Costa Rica and Panama.

and the valves are thicker (e.g., *Pierce s.n.*, *Troll 1738*, *Williams 241*).

7. **Zapoteca mollis** (Standley) H. Hern., Ann. Missouri Bot. Gard. 73: 755–763. 1986. *Calliandra mollis* Standley, Contr. U.S. Natl. Herb. 17: 431. 1914; Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 492. 1937. *Anneslia mollis* (Standley) Britton & Rose, N. Amer. Fl. 23: 65. 1928. TYPE: Costa Rica: buissons à Nicoya, Jan. 1900, *Tonduz 13536* (holotype, US no. 578114; isotypes, BM (2), F, G (3), GH, K (2), LE, NY (3), US (2)).

Erect shrubs to 3 m tall; branchlets terete, costate under magnification, abundantly villous with tawny hairs. Pinnae (3–)4–6-jugate; petioles eglandular, terete, with a conspicuous channel in the adaxial surface, 1.2–4.5 cm long, abundantly villous; rachis 3.5–9.5 cm long, abundantly villous; rachillae 4.5–12.5 cm long in well-developed leaves; leaflets 15–26 pairs per pinna, narrowly oblong, oblique at base, acute to rounded and mucronulate at apex, the median leaflets 7–18 × 2–5 mm, the proximal ones smaller, all membranous, drying a light green in the abaxial surface, densely pilose with white hairs on both surfaces; leaflet venation inconspicuous; stipules leafy, triangular-lanceolate, acute, ca. 6–14 mm long, parallel-veined, pilose, ciliate. Capitula in simple, rarely compound, pseudopanicles 3.5–15 cm long; peduncles usually fasciculate, rarely solitary, 2.5–4 cm long at anthesis, usually densely villous with tawny hairs. Calyx ca. 2–3 mm long, glabrous, the teeth lanceolate, acute, ca. 2 mm long; corolla infundibuliform, ca. 3–4 mm long, glabrous, the lobes ovate-lanceolate, acute; filaments about 2.5 cm long, the basal half white and the distal half ochroleucous, the staminal tube ca. 2 mm long; ovary ca. 2–3 mm long when fertile, glabrous, sometimes with fine translucent hairs, sessile. Pods to 9 × 0.7 cm when mature, with the apex rounded, rarely truncate, rostellate, thickly membranous, densely villous with long tawny hairs. Seeds widely rhomboid, flattened, ca. 4 × 3 mm, dark colored, the areola lighter, pleurogram irregular.

Distribution (Fig. 37). This species has been collected in tropical dry forests near Nicoya (Peninsula of Nicoya), in San Lucas Island (Gulf of Nicoya), and in Río Lagarto, all in Prov. Puntarenas, Costa Rica. Plants from a presumably disjunct population have been collected in Santa Cruz, near Panama City, Panama.

Additional specimens examined. COSTA RICA. PUNTARENAS: Island of San Lucas, Gulf of Nicoya, *Barclay 2756* (BM, MO, US); Isla de San Lucas, Golfo de Nicoya, along Quebrada Hacienda Vieja, 9°57′N, 84°54′W, *Grayum et al. 4164* (MEXU, MO); Isla de San Lucas, Golfo de Nicoya, between Playa Tumbabote and Punta Barrigona, *Grayum 4201* (MEXU, MO); Isla de San Lucas, Golfo de Nicoya, along trail to Punta Cirial, *Grayum 4290* (MEXU, MO); Río Lagarto, entronque a Monteverde y Guacimal, *Téllez 4307* (MEXU). PANAMA: Santa Cruz, *Arroyo 37* (MO).

This species closely resembles *Z. portoricensis* subsp. *flavida* in general characteristics of leaves and inflorescences, but it can be distinguished readily by having an erect habit, which contrasts with the scandent habit of the subspecies, and by being villous or pilose throughout, including the pods,

which are densely covered with long tawny hairs. Further, the filaments are white in *Z. portoricensis* subsp. *flavida*, but white in the basal half and ochroleucous in the distal half in *Z. mollis* (*Grayum 1162, 4290*). (It would be desirable to check more living individuals for this feature.) Contrasted with *Z. portoricensis* subsp. *flavida*, which is commonly found in thickets in wet lowland habitats (e.g., along water courses and near ponds), populations of *Z. mollis* usually occur in relatively dry habitats. With the exceptions of *Z. formosa* subsp. *salvadorensis*, *Z. caracasana* subsp. *weberbaueri*, and *Z. portoricensis* subsp. *pubicarpa*, this is the only species in the genus with hairy pods.

In addition to the few collections of this species from Costa Rica, there is a collection from Santa Cruz, near Panama City (*Arroyo 37*), which indicates a disjunction in its range. This collection, with immature pods, matches the plants collected in Costa Rica well. Recent attempts (1984) to recollect from this population have been unsuccessful, presumably due to widespread destruction of natural habitats in this part of Panama.

8. Zapoteca caracasana (Jacq.) H. Hern., Ann. Missouri Bot. Gard. 73: 755–763. 1986. *Mimosa caracasana* Jacq., Collectanea 4: 142. 1791. *Acacia caracasana* (Jacq.) Willd., Spec. 4: 1068. 1806; DC., Prodr. 2: 467. 1825; G. Don, Gen. Hist. 2: 419. 1832. *Calliandra caracasana* (Jacq.) Benth., London J. Bot. 3: 99. 1844; Benth., Trans. Linn. Soc. London 30: 543. 1875; Britton & Killip, Ann. New York Acad. Sci. 35: 137. 1936; J. F. Macbr., Fieldiana, Bot. 13: 69. 1943; Woodson & Schery, Ann. Missouri Bot. Gard. 37: 260. 1950; L. Cárdenas, Revista Fac. Agron. (Maracay) 7: 131. 1974. *Feuilleea caracasana* (Jacq.) Kuntze, Revis. Gen. Pl. 184. 1891. *Anneslia caracasana* (Jacq.) Britton & Rose, N. Amer. Fl. 23: 65. 1928. TYPE: Jacq., Icon. Pl. Rar. 3: 20, t. 632. 1793 (neotype here designated, copies at MO, NY, U). I have designated this excellent illustration as neotype (Fig. 38) because no other element on which the description of *Mimosa caracasana* was based appears to have survived.

Scandent, subprostrate or prostrate shrubs; stems usually branching shortly above soil level, ca. 2 cm diam.; branchlets flexible, elongate, usually to 3(–5) m long, terete, sometimes angulate, costate, glabrous to densely villous. Pinnae (1–)2–7-jugate; leaf primordia usually densely villous or pilose; petioles eglandular, terete, with a conspicuous channel adaxially, 0.9–5 cm long, usually villous or pilose; rachis (0.4–)1–7.5 cm long; rachillae 2–6(–7.5) cm long; leaflets 10–26(–37) pairs per pinna, narrowly oblong, oblique at base, rounded to acute at apex, the median ones (4–)5–10(–11) × (1–)1.5–2.5(–3) mm, the proximal ones smaller, all membranous, glabrous to short-villous, usually ciliate; leaflet venation usually conspicuous abaxially, the primary and secondary veins prominent; stipules leafy, narrowly triangular to linear-triangular, sometimes subauriculate at base, acuminate, parallel veined, to 7(–12) mm long, glabrous to villous, usually ciliate. Capitula axillary or in simple or, less frequently, compound pseudopanicles to 20(–26) cm long; peduncles fasciculate at distant nodes, 1.5–6.5 cm long at anthesis. Flowers pentamerous, sometimes hexamerous; calyx cup-shaped, deeply divided to the base, 1.5–2 mm long, glabrous to densely covered with relatively long wavy hairs in bud, glabrous, villous or ciliate at anthesis, the teeth lanceolate to linear-lanceolate; corolla campanulate, 3–4 mm long, glabrous, the lobes lanceolate; filaments ca. 2.5 cm long, white in the basal half, purple-red in the distal half, the staminal tube ca. 1.5 mm long; ovary ca. 1 mm long when fertile, glabrous or occasionally with a few hyaline hairs, shortly stipitate. Pods straight, sometimes slightly curved, apex usually curvedly rostrate, 10(–11) × 0.7(–0.8) cm, thickly membranous, glabrous, glabrate, or canescent, becoming densely short-pubescent. Seeds ovoid to rhomboid-ovoid, 4–6 × 3–4 mm, mottled or brown; pleurogram irregular. Somatic chromosome number $2n = 26$.

Distribution (Fig. 39). Populations of this species occur primarily in disturbed habitats derived from a wide variety of vegetation types, ranging from dry scrubby vegetation to wet evergreen forests. Its range extends from northern Venezuela (including Isla Margarita) southwest to Colombia, Ecuador, and Peru, where it has been collected in scattered localities. It has also been found in Hispaniola and in a distant disjunct population in Honduras. Perhaps this is the species within *Zapoteca*

→

FIGURE 38. "*Mimosa caracasana*" (= *Zapoteca caracasana* subsp. *caracasana*), from Jacquin's *Icon. Pl. Rar.* 3: 20, t. 632. 1793.

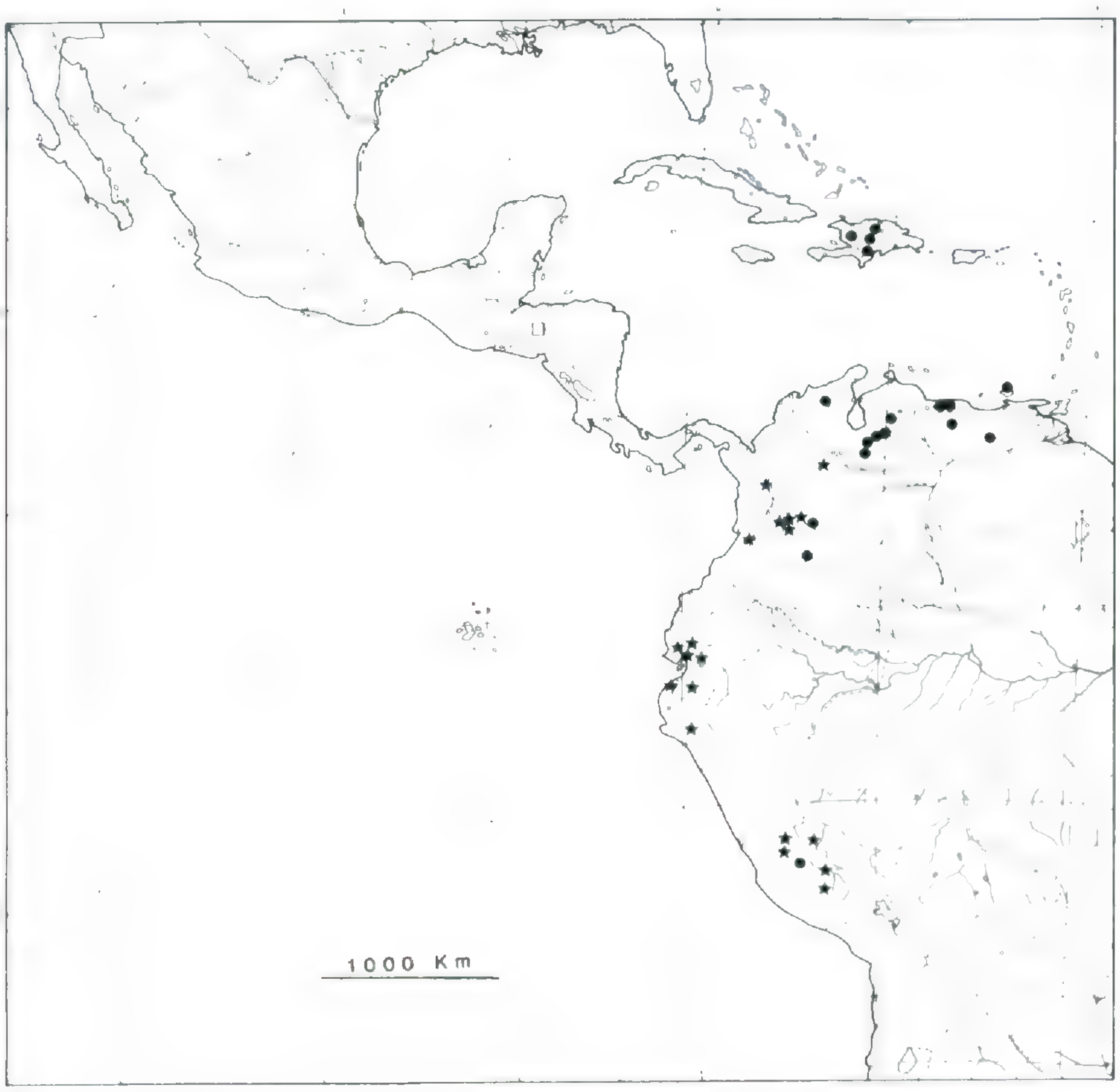


FIGURE 39. Distribution of *Zapoteca caracasana* subsp. *caracasana* (dots), *Z. caracasana* subsp. *weberbaueri* (stars), and *Z. caracasana* of unknown subspecific affinity (open square).

of which populations occupy the widest altitudinal range: 0–2,500 m. Woodson & Schery (1950) incorrectly included this species in the *Flora of Panama*.

Zapoteca caracasana is closely related to *Z. portoricensis*, and these two species have been merged at times. For instance, Bentham (1844) considered *Z.* (*Calliandra*) *caracasana* as a synonym of *C. portoricensis*, although subsequently, in his revision of Mimosoideae (Bentham, 1875), he recognized them as distinct species. Later, Woodson & Schery (1950) treated *Calliandra portoricensis* as a synonym of *C. caracasana*. The most important characters distinguishing these two species are outlined in Table 13. Although identification of herbarium specimens is admittedly difficult in some cases, *Z. caracasana* can be distinguished from *Z. portoricensis* by its presumably constant scandent or prostrate habit, usually smaller leaflets, and capitula with more slender peduncles, which are usually arranged in pseudopaniculate inflorescences, a condition rarely found in *Z. portoricensis*. Observations on cultivated material and information from herbarium specimens suggest that the scandent/prostrate habit of *Z. caracasana* is widespread throughout its range; however, it is uncertain whether it is characteristic of all the populations or if erect plants occasionally occur, as indicated by label information on a few specimens. Within *Z. portoricensis*, the scandent habit occurs only in subsp. *flavida*. There are, however, important differences in growth habit between that entity and *Z. caracasana*: cultivated specimens of of *Z. caracasana* (*H. Hernández 961*) had extremely short primary stems, usually giving rise to drooping, very elongate branchlets ca. 10 cm above the soil level, while those of *Z. portoricensis* subsp. *flavida* develop very long, flexible primary stems, sometimes reaching several meters before giving rise to secondary branches.

The flowers of *Z. caracasana* are generally smaller than those of *Z. portoricensis*, and the calyces are consistently deeply divided to the base, with the teeth lanceolate to linear-lanceolate. In addition, the two species are easily distinguished by their filament colors (Table 13) and by the usually smaller pods in *Z. caracasana*. Pod size, however, is highly variable in *Z. portoricensis*.

Although the degree of pubescence of stems and leaves is extremely variable in *Z. caracasana* and in *Z. portoricensis*, the branchlets of the former

TABLE 13. Comparison of *Zapoteca caracasana* with *Z. portoricensis*.

	Z. caracasana	*Z. portoricensis*
Habit	scandent, prostrate	scandent, erect
Leaflet l × w	4–11 × 1–3 mm	4–20 × 1–6 mm
Capitula	commonly arranged in pseudopanicles, or axillary	usually axillary, rarely in pseudopanicles
Calyx	deeply divided with the teeth lanceolate to linear-lanceolate	teeth triangular or deltate, rarely lanceolate to linear-lanceolate
Corolla length	3–4 mm	3–8(–10) mm
Filament color	white–red-purple	white
Maximum pod length	to 11 cm	to 16.5 cm

are never as densely villous as commonly in the latter. Similarly, the indumentum of the calyx is highly variable in *Z. caracasana*, most of the collections with completely glabrous calyces being concentrated in Ecuador. However, the peculiar vestiture observed in the flower buds of this species has never been observed in *Z. portoricensis*. Further discussion of the relationships between these two species is under *Z. portoriensis*.

Zapoteca caracasana consists of two closely related subspecies: *caracasana* (with glabrous pods) and *weberbaueri* (with canescent or pubescent pods). As in the other taxa of *Zapoteca* with pubescent pods (*Z. mollis*, *Z. portoricensis* subsp. *pubicarpa*, *Z. formosa* subsp. *salvadorensis*), the ovaries of *Z. caracasana* subsp. *weberbaueri* are glabrous, and the hairs of the pods presumably develop after fertilization. However, the ovaries in this subspecies occasionally have a few hairs.

KEY TO THE SUBSPECIES OF *ZAPOTECA CARACASANA*

1a. Pods glabrous or nearly so ..... 8a. subsp. *caracasana*

1b. Pods canescent or pubescent ..... 8b. subsp. *weberbaueri*

8a. Zapoteca caracasana (Jacq.) H. Hern. subsp. **caracasana.**

Branchlets villous to glabrate, usually glabrate, rarely densely villous. Calyx densely covered with usually wavy, long hairs or glabrous in bud, the teeth usually ciliate at anthesis; ovary glabrous. Mature pods to 10(–11) × 0.7(–0.8) cm, glabrous, rarely glabrate. Seeds 5–6 × 4 mm.

Distribution (Fig. 39). Relatively common along roadsides, in cultivated fields and thickets, and in shady sites. In the West Indies it occurs on Hispaniola. On the mainland, it has been collected in northern Venezuela (including Isla Margarita), in a few presumably disjunct localities in the departments of Magdalena and Meta, Colombia, and the Department of Ayacucho, Peru. *Zapoteca caracasana* subsp. *caracasana* appears to be allopatric with *Z. caracasana* subsp. *weberbaueri*, although their ranges come into proximity in Colombia and Peru. Collections come from altitudes of 200–1,300(–2,500) m. This subspecies has also been collected from cultivated individuals at the Botanical Garden of Pará, Brazil (*Huber 2078*). Given the fact that the only collection from Honduras lacks pods, it is not possible to assign it to a subspecies.

Common name. Cujicillo (Dominican Republic).

Additional specimens examined. HAITI: Massif des Cahos, Les Gonaives, *Ekman 9081* (GH, K, MO, NY, S, US). DOMINICAN REPUBLIC. MONTE CRISTI: Santo Domingo, Cordillera Central, Monción, *Ekman 12612* (S). AZUA: Río del Medio, *Ekman 13733* (GH, S, US). BAHORUCO: between El Aguacate and Sapotén, *Liogier 19782* (F, NY). SANTIAGO: Hato del Yaqua, Valle del Cibar, *Ekman 16527* (A, F, G, GH, S, US); Cerro de la Culebra, *Jiménez 910* (US); Constanza, El Chorrito, *Liogier 12230* (NY); near Las Mercedes, Pedernales, *Liogier 16687* (NY); near Sapotén, *Liogier 18190* (NY). VENEZUELA. ARAGUA: Carmen, *Williams 10411* (F, US). DISTRITO FEDERAL: Naiquetia, *Gentry & Morillo 10326* (MO); near Caracas, Lower Cotiza, *Pittier 7307* (G, GH, P, US); Losa, *Tamayo 572* (A, S, UC, US); between Sabana Grande and Baruta, *Williams 10592* (F, US). MERIDA: near Barinitas (8°45′N, 70°40′W), *Breteler 3149* (MO, NY, S); Tycoporo Forest Reserve (8°15′N, 70°45′W), *Breteler 3445* (US). NUEVA ESPARTA: El Valle, *Miller & Johnston 261* (F). PORTUGUESA: Guanare, 17 km NW of Tucupido, *Davidse et al. 21420* (MO). COLOMBIA. META: Villavicencio, *Cuatrecasas 4691* (F, US); Sierra de la Macarena, Río Guapaya, *Philipson et al. 1626* (F, US). MAGDALENA: Manaure, Sierra de Perijá foothills, *Cuatrecasas & Castañeda 25013* (US). PERU. AYACUCHO: Estrella, between Huanta and Río Apurimac, *Killip & Smith 23091* (NY, US). HONDURAS: COPÁN(?): Quebrada N of Copán, *Poole & Watson 1034* (LL).

8b. Zapoteca caracasana subsp. **weberbaueri** (Harms) H. Hern., comb. et stat. nov.

Calliandra weberbaueri Harms, Repert. Spec. Nov. Regni Veg. 17: 88. 1921. TYPE: Peru. Huancavélica: Prov. Tayacaja, Valley of the Mantaro, northeast of Pampas, 1,600 m, Mar. 1913, *Weberbauer 6511* (lectotype, GH, here designated; isolectotypes, F, G (fragm.), S, US).

Branchlets densely villous to usually glabrate. Calyx very densely covered with usually wavy, long hairs, or glabrous in bud, the teeth ciliate or glabrous at anthesis; ovary glabrous, very rarely with a few, translucent hairs. Mature pods to 10 × 0.7 cm, usually canescent when young, densely short-pubescent at maturity. Seeds 4–5 × 3–3.5 mm. Somatic chromosome number $2n = 26$.

Distribution (Fig. 39). This subspecies occurs primarily in relatively dry, scrubby vegetation. It has been collected from scattered localities in Colombia, in the departments of Antioquia, Cauca, Cundinamarca, Santander, Tolima, and Valle; in Ecuador, in the provinces of Chimborazo, Guayas and Loja; and in Peru, in the departments of Apurímac, Cuzco, Huancavélica, Lambayeque, and Tumbes. Collections come from elevations of 0 2,500 m.

Additional specimens examined. COLOMBIA. ANTIOQUIA: vicinity of Medellín, *Toro 787* (NY, US). CUNDINAMARCA: alrededores de Puente de San Antonio de Tena, *Cuatrecasas 8284* (F, US); La Esperanza, *García 4675* (US); Santandercito, *Uribe 467* (US). SANTANDER: Río Suratá valley, between El Jaboncillo and Uratá, *Killip & Smith 16433* (GH, NY, US); between El Roble and Tona, *Killip & Smith 19392* (A, GH, NY, US). TOLIMA: Chicoral, *Haught 6442* (US). VALLE: 30–35 km E Palmira, *Johnson 2494-82* (MO). ECUADOR: CHIMBORAZO: between Huigra and Naranjapata, *Asplund 15503* (G, LL, NY, S); canyon of the Río Chanchan, near Huigra, *Camp E-3107* (F, GH, MO, NY, US); Ventura, *Rose & Rose 23517* (GH, NY, US). GUAYAS: between Chongón and Ceresita, *Asplund 15335* (B, NY, S); Guayaquil, *Asplund 15982* (B, G, LL, NY, P, S, US); km 19 W of Pasquales on Guayaquil-Daule road, *Dodson et al. 13596* (MO); Capeira, km 21, Guayaquil to Daule, *Dodson & Gentry 13862* (MO). LOJA: 55 km W of Loja, between San Pedro and Chinchas, *Espinosa 1295* (US). PERU. APURIMAC: Casinchihua in Río Pachachaca Valley, 33 km SW of Abancay, *Iltis et al. 838* (NY, WIS); Abancay, *Vargas 9154* (MO); Hacienda Lucre, Oropeza Valley, *Vargas 9773* (F, G, UC). CUZCO: Prov. Convención, Rosario Mayo, *Alfaro 361* (MO); Prov. Convención, Echarate, *Vargas 10455* (F, G, GH, UC); Prov. Convención, alrededores de Quillabamba, *Vargas 249* (F); Prov. Convención, Chauca Mayo, *Vargas 5471* (MO). HUANCAVÉLICA: Tayacaja, Huachocolpa, Quintabamba, *Tovar 4145* (US); Tayacaja, between Chejyaj and Surcubamba, *Tovar 4579* (US). LAMBAYEQUE: km 28 E of Olmos, between Olmos and Jaen, *Hutchison & Wright 3411* (NY, UC). TUMBES: between Quebrada Seca y Matapalo, *Ferreyra et al. 10685* (MO, US).

This epithet has traditionally been associated with *Z. portoricensis* (Macbride, 1943), perhaps because of the superficial similarities between this species and *Z. caracasana*. The type material of "*Calliandra weberbaueri*," however, has a number of features suggesting its inclusion within *Z. caracasana*. For instance, the calyx is deeply divided, and the filaments are "white/pinkish-red" as indicated in Weberbauer's collection. In addition, the "prominent" leaflet veins in the type collection, as seen under magnification, are like those observed in many other collections of *Z. caracasana*.

Acacia fragrans Ten. nom. nud., Cat. Ort. Nap. 1 was apparently never described. There is, however, one specimen at K, clearly identified as *Z. caracasana* subsp. *weberbaueri*, which was presumably collected by Michele Tenore in the Orto Botanico di Napoli; its original source is unknown.

9. Zapoteca tetragona (Willd.) H. Hern., Ann. Missouri Bot. Gard. 73: 755–763. 1986. *Acacia tetragona* Willd., Sp. Pl. 4(2): 1069. 1806. *Calliandra tetragona* (Willd.) Benth., J. Bot. (Hooker) 2: 139. 1840; Benth., London J. Bot. 3: 99. 1844; Benth., London J. Bot. 5: 102. 1846; Benth., Trans. Linn. Soc. London 30: 543. 1875; S. Watson, Proc. Amer. Acad. Arts 22: 410. 1887; Britton & Killip, Ann. New York Acad. Sci. 35: 137. 1936; Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 493. 1937; Standley & S. Calderón, Fl. Salvadoreña 125. 1941; Standley & Steyerm., Fieldiana, Bot. 24: 27. 1946; Woodson & Schery, Ann. Missouri Bot. Gard. 37: 261. 1950; L. Cárdenas, Revista Fac. Agron. (Maracay) 7: 131. 1974. *Feuilleea tetragona* (Willd.) Kuntze, Revis. Gen. Pl. 189. 1891. *Anneslia tetragona* (Willd.) J. D. Smith, Enum. Pl. Guat. 1: 10. 1889. Britton & Rose, N. Amer. Fl. 23: 64. 1928. *Mimosa quadrangularis* Poiret in Lam., Encycl. Suppl. 1: 72. 1810, nom. illeg. (This superfluous epithet was based on Willdenow's *Acacia tetragona*.) TYPE: Venezuela. Caracas: in ripis arenosis fluvii Guairito, *Bredemayer 17* (lectotype designated by Hernández (1986a), B-W cat. no. 19147, not seen; photos at MEXU, MO).

Calliandra portoricensis var. *multijuga* M. Micheli, Bot. Gaz. (Crawfordsville) 20: 285. 1895. TYPE: Guatemala. Santa Rosa: San Juan Utapa, 4,500 ft., Oct. 1893, *Heyde & Lux 6098* (lectotype here designated, G; isolectotypes, GH, US (2)).

Calliandra toroana Britton & Rose in Britton & Killip,

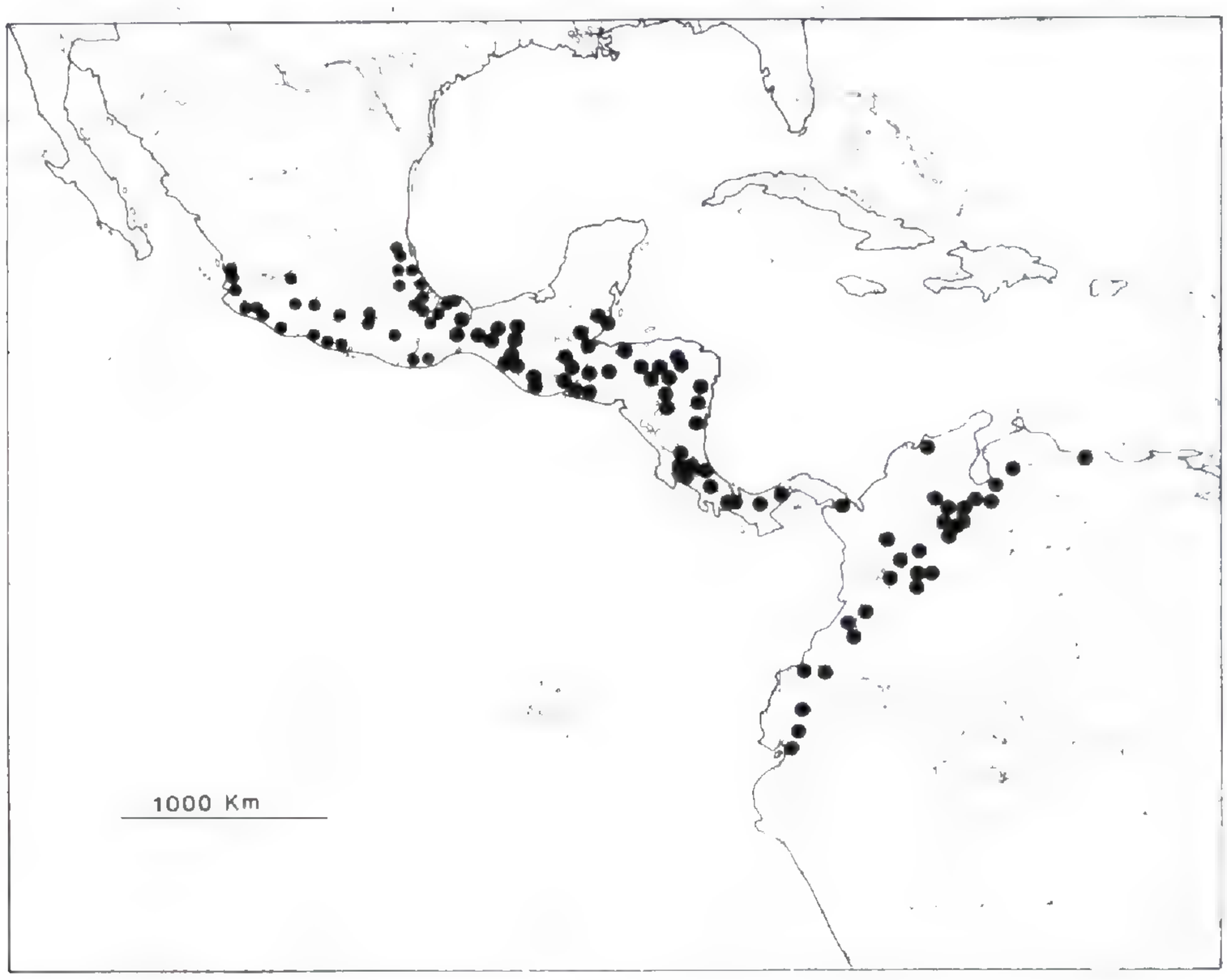


FIGURE 40. Distribution of *Zapoteca tetragona*.

Ann. New York Acad. Sci. 35: 137. 1936. TYPE: Colombia. Antioquia: vicinity of Medellín, 18 Aug. 1927, *Toro 465* (holotype, NY, photo, G).

Mostly shrubs to 5 m tall, rarely trees to 12 m tall; stems 2–4(–20?) cm diam.; branchlets conspicuously 4-angled, sometimes herbaceous in the younger parts, with the surface costate under magnification, mostly densely villous with tawny hairs when young, becoming glabrate. Pinnae (3–)4–7-jugate; petioles eglandular, with a conspicuous adaxial channel, angled, 1.7–6 cm long, glabrous to densely villous; rachis (1.5)3 9(–11.5) cm long, glabrous to densely villous; rachillae (3.5–)4.5–10(–13) cm long; leaflets 10–35 pairs per pinna, narrowly oblong, oblique at base, rounded to acute at apex, the median leaflets (5–)8–18 × 1 4 mm, the proximal smaller, all membranous, glabrous or ciliate marginally, always glabrous on both surfaces; leaflet venation inconspicuous; stipules leafy, adpressed, triangular-linear to triangular-lanceolate, acute at apex, straight or curved, parallel-veined, (0.5–)0.8–2.5 cm long, ciliate, villous or glabrous. Capitula axillary, rarely arranged in pseudopanicles 6–22 cm long; peduncles fasciculate, (2.5–)5–12 cm long at anthesis. Calyx 2–3 mm long, the teeth deltate, ciliate; corolla funnelform, (5–)8 mm long, glabrous, the lobes lanceolate, sometimes with tufts of hairs apically; filaments usually ca. 40 mm long, white, the staminal tube ca. 3 4 mm long; ovary 2 2.5 mm long, glabrous, shortly stipitate. Pods to 16.5 × 1.4 cm, at apex truncate to obtuse, rostellate, thickly membranous, glabrous. Seeds usually ovoid, 5 6 × 3 5 mm, mostly black or dark brown; pleurogram regular, obscure. Somatic chromosome number $2n = 26$.

Distribution (Fig. 40). This widespread species has been collected primarily in moist thickets, along streams or river banks, and, in general, in ruderal habitats derived from tropical and subtropical evergreen forests. Its range extends from Mexico (Nayarit and northern Veracruz) southeast through Central America along the Andean Cordillera in which it reaches southern Ecuador. Populations develop primarily at moderate and less frequently at low altitudes (0–1,500 m), although in some parts of Central and South America they can reach altitudes of 2,300 m.

Common names. Angel (Veracruz), atzalaquio (Puebla), barba de chivo (Veracruz), cabellito blanco (Oaxaca), cabellito de angel (Michoacán, Guerrero, Puebla), cabeza de viejo (Oaxaca, Veracruz), carbonero blanco (Colombia), carboncillo (Costa Rica), carboncillo de flor blanca (Costa Rica), cola de iguana (Jalisco), guaje silvestre (Oaxaca), guajillo (Jalisco), guajillo blanco (Oaxaca), lig tióu (Oaxaca), palo costillo (Guerrero), pelo de angel (Puebla), potosina (Jalisco), quebracho de montaña (Honduras), saqi c'alib (Quecchí name, Guatemala).

Additional specimens examined. MEXICO. CHIAPAS: Mpio. Tenejapa, Paraje Mahben Chauk, *Breedlove 7601* (DS, ENCB, MICH, US); Mpio. Ocozocoautla, 18 20 km N Ocozocoautla along the rd. to Malpaso, *Breedlove & Thorne 20995* (DS, LL, MEXU, MICH, MO); Mpio.

Mapastepec, along Río Testecapa, 10 km SE Mapastepec, *Breedlove & Thorne 30739* (MEXU); Mpio. Frontera Comalapa, along rd. to Ciudad Cuauhtemoc, *Breedlove 39086* (DS, MEXU); Mpio. Peltalcingo, Ahk'ulbal Nab above Peltalcingo, *Breedlove 56102* (MEXU); El Salvador, near Solosuchiapa, *Collins & Doyle 229* (US); Lago Suspiro, Reserva Montes Azules, *García et al. 211* (MEXU); Ixhuatán-N, *MacDougall 76* (NY, US); Escuintla, Turquía, *Matuda 17073* (DS, F, MEXU, NY); Guamuchil, SE de Mapastepec, *Miranda 6770* (MEXU); near Yajalón, *Nelson 3411* (NY, US); near Tapachula, *Nelson 3838* (NY, US); alrededores de Rayón, *Ramos & Funk 501* (MO); Mpio. Venustiano Carranza, above Soyatitán, along rd. from Las Rosas to Pugiltik, *Ton 3135* (DS, ENCB, F, LL, MICH). COLIMA: Mpio. Comala, a 5 km al N de El Naranjal, *Magallanes & Lott 2820* (MEXU, MICH). GUERRERO: Dist. Galeana, Alparosa, *Hinton 10847* (BM, F, G, GH, MO, NY, US); Dist. Galeana, Plan de Carrizo, *Hinton 11059* (DS, F, GH, MICH, US); Dist. Montes de Oca, Vallecitos, *Hinton 11780* (DS, GH, NY, US); Atoyac, *Kerber 169* (BM, BR, K, MICH, US). JALISCO: W slopes of Cerro San Miguel, central segment of Sierra de Manantlán, *Iltis et al. 470* (MICH); Mpio. Pihuamo, El Agostadero camino a Pihuamo, *Martínez et al. 4404* (MEXU); 16 mi. SW Autlán, *McVaugh et al. 19858* (MICH); Guadalajara, *Palmer 635* (BM, GH, NY, US). MÉXICO: Dist. Temascaltepec, Bejucos, *Hinton 2019* (F, MEXU); Dist. Temascaltepec, Tejupilco, *Hinton 2207* (A, BM, F, G); Dist. Temascaltepec, Acatitlán, *Hinton 7101* (A, BM, F, G, MICH, US). MICHOACÁN: Dist. Coalcomán, Zarzamora, *Hinton 12274* (DS, GH, MICH, NY, US); Dist. Coalcomán, Coalcomán, *Hinton 12331* (DS, F, GH, MICH, NY, T, US); Dist. Coalcomán, Sierra Torrecillas, *Hinton 15278* (GH, US); Puente Alto, 14 km S Ario de Rosales, *Sousa & Soto 8008* (CAS). MORELOS: Alpuyeca, *Atmar 17* (MEXU); Cuautla, Las Tazas, *Levy 13* (ENCB); Huajintlán, *Lyonnet 314* (BM, MO, US); Yautepec, *Pringle 9727* (F, G, GH, K, MO, NY, US). NAYARIT: carretera Puerto Vallarta-Jaltemba, *Puga 28* (ENCB); San Blas, *Rudd 3029* (MEXU, US). OAXACA: Mpio. Pochutla, 2 km NE Chacalapilla, o séa 3 km Puente de San Juan, *Delgado 694* (CAS, MO, UC); Dist. Juchitán, Mpio. Sta. María Chimalapa, Matías Romero, Colonia Cuauhtemoc, *Delgado 923* (ENCB, F, MEXU, MO, NY); Dist. Putla, 11.5 km NE de Putla por carr. a Tlaxiaco, *H. Hernández & Torres 153* (MEXU, MO); Sierra de San Pedro Nolasco, Talea, *Jurgensen 792* (BM, CGE, G, K, MO); Tuxtepec, Chiltepec and vicinity, *Martínez-Calderón 297* (A, LL, UC, US); Choapam, Yaveo, near Río Yaveo, *Mexia 9216* (B, CAS, F, G, GH, MO, NY, S, UC, US); Ranchería Toltepec, camino a Pluma Hidalgo, 19 km N Pochutla, *Sousa et al. 5338* (CAS, US, WIS); Dist. Juquila, 8 km NW de San Gabriel Mixtepec, *Sousa et al. 6375* (MEXU, MICH, MO); Dist. Teotitlán, 2 km al N de Puente de Fierro, en la carr. a Sta. Ma. Chilchotla, o séa a 10 km al NE de Huautla, *Sousa et al. 8153* (BM); Dist. Jamiltepec, 11 km SE de San Sebastián Ixcapa, *Sousa 8456* (ENCB, MEXU); Dist. Putla, 2 km Putla de Guerrero, *Sousa et al. 8480* (ENCB, MEXU, MICH); Dist. Juchitán, 10 km NW de Palomares, *Sousa & Téllez 8791* (MO); Dist. Tuxtepec, Mpio. Loma Bonita, San Felipe de la Peña, 9 km NW del límite Oaxaca-Veracruz, carr. Matías Romero-Tuxtepec, *Sousa & Téllez 8806* (MO); Dist. Tuxtepec, Monte Soria, 5 km NE de Valle Nacional, *Sousa & Rico 9265* (CAS, ENCB); Dist. Jamiltepec, 1.2 km N de desviación al Vivero Guapinol hacia San Agustín Chayuco, *Torres et al. 1636* (MO). PUEBLA: Mpio. Pantepec, 1 km N de Mecapalapa, *Basurto & Durán 118* (CAS, ENCB, MO); Mpio. Xilotepec de Juárez, 1 km S de Villa Avila Camacho, *Basurto & Durán 498* (CAS, ENCB, MO); SE Alpuyeca, *Miranda 4108* (MEXU). VERACRUZ: km 6 carr. Mizantla-Naolinco, *Avendaño 111* (ENCB, F, NY); Valle de Córdoba, *Bourgeau 1544* (G, GH, K, NY, P, S); 1 km N Sihuapán, *Calzada 895* (CAS, ENCB, F, MO, NY); San Andrés Tuxtla, Rancho Palzoquiapan de Don Aristeo (18°27′N, 95°13′W), *Calzada 4220* (F, WIS); 1 mi. E de Papantla, *Crutchfield & Johnston 5223* (TEX); Mpio. de la Palma, La Palma, Potrero, *Delgado et al. 896* (CAS, ENCB, MO); km 10 del camino Cedillo-La Laguna, Hidalgotitlán, *Dorantes et al. 4079* (F, MO, NY); Mizantla, camino a Tenochtitlán, *C. Hernández et al. 203* (F, NY); Mpio. Catemaco, 1 km de Sontecomapan por camino a Coxcoapan, *H. Hernández & Torres 167* (MEXU, MO); Mpio. Cabadas, 12.6 km NW de Santiago Tuxtla por carr. a Lerdo de Tejada, *H. Hernández & Torres 776* (MEXU, MO); Mpio. Catemaco, Rancho la Palma, 25 km de Catemaco por camino a Montepío, entre la Estación de Biología Los Tuxtlas y Sontecomapan, *H. Hernández & Torres 799* (MEXU, MO); Mpio. Catemaco, 5.7 km de Catemaco por camino a Montepío, *H. Hernández & Torres 800* (MEXU, MO); Mpio. Córdoba, sobre la autopista Fortín-Córdoba, *H. Hernández & Torres 827* (MEXU, MO); La Higuera, entre San José Acateno y Huaytamalco, *Márquez et al. 651* (F); Ignacio de la Llave, *Martínez-Calderón 1549* (A, BM, CAS, F, LL, MO, NY, US); Mpio. Catemaco, Playa Azul, *Martínez-Calderón 1803* (A, CAS, ENCB, F, MO, NY, US); Mpio. Tantoyuca, 10 km SE Tantoyuca, along Hwy. 105 (21°16′N, 98°09′W), *Nee et al. 19539* (F); 5 km E of Angel Cabada, *Veill 5388* (MO); Barranca del Fortín, near San Martín Tlacotepec, *Purpus 16439* (A, F, US); Mizantla and Papantla, *Schiede & Deppe 691* (BM, G, GH, K, MO, NY); Zongolica, camino rumbo a Zamajapan Nacaxtla (18°40′N, 96°59′W), *Vázquez 192* (ENCB, F); Río Solosúchil, entre Cedillo y La Escuadra, Hidalgotitlán (17°16′N, 94°37′W), *Vázquez et al. 1314* (BM, MO); Ursulo Galván, Loma de San Rafael, *Ventura 4565* (CAS, ENCB, LL); Amatlán, Río Seco, *Ventura 4976* (CAS, ENCB, MICH, TEX). GUATEMALA. ALTA VERAPAZ: Cobán, *Turckheim 691* (GH, P, US); near San Juan Chamelco, *Wilson 4094* (F). CHIQUIMULA: Volcán Ipala, near Amatillo, *Steyermark 30585* (F). PETÉN: Dolores, river bank of Río Mapán, *Contreras 10584* (F, LL, MEXU, S). ESCUINTLA: San Juan Mixtán, *Donnell Smith 2282* (K, US); near Escuintla, *Standley 63903* (F); La Trinidad, rd. between Escuintla and Finca Zapote, *Standley 64916* (A, F); near Río Sinacapa SE Escuintla, *Standley 89266* (F). IZABAL: El Estor, *Contreras 11112* (F, LL, MEXU, S). QUEZALTENANGO: between Colomba and Mercedes, *Standley 87972* (F). RETALHULEU: Retalhuleu, *Bernoulli & Cario 1155* (K); Las Victorias, *Rojas 240* (G); vicinity of Las Delicias, S Retalhuleu, *Standley 88007* (F). SACATEPÉQUEZ: near Las Lajas, *Standley 58101* (F). SAN MARCOS: Finca El Porvenir, Potrero Tojó, Volcán Tajamulco, *Steyermark 37648* (F). SANTA ROSA: Casillas, *Heyde & Lux 4148* (G, GH, US); región of Platanares, between Taxico and Guazacapan, *Standley 79083* (F, G); near El Molino, *Standley 78341* (F, US). SUCHITEPÉQUEZ: near Mazatenango, *Standley 66987* (F); San Francisco Zapotitlán, *Steyermark 52143* (F). BELIZE. EL CAYO: El Cayo, Grano de Oro, rd. to Río La Flor vicinity lumber mill, *Dwyer 10893* (F, NY); Vaca, *Gentle 2183* (A, MICH); 37 mi. section, Hummingbird highway, *Gentle 8998* (F, LL, MEXU, MICH, S); 6 km

E Cave's Brand, *Sousa et al. 12189* (MEXU); Macal River bottoms at the end of Kinloch Rd., *Spellman 1424* (MO); Barton Creek, *Whiteford 2897* (BM). EL SALVADOR. AHUACHAPÁN: vicinity of Ahuachapán, *Standley 19814* (GH, NY, US); near Salto Atehuecia, *Standley & Padilla 2873* (F, NY). LA LIBERTAD: San Andrés, Río Sucio, *Clausen & Kovar 6208* (MEXU, NY). SAN SALVADOR: vicinity of San Salvador, *Standley 19206* (GH, NY, US). SANTA ANA: S of Santa Ana, *Allen & Armour 7009* (F, LL, NY, US). HONDURAS. ATLÁNTIDA: vicinity of Tela, *Standley 55164* (A, F, NY, US). COMAYAGUA: 3 km to San José Comayagua, *Molina & Molina 31472* (F, MO). COPÁN: between Copán ruins and Santa Rita, *Molina & Molina 24661* (F, MO, NY, US). CORTÉS: near Lake Yojoa, *Williams & Williams 18798* (F, GH, US). SANTA BÁRBARA: Río Sisicarpa, *Molina 3738* (F). OLANCHO: between Juticalpa and Campamento, along Río Juticalpa, *Blackmore & Heath 1957* (BM, MO); Dulci Nombre de Culmi, near Las Marías, *Blackmore & Heath 1665* (BM); vicinity of Catacamas, *Standley 18146* (F). YORO: Pijol, Subirana, *von Hagen & von Hagen 1109* (F, NY). NICARAGUA. JINOTEGA: entre Wiwili y El Carmen, márgenes Río Coco (13°37′N, 85°50′W), *Araquistain & Moreno 1587* (MEXU, MO); ZELAYA: Bluefields, Cukra, *Long 100* (F); La Pastorela, 5 km W de Waslala, carretera Waslala a El Tuma, *Moreno 19135* (MO); carretera nueva a Wani, El Hormiguero, *Ortiz 1215* (MO); Amparo, *Ortiz 1304* (MO); Mpio. Siuna, Siunawas arriba, *Ortiz 1513* (MO); sector de Negro Was, entre El Empalme y Rosita (13°45′N, 84°25′W), *Ortiz 2181* (MO); El Salto, along Río Pis Pis and surrounding hills ca. (14°04′N, 84°38′W), *Pipoly 3633* (MO); Caño Corozal, near Río Kuzali, *Stevens & Moreno 19711* (MO). COSTA RICA. ALAJUELA: San Pedro de San Ramón, *Brenes 14974* (NY); borde del Río Burio, *Jiménez 1769* (F, NY, US); Alfaro Ruiz, Palmira, *Smith 1292* (F, NY). CARTAGO: vicinity of Turrialba, *Godfrey 66192* (MO); Finca Perla, entre Reserva de Vida Silvestre Tapantí y Purisil, *H. Hernández et al. 675* (MEXU, MO); 2 km de Cervantes por carr. a San José, *H. Hernández et al. 730* (MEXU, MO). GUANACASTE: Finca la Pacífica, *Opler 858* (F); entre Liberia y Quebrada Grande, *Poveda 1137* (F, MO); Quebrada Zopilote, Parque Nacional Rincón de la Vieja, *Sousa et al. 12750* (MO); vicinity of Tilarán, *Standley & Valerio 15021* (NY, US). HERLDIA: Barba, Río Segundo, *León 82* (F). LIMÓN: Los Diamantes (US rubber station) on r.r. to Guapiles, *Carlson 3449* (F, MEXU, US). SAN JOSÉ: Río Herradura, tributary Río Chiripó del Pacífico, NW Canaán, General Valley (9°29′N, 83°37′W), *Burger & Liesner 7083* (BM, F, MO, NY, US); San José, *Tonduz 1505* (BM, BR, G, US); Río Torres, *Tonduz 9800* (BM, BR, F, GH, MO NY, US); along Río Hermoso, Finca El Quizarra, *Williams et al. 28404* (F, NY, US). PANAMA. CHIRIQUÍ: Cerro Horqueta, *Blum & Duyer 2610* (LL); Dist. Boquete, above El Cantinero, *D'Arcy 9826* (MO); Dist. Boquete, Bajo Mono, *Davidson 520* (A, F, MO); along Highway to Concepción at Cuesta de Piedra, *King 5308* (TEX, UC, US); between Hato del Jobo and Cerro Vaca, *Pittier 5423* (US); 3 mi. S El Volcán, *Tyson 873* (MO). COCLÉ: El Valle, upper Río Antón, *Allen 3819* (G, GH, MO, S); along road 2 mi. above El Valle on road to La Mesa, *Croat 13297* (MO, NY). DARIÉN: Río Pucuro, between Cerro Mali and Cerro Tacarcuna, *Gentry & Mori 13873* (MO). VERAGUAS: 5 mi. W Santa Fe, on rd. past Escuela Agrícola Alto Piedra, *Croat 23106* (CAS, F, MO, NY). VENEZUELA. DISTRITO FEDERAL: Cordillera de Avila, dry south-facing slopes above Caracas, *Steyermark 55147* (F, MO). MÉRIDA: Depto. Tovar, alrededores de Tovar, *Badillo 5862* (F). MIRANDA: Los Guayabitos, arriba de Baruta, *Aristeguieta 5932* (NY); Petare and vicinity, near Caracas, *Pittier 7471* (GH, US). TACHIRA: entre Palo Grande y Lobatera, La Llanada, *Cárdenas 1248* (F); between Las Delicias and Paraguita, along Río Tachira, *Steyermark 57420* (F); along highway, N edge of Delicias, *Steyermark & Liesner 118756* (MO). TRUJILLO: Depto. Carache, entre El Paramito y El Balcón, *Benítez de Rojas 1989* (MO); San Jacinto, *Tamayo 1697* (US); nacimientos del Río Momboy, La Puerta, *Tamayo 1811* (US). COLOMBIA. ANTIOQUIA: Itiribe, vicinity of Medellín, *Toro 577* (NY, US). BOYACA: Cordillera Oriental, vertiente oriental, entre Gueteque y Guayatá, márgenes del Río Súnuba, *Cuatrecasas 9701* (F, US). CALDAS: granja cafetera Chinchina, *Duque-Jaramillo 4617* (F, NY, US). CAUCA: Popaván, *Lehmann 5368* (F, GH, S, US); around Cali, W side of Cauca Valley, *Pittier 926* (US). CUNDINAMARCA: entre Chipaque y Caqueza, alrededores de Puente Serviez, *García-Barriga & Jaramillo 20536* (F). MAGDALENA: Sierra Nevada de Santa Marta, Quebrada La Sirena (10°59′N, 73°59′W), *Kirkbride 2165* (US). NORTE DE SANTANDER: vicinity of Chinácota, *Killip & Smith 20851* (A, GH, NY, US); Culagá Valley, near Tapatá, N of Toledo, *Killip & Smith 21141* (A, GH, NY, US). TOLIMA: El Líbano, *García-Barriga 12227* (US). VALLE: Cord. Occidental, vertiente occidental, Hoya del Río Sanquinini, La Laguna, *Cuatrecasas 15674* (F, US); Cordillera Occidental, Hoya del Río Albán, El Zancudo, *Cuatrecasas 22400* (F, S, US); Bitaco, *Johnson 2466* (MO). ECUADOR. AZUAY: along Río Patol, between Hacienda Yuba and Hacienda San José de Coimotan, in region of Sanaguin, *Steyermark 52757* (F, MO). BOLÍVAR: Cord. Occidental, Limón, *Acosta 6345* (F). CARCHI: trail from Chical to Maldonado, along Río San Juan, *Gentry & Shupp 26611* (MO). CHIMBORAZO: vicinity of Ventura, *Rose & Rose 23524* (GH, NY, US). COTOPAXI: Quevedo-Latacuna road, areas along Río Pilalo (79°10′W, 0°53′S), *Holm-Nielsen et al. 3075* (F, MO, NY). CULTIVATED: U.S.A. MISSOURI, Saint Louis, Missouri Botanical Garden, *H. Hernández 956* (MEXU, MO). JAVA. Mountaingarden Tjibodas (Mt. Gede), *van Ooststroom 13707* (BR).

Zapoteca tetragona is closely allied to *Z. portoricensis* but can be readily distinguished primarily by having conspicuously tetragonal branchlets, larger corollas, and longer filaments. Despite the opinion of Woodson & Schery (1950), who suggested that *Z. tetragona* (*Calliandra tetragona*) is distinguished "unnaturally" by its tetragonal branchlets, implying that it is not differentiated from what they call the "*caracasana portoricensis* complex," this entity is maintained here as a separate species. Discussion of the relationship between *Z. tetragona* and *Z. portoricensis* is provided under the latter species.

Zapoteca tetragona is probably also related to *Z. andina*, from which it can readily be distinguished by having adpressed, usually larger, triangular-linear to triangular-lanceolate stipules, deltate calyx teeth, and totally white filaments. Discussion of the relationship between these two species is provided under *Z. andina*.

Acacia quadrangularis Link (Enum. Hort. Berol. Alt. 2: 445. 1822.) has traditionally been included in the list of synonyms of *Calliandra tetragona*, but I have been unable to confirm this synonymy. Link did not cite Willdenow's *Acacia tetragona*, nor Poiret's *Mimosa quadrangularis*, and given the fact that almost all of Link's personal herbarium was destroyed during World War II, there is no material available with which to evaluate this hypothesis.

10. Zapoteca andina H. Hern., sp. nov. TYPE: Ecuador. Azuay: valley of the Río Tarqui, a few km south of Cuenca, 2,500 m, 1–2 Feb. 1945, *M. A. Guiler 47* (holotype, US no. 2106703; isotype, NY). Figure 41.

Frutices ramulis praesertim juvenilibus conspicue tetragonis. Pinnae 3–6-jugae; foliolis 15–32-jugis in pinna utraque, angusto-oblongis; stipulae vadoso-triangulares basi auriculis duabus descendentibus vel depressis praeditae. Calyx ca. 2 mm longus, dentibus angusto-oblongis; filamenta basi alba ad apicem purpurea.

Shrubs to 2 m tall; branchlets conspicuously 4-angled, especially the younger ones, costate under magnification, glabrous to sparsely villous. Pinnae 3–6-jugate; petioles eglandular, with a conspicuous adaxial channel, 1.3–4 cm long, glabrous to villous; rachis 2–4 cm long; rachillae to 8 cm long; leaflets 15–32 pairs per pinna, narrowly oblong, oblique at base, acute at apex, the median leaflets 5–10 × 1–3 mm, all membranous, glabrous or ciliate; leaflet venation inconspicuous; stipules leafy, shallowly triangular, with 2 basal auricles, descending or depressed, parallel-veined, to 0.6 cm long, glabrous or ciliate. Capitula axillary; peduncles fasciculate, 3.5–7 cm long at anthesis. Calyx ca. 2 mm long, the teeth narrowly oblong, acute; corolla funnelform, ca. 4.5 mm long, glabrous, the lobes lanceolate; filaments white in the basal half, red-purple in the distal half, the staminal tube ca. 2 mm long; ovary glabrous. Pods ca. 7 × 1 cm, acute at apex, rostellate, thickly membranous, glabrous, reticulate-veined. Seeds ovoid, ca. 5 × 3 mm, mottled; pleurogram irregular.

Distribution (Fig. 42). *Zapoteca andina* is endemic to restricted areas of the Andes, in the provinces of Azuay and Loja, Ecuador; the departments of Cajamarca, La Libertad, and Piura in northern Peru; and the department of La Paz, Bolivia. This species is allopatric with *Z. tetragona*; taken together, the two species occupy a nearly continuous area of the northern Andes (Figs. 40, 42); 1,400–2,650 m.

Additional specimens examined. ECUADOR. LOJA: Hac. Huaico-Pamba, 55 km S de Loja, *Espinosa 2329* (MICH). PERU. CONTUMAZÁ: Depto. Cajamarca, La Montaña (Guzmango-Contumazá), *Sagástegui et al. 9301* (MO); Yetón-Guzmango, *Sagástegui 10321* (MO); Depto. Cajamarca, Quebrada Honda (Santiago-Yumal), *Sagástegui & López 10627* (MO). LA LIBERTAD: Prov. Otuzco, Huaranchal, *López et al. 2648* (US). PIURA: Prov. Canchaque, *Ferreyra 3133* (MO); entre Palambla y Faique, cerca a Canchaque, *Ferreyra 10920* (US). BOLIVIA. LA PAZ: Sorata, *Holway & Holway 520* (GH, US); Sorata, prope Espada, *Mandon 759* (BM, BR, GH, K, NY); without locality, *Bang 1812* (BM, F, GH, MO, NY, US).

Zapoteca andina resembles *Z. tetragona* in most of its vegetative features, although the branchlets are sometimes visibly four-angled only in the youngest parts. It differs from *Z. tetragona* primarily by having smaller, triangular, descending or depressed, auriculate stipules and by having narrowly oblong calyx teeth, smaller floral dimensions, and white/red-purple filaments. Available collections of *Z. andina* do not reveal the habit, and it is uncertain whether plants of *Z. andina* are erect shrubs or low, subprostrate or prostrate shrubs, as suggested by the aspect of some of the Bolivian collections (e.g., *Bang 1812, Mandon 759*).

11. Zapoteca costaricensis (Britton & Rose) H. Hern., comb. nov. *Anneslia costaricensis* Britton & Rose, N. Amer. Fl. 23: 67. 1928. *Calliandra costaricensis* (Britton & Rose) Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 492. 1937. TYPE: Costa Rica: bords du Río Convento, Jan. 1897, *Pittier 10643* (lectotype, US no. 577350 here designated; isolectotypes, BR (2), US (2)).

Shrubs; branchlets slender, terete, smooth, glabrous. Pinnae (2–)3-jugate; petioles very slender, terete to tetragonal, with a conspicuous adaxial channel, 4.3–7 cm long, glabrous; rachis 2–2.5 cm long in 2-jugate leaves, 4.3–6.2 cm long in 3-jugate ones, glabrous or glabrate; rachillae 7–13 cm long; leaflets 10–13 pairs per pinna, the median ones narrowly oblong, the distal ones oblong-obovate, oblique at base, acute at apex, 2–2.7 × 0.5–0.7 cm, the proximal pairs smaller and narrower, all olive-green adaxially, pale-green abaxially, membranous, glabrous; leaflet venation inconspicuous; stipules leafy, ovate to widely ovate, rounded to cordate at base, acute at apex, to 13 × 8 mm, glabrous, palmately veined. Capitula axillary; peduncles 4.5–6.5 cm long in fruit. Pods to ca. 15 cm long when mature, acute, rostrate, thickly membranous, glabrous. Seeds ovoid, 7 × 4 mm, brown; pleurogram irregular.

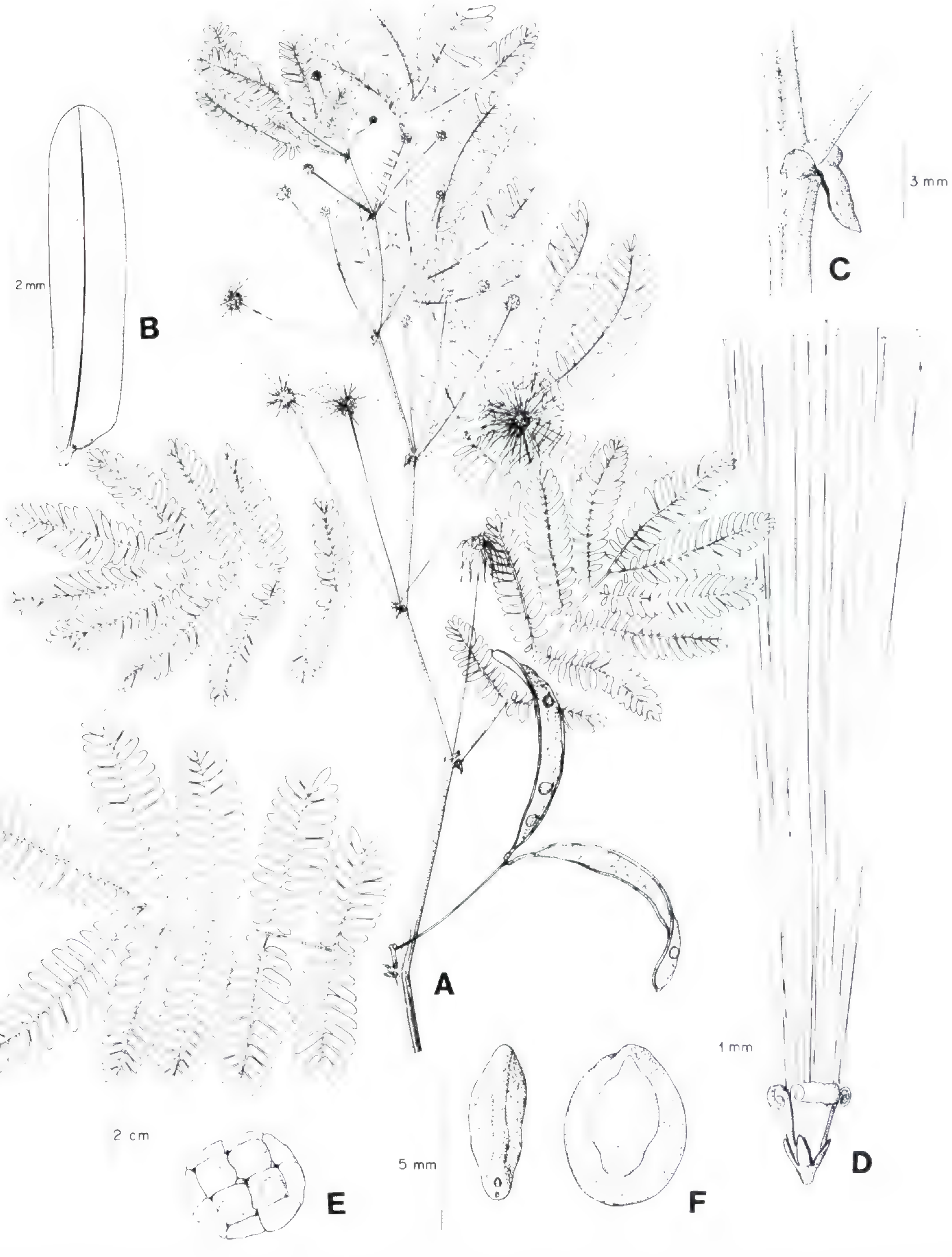


FIGURE 41. *Zapoteca andina.*—A. Branchlet with inflorescences at anthesis, and dehisced pod.—B. Leaflet. C. Stipule.—D. Flower.—E. Polyad.—F. Seeds. (From *Espinosa 2329* (MICH); pod from *Sagástegui et al. 10321* (MO).)

Distribution (Fig. 37) *Zapoteca costaricensis* is endemic to Costa Rica, where it is known from only two collections, one from Valle del Río Diquís (Río Convento) near San José and the other from near Siquirres, Province of Limón.

Additional specimen examined. COSTA RICA. LIMÓN: bord de la voie ferrée de l'Atlantique à Siquirres, 19 Nov. 1890, *Pittier 3154* (BR).

The relationships of this species with other members of *Zapoteca* are difficult to establish, espe-

FIGURE 42. Distribution of *Zapoteca andina*.

cially due to the paucity of material. On the basis of leaflet morphology and obscure leaflet venation patterns, *Z. costaricensis* is probably related to *Z. portoricensis* subsp. *flavida*. *Zapoteca costaricensis* can be easily distinguished from that entity, however, by its much larger leaflets and characteristic ovate/widely ovate, cordate stipules. The narrowly oblong leaflets of *Z. costaricensis* contrast with those of *Z. formosa*, which are almost always obovate.

12. Zapoteca formosa (Kunth) H. Hern., Ann. Missouri Bot. Gard. 73: 755 763. 1986. *Acacia formosa* Kunth, Mimoses 102, t. 32. 1822; Kunth, Nov. Gen. Sp. 6: 278. 1824; DC., Prodr. 2: 466. 1825. *Calliandra formosa* (Kunth) Benth., London J. Bot. 3: 98. 1844; Benth., London J. Bot. 5: 102. 1846; Benth., Trans. Linn. Soc. London 30: 542. 1875; Benth. in C. Martius, Fl. Bras. 5: 411. 1876; León, Contr. Ocas. Mus. Hist. Nat. Colegio "De la Salle" 10: 237. 1951. *Feuilleea formosa* (Kunth) Kuntze, Revis. Gen. Pl. 187. 1891. *Anneslia formosa* (Kunth) Britton & Millsp., Bahama Fl. 159. 1920; Britton & Rose, N. Amer. Fl. 23: 67. 1928. TYPE: Mexico, Guanajuato: *Bonpland 4288* (holotype, P, seen in microfiche; isotype, P). The label information on these specimens does not indicate the locality, but according to the description, it was collected in Guanajuato 1,068 hex (1,922 m) elevation. The holotype is extremely similar to and presumably served as the model for the illustration in Kunth's work (Fig. 43).

Erect shrubs to 5 m tall; stems erect, sometimes drooping, usually slender, sometimes to 5 cm diam.; branchlets terete to angular. Leaves eglandular, the pinnae 1–3(–4)-jugate; petioles terete, with a conspicuous adaxial channel, 0.3–7.8 cm long, glabrous to villous; rachis 0.3–6.8 cm long; rachillae 0.6–12.5 cm long; leaflets (2–)3–15 (–17) pairs per pinna, oblong to oblong-obovate or very widely obovate, the proximal ones sometimes

→

FIGURE 43. "*Acacia formosa*" (= *Zapoteca formosa* subsp. *formosa*), from Kunth's *Mimoses* t. 32. 1822. This plate was probably based on *Bonpland 4288*, a collection made in Guanajuato, Mexico.

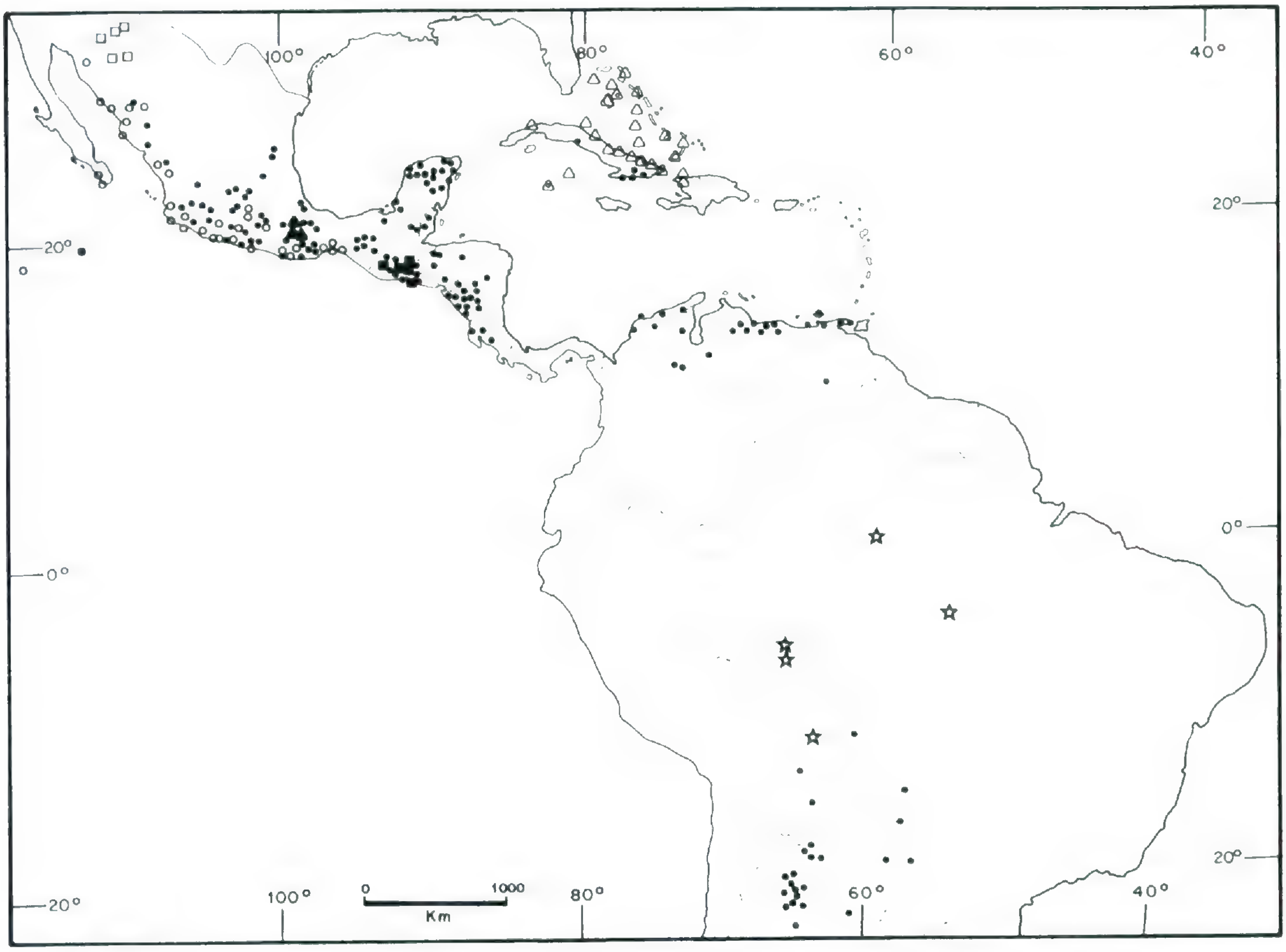


FIGURE 44. Distributions of *Zapoteca scutellifera* (stars), *Z. formosa* subsp. *formosa* (dots), *Z. formosa* subsp. *salvadorensis* (solid squares), *Z. formosa* subsp. *gracilis* (open triangles), *Z. formosa* subsp. *rosei* (open circles), *Z. formosa* subsp. *mollicula* (solid triangles), and *Z. formosa* subsp. *schottii* (open squares).

becoming elliptic or widely obovate, all oblique at the base or the proximal ones sometimes becoming acute, rounded to acute at apex, usually mucronate, the distal leaflets 0.4–5.9 × 0.2–3.6 cm, the proximal ones smaller, mostly membranous, glabrous to pubescent, pilose or villous; leaflet venation mostly inconspicuous, primary and secondary veins occasionally conspicuous; stipules leafy, triangular to linear-triangular, or lanceolate to ovate-lanceolate, to 13 mm long, glabrous to villous. Capitula axillary or in simple pseudopaniculate inflorescences; peduncles usually fasciculate at distant nodes, 1–11 cm long at anthesis. Flowers pentamerous; calyx cup-shaped, 1.5–4 mm long, glabrous, the teeth triangular to oblong-lanceolate; corolla campanulate, 3–5 mm long, glabrous, the lobes elliptic to lanceolate; filaments ca. 2.5–3 cm long, white, greenish white, red-purple, or white in the basal half and red-purple or pink in the distal half, the staminal tube ca. 1–3 mm long; ovary ca. 1–3 mm long, glabrous. Pods to 13(–15) cm long when mature, at apex truncate to rounded or acute, usually rostrate, thickly membranous, glabrous, glabrate or densely pilose. Seeds rhomboid-ovoid, sometimes very widely so, 4–8 × 3–6 mm, brown or gray, the areola usually lighter; pleurogram irregular, sometimes semiregular. Somatic chromosome number $2n = 26$.

Distribution (Fig. 44). Usually common in disturbed or undisturbed habitats derived from arid scrub, tropical deciduous forests, and less frequently semievergreen forests. This species ranges from Arizona to Argentina and into the West Indies. Collections come from 0 2,000 m.

Zapoteca formosa as circumscribed here consists of six highly variable subspecies: *formosa*, *salvadorensis*, *gracilis*, *rosei*, *mollicula*, and *schottii*. This infraspecific classification is based primarily on leaf and flower characters (Table 14). Varying degrees of morphological intergradation occur between different pairs of subspecies. A total of 24 specific epithets have been published for plants that fall within *Z. formosa*. Most of these names really designate regional variations in leaflet characters. In light of the enormous degree of morphological variability within this widespread species and the relatively common occurrence of

TABLE 14. Comparison of the subspecies of *Zapoteca formosa*.

	Subspecies *formosa*	Subspecies *salvadorensis*	Subspecies *gracilis*	Subspecies *rosei*	Subspecies *mollicula*	Subspecies *schottii*
Pairs of pinnae	(1–)2–3(–4)	2–3	2–3(–4)	1–3	1(–2)	1–2
Petiole length	2.2–7.8 cm	(1.8–)3.1–4.5 cm	1.3–5.5 cm	1–4.2(–5) cm	0.3–1.1 cm	1.2–3.5 cm
Rachilla length	2.6–8(–12) cm	(1.8–)3.8–5.6 cm	3.5–12.5 cm	1.9–6.5(–11.3) cm	0.6–1.8 cm	1.9–4.5 cm
Leaflet						
Pairs/pinna	3–8(–11)	4–6	(5–)7–15	(3–)4–12(–17)	(2–)3–5(–6)	(3–)4–6(–7)
l × w	11–59 × 5–36 mm	16–26 × 7–19 mm	9–22 × 3.5–11 mm	8–31 × 3–21 mm	4–14 × 2–9 mm	4–12(–14) × 2–6(–7) mm
Indument	glabrous–hairy	hairy	glabrous	glabrous–hairy	glabrous–hairy	glabrous–hairy
Maximum stipule length	10(–13) mm	12 mm	5 mm	9 mm	3 mm	5 mm
Inflorescence organization	axillary, pseudo-paniculate	axillary, pseudo-paniculate	axillary	axillary, pseudo-paniculate	axillary	axillary
Filament color	white	white	white	white/red-purple, white/pink, red-purple	white/red-purple	white–pink
Maximum legume length	13(–15) cm	9 cm	11 cm	9 cm	7.5 cm	7 cm
Indument	glabrous	pilose	glabrous	glabrous	glabrous	glabrous

intermediates, a conservative approach has been chosen in this treatment. The following sequence of the subspecies reflects their putative relationships.

KEY TO THE SUBSPECIES OF *ZAPOTECA FORMOSA*

1a. Pods pilose; plants hairy throughout ..... 12b. subsp. *salvadorensis*
1b. Pods glabrous, rarely glabrate; plants glabrous to hairy.
2a. Filaments white or greenish white.
3a. Leaflets oblong, glabrous; stipules narrowly triangular, to 5 mm long ..... 12c. subsp. *gracilis*
3b. Leaflets oblong-obovate, glabrous to villous; stipule lanceolate to ovate-lanceolate, to 13 mm long ..... 12a. subsp. *formosa*
2b. Filaments either red-purple or white basally and red-purple or pink distally.
4a. Leaflets 4 14 × 2–9 mm; capitula axillary; filaments white basally and either pink or red-purple distally.
5a. Petioles 3–11 mm long ..... 12e. subsp. *mollicula*
5b. Petioles 12–35 mm long ..... 12f. subsp. *schottii*
4b. Leaflets 8–31 × 3 21 mm; capitula axillary or pseudopaniculate; filaments either wholly red-purple or white basally and red-purple to pink distally ..... 12d. subsp. *rosei*

12a. Zapoteca formosa (Kunth) H. Hern. subsp. **formosa**.

Calliandra capillata Benth., London J. Bot. 3: 98. 1844; Benth., Trans. Linn. Soc. London 30: 542. 1875. *Anneslia capillata* (Benth.) Britton & Rose, N. Amer. Fl. 23: 68. 1928. TYPE: Mexico. Oaxaca: ad radices Montis San Felipe, Julio, *Andrieux 404* (lectotype, K, here designated; isolectotypes, F (fragment), G, K, P).

Calliandra malacophylla Benth., London J. Bot. 3: 100. 1844; Benth., Trans. Linn. Soc. London 30: 544. 1875. TYPE: Mexico. Oaxaca: ad radices Montis San Felipe, Julio, *Andrieux 401* (lectotype, K, here designated; isolectotypes, F (fragment), G, K, P, US (fragment)).

Calliandra viridiflora Benth., London J. Bot. 3: 98. 1844; Benth., Trans. Linn. Soc. London 30: 542. 1875. TYPE: Brazil: *Tweedie s.n.* (lectotype, K, here designated; isolectotype, K).

Calliandra gracilis Klotzsch ex Baker, Refug. Bot. 5: t. 294. 1873, non Griseb., 1861, nec Standley, 1929, nec Renvoize, 1981; Benth., Trans. Linn. Soc. London 30: 542. 1875; L. Cárdenas, Revista Fac. Agron. (Maracay) 7: 131. 1974. *Calliandra formosa* var. *gracilis* (Klotzsch ex Baker) J. F. Macbr., Contr. Gray Herb. 59: 4. 1919. *Calliandra moritziana* L. Cárdenas, Ernstia 23: 40. 1984. (This name was published as a nomen novum for *Calliandra gracilis* Klotzsch ex Baker. The designation of *Moritz 887* (BM) as the lectotype made by Cárdenas is incorrect; the type collection is *Otto 404*, which Klotzsch explicitly cited in the original description of *C. gracilis*.) TYPE: Colombia: *Otto 404* (lectotype here designated, LE). The holotype, which presumably was at B, was probably destroyed in 1943 (P. Hiepko, pers. comm., 1986); additional duplicates of this collection were not found at GOET nor HBG.

Calliandra penduliflora Rose, Contr. U.S. Natl. Herb. 5: 193. 1899. *Anneslia penduliflora* (Rose) Britton & Rose, N. Amer. Fl. 23: 69. 1928. TYPE: Mexico. Jalisco: Bolaños, 10 19 Sept. 1897, *J. N. Rose 2924* (lectotype here designated, US no. 301875; isolectotypes, GH, K, NY).

Calliandra marginata Griseb. ex R. O. Williams, Fl. Trin. & Tob. 1: 299. 1931; Britton & Killip, Ann. New York Acad. Sci. 35: 137. 1936; L. Cárdenas, Revista Fac. Agron. (Maracay) 7: 131. 1974. *Anneslia marginata* (Griseb. ex R. O. Williams) Mold., Revista Sudamer. Bot. 6: 177. 1940. TYPE: British West Indies, Trinidad, *Crueger 326* (lectotype here designated, K; isolectotypes, NY, US). The specific epithet was provided by Grisebach in his *Fl. Brit. W.I.* 710. 1864.

Calliandra gentryi Standley, Field Mus. Nat. Hist., Bot. Ser. 17: 261. 1937; Gentry, Publ. Carnegie Inst. Wash. 527: 122. 1942. TYPE: Mexico. Chihuahua: Guasaremos, Río Mayo, Canyon Chanate, tropical Sonora, 5 Aug. 1936, *H. S. Gentry 2363* (holotype, F; isotypes, A, MEXU, MO, S, UC, US).

Anneslia chapaderoana Britton & Rose, N. Amer. Fl. 23: 69. 1928. TYPE: Guatemala. Santa Rosa: Chapadero, 5,000 ft., Aug. 1892, *Heyde & Lux 3740* (lectotype here designated, US no. 942577; isolectotype, G).

Anneslia cookii Britton & Rose, N. Amer. Fl. 23: 68. 1928. *Calliandra cookii* (Britton & Rose) Standley, Publ. Field Columbian Mus., Bot. Ser. 3: 277. 1930. TYPE: Guatemala. Petén: between Yaxmuxán and Yaxhá, 9 Apr. 1922, *Cook & Martin 209* (lectotype, here designated, US no. 1084668).

Anneslia izalcoensis Britton & Rose, N. Amer. Fl. 23: 69. 1928; León, Contr. Ocas. Mus. Hist. Nat. Colegio "De la Salle" 10: 237. 1951. TYPE: El Salvador. Sonsonate: vicinity of Izalco, in thicket, 19–24 Mar. 1922, *Standley 21818* (lectotype here designated, NY; isolectotypes, GH, US).

Anneslia orientalis Britton & Rose, N. Amer. Fl. 23: 69. 1928. *Calliandra orientalis* (Britton & Rose) León, Contr. Ocas. Mus. Hist. Nat. Colegio "De la Salle" 9: 7. 1950. TYPE: Cuba. Sevilla Estate, near Santiago, 27 Aug. 1906, *N. Taylor 4* (holotype, NY).

Anneslia suborbicularis Britton & Rose, N. Amer. Fl. 23: 69. 1928. TYPE: Mexico. Veracruz: Baños del Carrizal, Aug. 1912, *Purpus 6084* (lectotype here designated, NY; isolectotypes, F, GH, UC, US).

Anneslia yoroensis Britton, N. Amer. Fl. 23: 193. 1928. *Calliandra yoroensis* (Britton) Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 309. 1929. TYPE: Honduras. Yoro: near Progreso, 30 m, wet thicket, 24 Jan. 1928, *Standley 55053* (lectotype here designated, NY; isolectotypes, A, F, US).

Erect shrubs to 3(5) m tall; stems usually slender, sometimes reaching 5 cm diam.; branchlets

generally ascending, sometimes drooping. Pinnae (1–)2–3(–4)-jugate; petiole 2.2–7.8 cm long; rachis 1.7–6.8 cm long; rachillae 2.6–8(–12) cm long; leaflets 3–8(–11) pairs per pinna, the distal leaflets 1.1–5.9 × 0.5–3.6 cm, oblong-obovate to very widely obovate, sometimes falcate, the proximal ones elliptic to widely obovate, the distal ones oblique at base, usually becoming acute proximally, rounded to acute at apex, usually mucronate, the proximal leaflets smaller, all glabrous to short-pubescent or finely villous; stipules lanceolate to ovate-lanceolate, sometimes slightly curved, to 10(–13) mm long, glabrous to pubescent or villous. Capitula axillary or in pseudopanicles to 22 cm long; peduncles 2.1–11 cm long at anthesis. Calyx 2–4 mm long, the teeth triangular to oblong-lanceolate, sometimes deeply divided; corolla 4–6 mm long; filaments white, sometimes greenish white. Pods to 13(–15) × 1(–1.2) cm, glabrous when mature, but occasionally villous or sparsely villous in early developmental stages. Seeds rhomboid-ovoid to widely so, 6–7 × 3–6 mm, brown, the areola usually lighter; pleurogram strongly irregular. Somatic chromosome number $2n = 26$.

Distribution (Fig. 44). This subspecies has the widest distribution within *Z. formosa*. Its range extends from northern Mexico, in the states of Tamaulipas, Chihuahua, and Sinaloa, south and southeast through Central America to central Costa Rica. In South America it occurs in northern Venezuela and northern Colombia, and also in Brazil (Minas Gerais), Bolivia, Paraguay, and northern Argentina. It has been collected on Cuba, Trinidad, and other smaller islands in the West Indies. This subspecies has not been collected in Panama, most of Colombia, Ecuador, or Peru. It is relatively common in open sites in seasonal, dry environments such as tropical dry forests, coastal thickets, and arid thorn scrub, although occasionally it is found in wetter disturbed or undisturbed habitats, in semi-evergreen or evergreen tropical or subtropical forests. It has also been collected occasionally in pine and pine–oak forests in Mexico. Collections come from altitudes of 0–2,000 m. Cultivated individuals in Guanajuato, Mexico yielded the collection *Dugès s.n.*

Common names. Bellotica (Atlántico, Colombia), caba pixoy (Yucatán), cabellera (Oaxaca), chipilín de monte (Guatemala), chapuli (Guerrero), claveyino (Chihuahua), barbón montañés (El Salvador), huaje (Sinaloa), ibche (Yucatán), tamanché (Yucatán), tepehuaje (Guanajuato), veranero (Bolívar, Colombia), yag civ (Oaxaca), yaque (Sucre, Venezuela).

Additional specimens examined. MEXICO. CAMPECHE: alrededores de las Grutas de Xtacumbilxunam, a 3 km W de Bolonchén de Rejón, *Cabrera & Cabrera 9514* (MEXU); 8 km SE de Conhuas sobre el camino al Centro Regional Calakmul, en km 99 de la carr. Escarcega-Chetumal, *Cabrera & Cabrera 10973* (MEXU); Reforma, *Lundell 835* (CAS, F, GH, MICH, MO, NY, UC, US, WIS); Tuxpeña, *Lundell 1073* (F). CHIAPAS: Mpio. of Tuxtla Gutiérrez, 15 km N of Tuxtla Gutiérrez along road to El Sumidero, *Breedlove 10635* (LL, MO, US); Mpio. of Chiapa de Corzo, Mexican hwy. 190 in the Zinacantán paraje of Muktajok, *Breedlove 36531* (MO, NY); Mpio. of Ocozocoautla de Espinosa, 13–18 km S of Ocozocoautla, *Breedlove 37844* (MEXU, MO); Mpio. La Trinitaria, 6 km al S de La Trinitaria por carr. a Frontera Comalapa, *H. Hernández & Chacón 546* (MEXU, MO); Rancho Lindavista, 24 km E de Villa Flores, *Miranda 5977* (MEXU); road between Tenejapa and Yajalón, *Nelson 3244* (GH, US); Mpio. of Ocosingo, near Rancho Mumuntik near Ocosingo, *Ton 3491* (LL, MO, NY, US). CHIHUAHUA: Wisiego, Río Mayo, *Gentry 2389* (A, MO); Mpio. Batopilas, entre Kirare y la Buta, *Tenorio & Romero 6585* (MEXU). COLIMA: SW foothills of the Nevado de Colima, 1–1.5 mi. S of Hacienda San Antonio, *McVaugh 16113* (MICH). DURANGO: *Rose 2332* (US). GUANAJUATO: Mpio. Guanajuato, Cañada de Pastita, *Arellano s.n.* (ENCB); 10 km SW of León, road to San Francisco del Rincón, *McVaugh 24272* (MICH). GUERRERO: 4 mi. SW of Garrapato, *Rowell 107* (MICH); 2.5 mi. N of Acahuizotla, *Herold & Clark 449* (MEXU, MICH); Distr. Montes de Oca, Vallecitos, *Hinton 11626* (CAS, GH, MEXU, MICH, NY, US); Tecpan El Verde, *Hinton 14335* (CAS, GH, MEXU, MICH, NY, UC, US); Mazatlán, *Kruse 1121* (ENCB); La Corréa, *Langlassé 271* (F, G, GH, K, US); Distr. Aldama, Sierra Madre del Sur, N of Río Balsas, Temisco, Barranca de la Julia, *Mexia 8942* (B, CAS, F, G, GH, K, LL, MO, NY, UC, US); near Iguala, *Rose et al. 9417* (US); Mpio. de Tecpan de Galeana, El Pusulmiche 3 km del entronque de la brecha a Corinto con la carr. Tecpan de Galeana-Zihuatanejo, *Tenorio et al. 1337* (MO); Mpio. de Zihuatanejo, 17 km al NE de Zihuatanejo, por la carr. Zihuatanejo Cd. Altamirano, *Tenorio et al. 398* (MO); 1.5 km al N de Chilpancingo, *Torres et al. 1205* (MO); 24 km al N de Zumpango del Río hacia Iguala, *Torres 1247* (MO). JALISCO: above Lake Chapala, *Barkley et al. 7615* (F, TEX); Barranca de la Cruz, La Cruz, Tonalá, *Luna 5485* (MEXU); S and W facing slopes, 11–12 mi. SW of Autlán, *McVaugh & Koelz 883* (MICH); 16 mi. SW of Autlán, *McVaugh 19857* (MICH); 5–8 mi. N of La Cuesta below the pass to Talpa de Allende, *McVaugh 20327* (MICH); near Guadalajara, *Rose & Painter 7364* (GH, US); near Etzatlán, *Rose & Painter 7524* (NY, US). MICHOACAN: vicinity of Morelia, *Arsène 5906* (A, BM, G, GH, MO, NY, US); Aquila, La Mina, *Guerrero et al. 494* (MEXU); Distr. Coalcomán, Sierra Naranjillo, *Hinton et al. 15131* (GH, LL, NY, US); between San Juan de los Plátanos and Amatlán (Sta. Ana), *McVaugh 17950* (MICH); around Lake Cuitzeo, *Pringle 4161* (BM, BR, F, G, GH, MEXU, MICH, MO, NY, P, UC, US); Monteleón, *Pringle 9725* (F, GH, MICH, MO, NY, US); 17 mi. E of Jiquilpan, *Waterfall 16404* (US). MORELOS: 6 mi. W of Yautepec, *Hunt 93* (MEXU, MICH); Cuernavaca, *Rose & Rose 11074* (US). NAYARIT: Laguna de Santa María del Oro, *Luna 9084* (MEXU); 10 mi. SE of Ahuacatlán on the road to Barranca de Oro and Amatlán, *McVaugh & Koelz 759* (MICH). OAXACA: Distr.

Tlacolula, enfrente de la Virgen Juovila, 12 km E de Totolapan, *H. Hernández & Torres 216* (MEXU, MO); Dist. Pochutla, a 4 km NE de Chacalapa por camino a Finca Monte Cristo, *H. Hernández & Torres 394* (MEXU, MO); Dist. Putla, 20 km NE de Putla por carr. a Tlaxiaco, *H. Hernández & Torres 443* (MEXU, MO); Teotitlán del Valle, 10 mi. E of city, *Kenoyer 1629* (A); vicinity of Mitla, *Messer 247* (MICH); vicinity of Yalalag, *Nelson 945* (US); near Oaxaca, *Pringle 4801* (A, BM, BR, F, G, GH, MEXU, MICH, MO, NY, P, UC, US); a 10 km al NE de Teotitlán del Camino, *Rico et al. 251* (BM, MEXU, MO); Monte Albán, *Smith 115* (GH, US); Mpio. de Tututepec, 27 km al E de Río Verde, *Sousa et al. 5271* (MEXU); Distr. de Tuxtepec, Mpio. de Loma Bonita, San Agustín, 4 km al S de Mano Marquez, *Sousa et al. 7288* (MO); Desv. a Bahía de Santa Cruz, a 5 km al N de Santa Cruz, *Sousa et al. 7599* (CAS, MEXU); Distr. Tuxtepec, a 3 km al N de San Matéo Yetla, *Sousa 7955* (CAS, MEXU); Distr. de Tlacolula, Santa Rosa, a 3 km al E de Totolapan, *Sousa & Téllez 8561* (MO); Distr. de Yautepec, Mpio. Asunción-Tlacolulita, Los Tunillos, 2 km al ENE de La Reforma, *Sousa & Téllez 8616* (MEXU); Distr. Zimatlán, Santa Cruz Mixtepec, *Sousa et al. 10454* (CAS, MEXU, TEX); 1 km al SW de San José de Gracia, *Téllez & Magallanes 111* (CAS, MEXU, MO, NY); Dist. Tehuantepec, ladera W del Cerro Guingola, *L. Torres 395* (MEXU). PUEBLA: Acatlán, *Miranda 3025* (MEXU); behind Cerro Colorado between Nacozcalco and San Antonio Cañada, along the Barranca de los Mangos, *Smith et al. 4073* (G, GH, MEXU, NY, TEX, US). QUERÉTARO: Mex. hwy. 57, 21 km N of Querétaro on road to San Luis Potosí, *Anderson & Anderson 5041* (ENCB, GH, MICH, NY); Hacienda Rivera, *Arsène 10061* (A, BM, F, MO, NY, US); El Batán, *Arguelles 615* (CAS, MEXU); Pénjamo, *Magallanes 2672* (MEXU). QUINTANA ROO: Mpio. Carrillo Puerto, Rancho El Ramonal, *Durán & Olmsted 694* (MEXU); 22 km al ENE de Felipe Carrillo Puerto, camino a Vigía Chico, *Grether et al. 1317* (MEXU); 1 km al SW de Xel-Ha, *Grether et al. 1327* (MEXU, MO); Cobá, along Dzitnup trail, *Lundell & Lundell 7846* (A, LL, MICH, US); Cozumel, km 17 de la carr. costera W, *Pérez & Ramos 1063* (LL, MEXU, MO); 18 km al S de las Ruinas de Tulum, *Quero & Grether 924* (MEXU, MO); 3 km al S de Cancún, *Sousa et al. 10804* (MEXU, NY); Lázaro Cárdenas, en el camino blanco de Kantunilkin rumbo San Arseño, *Ucan & Chan 2926* (XAL). SAN LUIS POTOSÍ: 13 mi. W of Nuevo Morelos, *Kenoyer & Crum 3953* (A). SINALOA: Imala, *Gentry 4959* (CAS, GH, MEXU, MICH, MO, NY, UC); Las Mesas, Sierra Surutato, *Gentry 6156* (GH, MICH, MO, NY). TABASCO: San Pedro Balancán, límite N de la zona de Reserva Federal, S ejido Naranjito, *García & Palma 119* (XAL). TAMAULIPAS: Mpio. Gómez Farías, 3 km NW de Gómez Farías por camino corto al Rancho del Cielo, *H. Hernández & Torres 145* (MEXU, MO); 10 km NW of El Progreso which is 18 km NW of Ocampo (23°N, 99°30′W), *Stanford et al. 1095* (CAS, GH, MEXU, MO, NY, UC). VERACRUZ: Buena Vista, *Dorantes et al. 1430* (LL, MEXU); Mpio. de Jalcomulco, alrededor de Jalcomulco, *Gándara & Dorantes 100* (MEXU); Zacuapán, *Purpus 8401* (GH, UC); Mpio. Zapata, La Laja, entre Corral Falso-Pinoltepec, desv. a 16 km al SE Jalapa, *Sousa & Ramos 4899* (MEXU). YUCATÁN: en los alrededores de las Grutas de Balancanché, a 36 km W de Valladolid, *Cabrera & Cabrera 9733* (MEXU); Cantamayec, 1 km después de Cantamayec–camino a Peto, *Chan 1814* (XAL); Hunuema, km 12 carr. Hunuema a Sisal, *Chan 2827* (XAL); Chikindzonot, Xcocmil, *Chan 3536* (XAL); 5 km E of Motul, *Conway & Johnson 490-78* (MO, NY) Chankom, *Enríquez 690* (MEXU, US); Progreso, *Gaumer 1178* (A, BM, BR, CAS, F, GH, K, MA, MICH, MO, NY, UC, US); Suitún, *Gaumer et al. 23410* (F, G, GH, MA, MO, US); Kantunil, *Gaumer et al. 23431* (A, F, G, US); 2 km al NW de Ticul, Sierra de Ticul, *Grether 523* (MEXU); 7 km al N de Colonia Yucatán, brecha de Colonia Yucatán a El Cuyo, *Grether 557* (MEXU); 5 km al W de Chimax, *Grether 1333* (MEXU, MO); 3 km W of Valladolid, *Johnson & Conway 441-78* (MO); Oxkutzcub, Xul, *May 74* (XAL); Chichen Itzá, *Steere 1438* (BM, F, MEXU); Uxmal, *Steere 2078* (MICH); Muna, *Steere 2152* (MICH); Dzetás, *Stewart 235* (GH); Valladolid, Pixoy, *Ukanek 40* (XAL); Mpio. de Yaxcabá, al E de Yaxcabá, *Lara et al. 588* (F, MO, NY). GUATAMALA. ALTA VERAPAZ: between San Cristóbal Verapaz and Chixoy, *Steyermark 43911* (F, US). CHIMALTENANGO: Alameda, *Johnston 925* (F); San Martín, *Morales 1302* (F). CHIQUIMULA: Cerro Brujo, vicinity of Río Negro, below Montaña Montenegro, *Steyermark 30954* (F). GUATEMALA: 2.5 km S of Amatitlán, *Harmon & Dwyer 2987* (F, GH, LL, MO, NY, US). JALAPA: vicinity of Jalapa, *Standley 77380* (F, NY). PETÉN: Tikal, entrada de Baja de Santa Fe, *Contreras 191* (F, LL, MEXU); Dos Lagunas, on Ixcanrio Road, 3 km NE of the village, *Contreras 1544* (F, LL, MEXU); Uaxactún, *Contreras 3594* (F, LL, MEXU); Milpa Grande, Macanché, *Contreras 5487* (F, MO, NY); Guayacán, La Pita, bordering Laguna Guayacán, *Contreras 7409* (F, LL, MEXU); road to Flores from Melchor de Mencos, 7 km W of the Belize Guatemala border, *Ramos & Funk 519* (MO). SACATEPÉQUEZ: near Tejar, Baños de San Lorenzo, *Standley 59866* (A, F). SANTA ROSA: near Cuilapa, *Standley 78533* (F); between Santa Ana Huista and woods of Rancho Lucas, Sierra de los Chuchumatanes, *Steyermark 51357a* (F). BELIZE. Indian Church, road to Seibal, *Arnason & Lambert 17882* (MO); El Cayo, *Chanek 108* (MEXU?). HONDURAS. COMAYAGUA: near Lake Yojóa, *Hazlett 1079* (MO). CORTÉS: 3 km de San Pedro Sula, Montaña La Zona, cañon del Río Piedras, *Molina 3435* (F, GH, US); faldas de San Juan Lindo, cerca de Sta. Ana, *Molina 3476* (F, GH, US). MORAZÁN: near San Francisco, Río Yeguare Valley, *Williams & Molina 11482* (F, GH, LL, MEXU, MICH, MO, UC). OLANCHO: carr. a San Francisco La Paz, Montaña Uval, *Molina 13337* (F, LL, NY, US). EL SALVADOR. AHUACHAPÁN: *Padilla 88* (US). CHALATENANGO: La Reina, *Calderón 2468* (F, US). LA LIBERTAD: Santa Tecla, slopes of Volcán San Salvador, *Williams & Molina 15229* (GH). NICARAGUA. BOACO: Las Pitas (12°28′N, 85°35′W), *Moreno 10642* (MO); Santa Cruz (12°24′N, 85°49′W), *Moreno 18619* (MO). CARAZO: entrada a La Paz de Oriente, 1 km de la carr. S (11°49′N, 86°08′W), *Moreno 10710* (MO); Comarca El Aguacate, 4 km S of Jinotepe, *Neill 1058* (MO). CHINANDEGA: SE del Cosiguina, *Fonseca 146* (MO); Volcán San Cristóbal, Finca Los Rojos, a 20 km de Chinandega (12°42′N, 87°02′W), *H. Hernández et al. 582* (MEXU, MO); falda SE del Volcán Casita, 1 km antes de Argelia (12°70′N, 86°57′W), *Moreno 1572* (MO); La Suiza, 13 km al NE de Chinandega (12°41′N, 87°00′W), *Moreno 25040* (MO); km 146.5 carr. a Guasaule, camino al Volcán Chonco (12°43′N, 87°04′W), *Sandino 1357* (MO). CHONTALES: Puerto Monota N of Acoyapa (11°58′N, 85°10′W), *Stevens 10942* (MO); Hda. San Martín, near confluence of Río El Jordán and Río La Pradera (12°17′N, 85°15′W), *Stevens 22620* (MO). ESTELÍ: Salto de Estanzuela, 5 km

S Ciudad de Estelí, *H. Hernández et al. 634* (MEXU, MO); 6 km de Pueblo Nuevo carr. a Limay Cerro San Ramon (13°21′N, 86°31′W), *Moreno 3140* (MO); La Gavilana (13°03′N, 86°19′W), *Moreno 21883* (MO); Mpio. de Condega, 5 km al NE de Condega (13°22′N, 86°20′W), *Moreno 25333* (MO). GRANADA: Isla Apatera, Cerro El Llano (falda norte), *Grijalva 808* (MO); San Agustín, camino a Cutirre, a 2.5 km de Granada (85°58′N, 11°55′W), *Moreno 2632* (MO); Volcán Mombacho, subiendo por la finca Las Delicias (11°51′N, 85°58′W), *Moreno 4089* (MO); 1 km al N de Casa de Teja (11°50′N, 86°01′W), *Moreno 5404* (MO). JINOTEGA: 7 km a la entrada del camino viejo a Jinotega (12°58′36″N, 85°58′36″W), *Vega & Robleto 106* (MO). LEÓN: carr. vieja a León, km 63, debajo del puente del Río Tamarindo (12°14′N, 86°43′W), *Guzmán et al. 1025* (MO); Carretera a El Tránsito San Pablo (12°05′N, 86°41′W), *Moreno 4841* (MO). MADRIZ: Cerro Quisuca (13°31′N, 86°31′W), *Stevens 22205* (MO). MANAGUA: Cuesta del Coyol (12°30′N, 86°03′W), *Araquistain 3614* (MO); San Isidro (12°05–06′N, 86°15′W), *Araquistain 3654* (MO); Cuenca sur (12°00–03′N, 85°15 19′W), *Araquistain 3749* (MO); Managua, Punta Chiltepe, costado W de Laguna Apoyeque, *Grijalva et al. 3104* (MO); carr. entre Las Conchitas y Masachapa, *Guzmán & Castro 1961* (MO); San Francisco de Bolas, *Méndez 54* (MO); carr. a San Francisco Libre, 3 km después del Río San Antonio (12°23′N, 86°09′W), *Moreno 3767* (MO); S of Villa Franca, *Sandino 349a* (MO); along hwy. 8 ca. 2.4 km SW of intersection with hwy. 2, km 28 (11°57′N, 86°20′W), *Stevens 3941* (MO). MATAGALPA: Ermita de Esquipulas, 20 km NE de El Tuma (13°30′20″N, 85°30′30″W), *Grijalva & Grijalva 1366* (MO); Carretera Panamericana, Cuesta El Venado, 4 km al E Las Delicias (12°41′N, 86°03′W), *Moreno 18366* (MO); 1 km al E de la Hacienda Los Angeles (13°12′N, 85°42′W), *Moreno 19004* (MO); carr. vieja a Jinotega, Las Trancas (12°59′N, 85°58′W), *Moreno 22927* (MO); El Tempisque, 3 km al E de Puertas Viejas (12°35′N, 86°00′W), *Moreno 24831* (MO); along hwy. 1 at entrance to La Cruz, ca. 1.8 km SE of Las Calabazas (12°39′N, 86°04′W), *Stevens & Montiel 18611* (MO); Macizos de Peñas Blancas, SE side, drainage of Quebrada El Quebradón, slopes N and W of Hda. San Sebastián (13°14 15′N, 85°38′W), *Stevens et al. 21271* (MO). NUEVA SEGOVIA: carr. a Dipilto, 3 km al N de Ocotal Santa Marta (13°39′N, 86°28′W), *Moreno 25253* (MO). ZELAYA: La Luz (13°44′N, 84°47′W), *Ortiz 1589* (MO); Suina, *Seymour 3200* (MO). COSTA RICA. GUANACASTE: Bahía El Coco, Bahía Playa Hermosa (10°32′N, 85°40′W), *Burger & Baker 9942* (F); Parque Nacional Santa Rosa, *H. Hernández et al. 698* (MEXU, MO). PUNTARENAS: Monteverde, *Haber 392* (MO). SAN JOSÉ: cerca Río Virilla, San José, *Brenes 20565* (NY); Planta Hidroeléctrica Brazil-Villa Colón, *Poveda 934* (F); La Caja, *Valerio 1315* (F). CUBA. SANTIAGO DE CUBA: Santiago Bay, *Clemente 4279* (US); Sardinero, *Clemente 6102* (GH, US); Finca El Salado, *Clemente 6268* (GH, US); Finca Caimanes, *Clemente 6319* (GH); Loma Colorada, *Clemente 7030* (GH); Jaraguá Beach, *Clemente 7439* (GH, NY); Bayate, *Ekman 6432* (NY); en la zona entre el Puente de la Mina y la Estación de Radio, carr. de Punta Gorda, *López 217* (US); bordes del camino en Santa María de Loreto, *López & Acuña 346* (US). VILLA CLARA: from Santos Espiritus to Loma de Cantú, *León 5359* (NY, US). TRINIDAD: Island of Huevos, *Friend 115* (NY). VENEZUELA. ANZOATEGUI: Isla Chimana Segunda, N of Guanta (10°18′N, 64°36′W), *Steyermark & Manara 107998* (US). ARAGUA: detrás del Instituto de Botánica Agrícola, Facultad de Agronomía U.C.V. Maracay, *Cárdenas 1979* (F); Magdaleno, *Williams 10303* (F, G, US). BOLÍVAR: headwaters of Río Saca, *Wurdack & Guppy 60* (F, NY, US). CARABOBO: alrededores de Mariara, *Rojas 1051* (F); Pto. Cabello, *Curran & Haman 1144* (A, F, GH, MO, NY, US); hacienda del Cura, near San Joaquín, *Pittier 7902* (F, GH, US); La Cabrera, on Lake Valencia, *Pittier 12212* (A, CAS, G, US). DISTRITO FEDERAL: between Caracas and Blandin, road to La Guaira, *Pittier 11619* (A, F, MO, NY, US). MÉRIDA: Península Paraguaná, La Ciénaga, between Pueblo Nuevo and Santa Ana, *Breteler 4373* (F, MO, NY, UC, US); Chama Valley between Estanques and La Victoria, *Breteler 4562* (F, MO, UC, US). MIRANDA: Parque Nacional Guatopo, 22 km N of Altagracia de Orituco, N of the border with Estado de Guárico, *Vee 17935* (NY); Guarenas Valley, *Pittier 11903* (A, NY, US). NUEVA ESPARTA: Isla Margarita, *s. leg. 2419* (NY). SUCRE: Puerto de Hierro, hacia el valle y serranías de Patáo, *Aristeguieta 4719* (NY, UC, US); Península de Araya, 20 km NW of Cariaco, 2 km W of corner where road from Cariaco to Chocopata meets ocean (10°38′N, 63°40′W), *Liesner & González 12037* (MO). TACHIRA: S of La Mulata, near Venezuelan Colombian border (7°50′30″N, 72°27′3″W), *Steyermark et al. 120263* (MO). YARACUY: Hacienda Iboa, near Guama, *Pittier 11160* (GH, NY, US). ZULIA: San Martín, on Río del Palmar, *Pittier 10531* (GH, US). COLOMBIA. ATLÁNTICO: Canacoima, *Dugand 678* (F); Los Pendales, Hacienda Riodulce, *Dugand & Jaramillo 4104* (US); Costa del Caribe, arriba de Salgar, *Dugand 6421* (US); Costa del Caribe, carr. a Puerto Colombia, km 5, *Dugand 6574* (US); Barranquilla, *Elías 314* (NY, US). BOLÍVAR: La Popa, near Cartagena, *Killip & Smith 14068* (A, BM, G, GH, NY, US); Torrecilla, near Turbaco, *Killip & Smith 14388* (A, GH, NY, US). GUAJIRA: between Cuestecita and Carraipía, Río Cesar, *Cuatrecasas & Castañeda 25525* (US). MAGDALENA: Becerril, *Haught 3689* (A, US); trail to Pueblito, Parque Nacional Tayrona (11°19′N, 73°58′W), *Kirkbride 2513* (F, MO, NY, US); 0.5 km E of Aeropuerto Simón Bolívar and 14 km S of Santa Marta (11°07′N, 74°15′W), *Kirkbride 2606* (MO, NY, US); Mpio. de Santa Marta, Don Jaca, *Romero 10595* (F, MO, NY) NORTE DE SANTANDER: Valle del Río Peralonso, en los alrededores de Santiago, *Molina & Barkley 18* (US). BRAZIL. MATTO GROSSO: Corumbá, *Robert 755* (K). BOLIVIA. COCHABAMBA: Saipina, *Cárdenas 5753* (US). SANTA CRUZ: Prov. Cordillera, Camiri, *Cárdenas 4775* (US); Alto Parapetí, *de Michel 125* (NY). PARAGUAY. Fuerte Olimpo-Chaco, *Rojas 13645* (MO, TEX); Zwischen Río Apa und Río Aquidabán, Estrella, *Fiebrig 4304* (BM, GH). ARGENTINA. CHACO: Las Breñas, *Venturi 10198* (A). JUJUY: Dique La Ciénega, *Krapovickas & Cristóbal 17540* (LL, UC, WIS), SALTA: Joaquín González, *Aguilar 252* (NY); Dept. de Orán, Caraparí, *Bridarolli 3262* (GH); Cerro 20 de Febrero, *Filipovich 255* (US); 10 km E de Tartagal, camino a Tonono, *Krapovickas & Schinini 39282* (WIS); 14 km E de Embarcación, *Krapovickas & Schinini 30871* (G); Depto. San Martín, Gral. Ballivín, prox. El Saladillo, *Lognamé-Medina & Cuezzo 10144* (WIS); Pasaje del Río Juramento, *Lorentz & Hieronymus 275* (BR, G, NY, UC); Depto. Orán, Ruta 50, Quebrada El Cebilar, *Maruñak et al. 504* (MO, P); Depto. Caldera, Mojotoro, *Meyer 35760* (GH, NY); El Tabacal a Río Santa María, *Meyer 4521* (UC); Depto. Orán, Urindel a Río San Francisco,

Meyer 8413 (A, NY); Depto. Orán, Bella Vista, *Pierotti 106* (NY, UC); Depto. Orán, Tartagal a Las Tablillas, *Schreiter 11052* (A, GH); Depto. Guachipas, Alemania, *Venturi 9812* (A, BM, GH, MO, NY, US); Depto. Antillas, Cerro Negro, *Venturi 10390* (BM, NY). SANTIAGO DEL ESTERO: Sierra de Guasayán, Ruta 64, 70 km SW de Sgo. del Estero, *Krapovickas et al. 37390* (MEXU). TUCUMÁN: San Pedro Colaláo a Chulcas, *Castillón 69574* (A); Depto. Trancas, Vipos, *Schreiter 69573* (A, F); Depto. Burruyaco, Timbó, *Venturi 1549* (BM, CAS, F, GH, MO, NY, UC, US); Depto. Trancas, Tapia, *Venturi 5824* (A, CAS, US); Depto. Burruyaco, Cerro del Campo, *Venturi 7525*(A, BM, CAS, GH, US). CULTIVATED. U.S.A. MISSOURI: St. Louis, Missouri Botanical Garden, *H. Hernández 946, 953, 954* (MEXU, MO). MEXICO. Guanajuato, Garden of the Alameda, *Dugès 1* (GH, NY, US).

Specimens not assigned to subspecific status, probably intermediate between Z. formosa *subsp.* formosa *and* Z. formosa *subsp.* rosei. MEXICO: GUERRERO: Distr. Coyuca, Pungarabato, *Hinton 6878* (A, BM, F, GH,LL, MEXU, NY, US); Distr. of Mina, Placeres Camerún, *Hinton 9191* (ENCB, K, LL, MICH, NY, UC); 13 km NE of Atoyac, *Johnson 1270-80* (MO, NY); Mpio. de Zumpango del Río, 8 km al N de Milpillas, carr. Iguala–Chilpancingo, *Ladd et al. 120* (MEXU, MO); Mpio. de Chilpancingo de los Bravos, sobre la desv. a Chichihualco, a 8 km al NW de Chilpancingo, *Ladd et al. 146* (MEXU, MO); Distrito Aldama, N of Río Balsas, Temisco, Barranca de la Julia, *Mexia 8731* (CAS, GH, MO, NY, UC, US); 4 mi. W de Zumpango del Río, *Rico & Funk 201* (CAS, MEXU).

Zapoteca formosa subsp. *formosa* is the most widespread and morphologically variable subspecies within the species. Fourteen names have been published that fall within the boundaries of this subspecies as I have defined it; most of them have been based primarily on regional variations in leaflet morphology and vestiture. These characters, along with the size of the flower parts and pods, are highly variable at an inter- and intrapopulation level, especially in the Mexican and Central American populations, and thus they are not useful taxonomically. Perhaps the most variable character is leaflet size, but the variation does not correspond to a geographical pattern. A similar situation occurs with variation in leaflet vestiture; plants with short-pubescent or villous leaflets occur in the same areas as plants with glabrous leaflets throughout most of the range. In addition there is continuous variation in leaflet apex morphology, ranging from rounded to acute. Plants from the southern limits of this subspecies are comparatively consistent morphologically. In this area, they usually have medium to relatively small leaflets, and the number of pairs of leaflets per pinna is quite regular.

The entity most closely related to *Z. formosa* subsp. *formosa* appears to be the Central American subsp. *salvadorensis*, which is distinguished by its densely pilose pods. *Zapoteca formosa* subsp. *formosa* is consistent in having glabrous pods, although in El Salvador and Venezuela, plants with glabrate pods have been collected. In a few collections of subsp. *formosa* from Oaxaca, Jalisco, Honduras, Venezuela, and Cuba, the pods are pilose or sparsely pilose when very young, but soon become glabrous.

Zapoteca formosa subsp. *formosa* also appears closely allied to subsp. *rosei*, from which it differs by having white or white-green filaments (Table 14). Plants of subsp. *formosa* also usually have larger leaflets and are generally more robust than those of subsp. *rosei*. In a number of instances, however, the identification of these two subspecies is troublesome if flowers are not available or if filament color is not known. In some areas of the Mexican Pacific slope, especially in the state of Guerrero, where these two subspecies presumably occur sympatrically, hybridization probably takes place, resulting in morphological intergradation. In this area, many collections of subsp. *rosei* have larger leaflets than normal in this entity, thus resembling those of subsp. *formosa*. Such areas of intergradation are in Tecpan de Galeana (e.g., *Hinton 14335, 10894, Ladd et al. 206*) and Zihuatanejo (e.g., *Tenorio et al. 398, Ladd et al. 216, Sousa 6159*). Similarly, in some localities of the District of Yautepec in Oaxaca, plants from the two subspecies have been found growing together (e.g., *H. Hernández & Torres 216, 217, Téllez Magallanes 111, 113*). The collections belonging either to *Z. formosa* subsp. *formosa* or to subsp. *rosei*, but of ambiguous identity, are listed separately under *Z. formosa* subsp. *formosa*.

Zapoteca formosa subsp. *formosa* is distinguishable from the West Indian subsp. *gracilis* by having oblong-obovate leaflets, usually larger, lanceolate to ovate-lanceolate stipules, and glabrous, pubescent, or villous leaflets, which contrast with the consistently glabrous ones of subsp. *gracilis*. Subspecies *formosa* differs from subsp. *mollicula* and subsp. *schottii* by its more robust habit, white filaments, and larger petioles, leaflets, stipules, flower parts, and pods (Table 14).

There is a wide disjunction in the South American distribution of *Z. formosa* subsp. *formosa*, from northern Colombia and Venezuela to Bolivia, southeastern Brazil and Paraguay (Fig. 44). Morphologically, the populations from the southern region clearly belong to the subspecies. Perhaps this geographical fragmentation is related to the current scarcity of relatively dry, seasonal, lowland habitats in the intervening region. As reviewed by Haffer (1982, and references therein), climatic fluctuations during the Pleistocene had a great

effect in tropical areas. In lowland areas of the Neotropics, alternating periods of cooler and drier climates probably caused extinction or displacement of species adapted to the warm-wet forest conditions during the interglacial periods, and only a few areas (forest refugia) remain relatively unchanged. Consequently, great expanses of wet forests were replaced by drier, more open vegetation in the Amazon Basin (Ab'Saber, 1982; Absy, 1982; Bigarella & Andrade-Lima, 1982; van der Hammen, 1982; Prance, 1982; and others). In light of this body of ideas, it can be postulated that the populations of *Z. formosa* subsp. *formosa* found a more suitable environment during the dry phases of the Pleistocene, and then were continuously distributed across the Amazon Basin; and that the present-day disjunction in South America is the result of fragmentation of a formerly more continuous range after the warm, wet present-day conditions were established.

12b. Zapoteca formosa subsp. **salvadorensis** (Britton & Rose) H. Hern., comb. et stat. nov. *Anneslia salvadorensis* Britton & Rose, N. Amer. Fl. 23: 68. 1928. TYPE: El Salvador: vicinity of San Salvador, 650 850 m, 2–7 Feb. 1922, *Standley 20452* (lectotype, NY, here designated; isolectotypes, GH, MO, US).

Erect shrubs to 4 m tall, usually finely to densely villous throughout, except for the flowers. Pinnae 2–3-jugate; petioles (1.8–)3.1–4.5 cm long; rachis (0.9–)1.6–4 cm long; rachillae (1.8)3.8 5.6 cm long; leaflets 4–6 pairs per pinna, oblong-obovate, oblique at base, rounded to acute at apex, usually mucronate, the distal leaflets 1.6 2.6 × 0.7–1.9 cm, the proximal ones smaller; stipules lanceolate, sometimes curved, to 1.2 cm long. Capitula usually axillary, occasionally in simple pseudopanicles to 7 cm long; peduncles 2.2 8.2 cm long at anthesis. Calyx 3–4 mm long, the teeth oblong-lanceolate, glabrous; corolla ca. 5 mm long, glabrous; filaments white. Pods to 9 × 0.8 cm, pilose to densely pilose with white hairs. Seeds rhomboid-ovoid, ca. 5 × 4 mm, sometimes red when immature, brown when mature, the areola lighter; pleurogram irregular.

Distribution (Fig. 44). Endemic to southern Guatemala and El Salvador, where it has been collected in the departments of El Progreso, Chiquimula, Quiché, Sololá, and Zacapa, Guatemala, and near San Salvador, El Salvador. It has been collected primarily in disturbed, brushy habitats at altitudes of 300 1,800 m.

Additional specimens examined. GUATEMALA. CHIQUIMULA: between Chiquimula and Sta. Rosalía, *Molina & Molina 25136* (F, MO, US); near divide on road from Zacapa to Chiquimula, *Standley 73743* (F). EL PROGRESO: Motagua Valley, *Breckon & Breckon 2118* (ENCB, MEXU, NY). QUICHÉ: near village of Río Blanco, *Williams et al. 22456* (BM, F, GH, NY, US). SOLOLÁ: village of San Pedro, Volcán San Pedro, north-facing slopes towards Lago de Atitlán, *Steyermark 47203* (F). ZACAPA: Río Hondo, base of Sierra de las Minas, *Standley 73979* (F); Río Hondo, *Steyermark 29494* (F).

Zapoteca formosa subsp. *salvadorensis* is closely related to subsp. *formosa*, from which it can be distinguished by having pilose or densely pilose pods and by being villous on all vegetative parts. By contrast, presence or absence of vestiture in subsp. *formosa* is expressed irregularly throughout its range. Geographically, these two subspecies are allopatric.

12c. Zapoteca formosa subsp. **gracilis** (Griseb.) H. Hern., comb. et stat. nov. *Calliandra gracilis* Griseb., Mem. Amer. Acad. Arts 8: 180. 1861, non Klotzsch, 1871, nec Standley, 1929, nec Renvoize, 1981. *Anneslia grisebachii* Britton & Rose, N. Amer. Fl. 23: 67. 1928. This was published as a nomen novum, because the name *Anneslia gracilis* was preoccupied by Britton & Rose for a species based on *Acacia gracilis* M. Martens & Galeotti (see synonymy under *Z. formosa* subsp. *rosei*). *Calliandra grisebachii* (Britton & Rose) Standley, Publ. Field Columbian Mus., Bot. Ser. 3: 277. 1930. *C. grisebachii* (Britton & Rose) León, Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle" 10: 237. 1951; Liogier, Fl. Cuba (Supl.). 72. 1969. TYPE: Prope Cuba Orientali, Sep. 1859 Jan. 1860, *Wright 151* pro parte (lectotype here designated, GH; isolectotypes, CGE, F, G, LE, MO). As León (1951; see synonymy below) pointed out, *Wright 151* includes two elements under the same number. In addition to the specimens considered here to represent the type of this taxon, there are five collections, also numbered as *151*, at G, GH, LE, NY (fragment), and S, that presumably came from another locality and belong to *Z. formosa* subsp. *formosa*. One additional specimen at G includes material from both.

Calliandra comosa Griseb., Cat. Pl. Cub. 83. 1866, non Benth., 1846. *Calliandra formosa* var. *cubensis* J. F. Macbr., Contr. Gray Herb. 59: 4. 1919. (Based on the same type as *Calliandra comosa.*) *Anneslia cubensis* (J. F. Macbr.) Britton & Rose, N. Amer. Fl. 23: 68. 1928. *Calliandra cubensis* (J. F. Macbr.) León, Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle" 9: 7. 1950; León, Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle" 10: 237. 1951; Liogier,

Fl. Cuba (Supl.). 72. 1969; Proctor, Kew Bull. 11: 481. 1984. TYPE: Cuba: *Wright 2406* (lectotype here designated, GH).

Erect shrubs to 2(5) m tall, glabrous throughout. Pinnae 2–3(–4)-jugate; petioles 1.3–5.5 cm long; rachis 0.7–5 cm long; rachillae 3.5–12.5 cm long; leaflets (5–)7–15 pairs per pinna, the median ones elliptic to elliptic-oblong, the distal ones oblique at the base, the proximal ones becoming acute, rounded to subacute, rarely acute at apex, sometimes mucronate, the median leaflets 9–22 × 3.5–11 mm, all usually drying light green; stipules linear-triangular, to 5 mm long. Capitula axillary; peduncles 3.5–10.5 cm long at anthesis; calyx 2.5–3 mm long; corolla 5–6 mm long; filaments white. Pods to 11 × 1.2 cm, glabrous. Seeds ovoid, 5–6 × 3–4 mm, usually mottled, pleurogram semiregular.

Distribution (Fig. 44). Restricted to several islands of the West Indies: Cuba, Bahamas, Cayman Islands, and Haiti, where it primarily occurs in rocky, calcareous areas, in dense thickets, and, in general, in secondary, arid habitats at elevations of 0–600 m.

Additional specimens examined. BAHAMA ARCHIPELAGO. ABACO: Eight Mile Bay, *Brace 1854* (F, NY). ANGUILLA ISLAND: south end, *Wilson 8025* (F, NY). ANDROS: road to Morgan's Bluff, *Brace 6661* (F, NY); Behring Point, *Godfrey 41444* (NY); South Andros, S of Little Creek, *Correll 43481* (NY); 2 mi. E of Andros Town airport, *Hill 3003* (NY); Mangrove Cay, near Lisbon Creek, *Small & Carter 8439* (F, GH, NY, US). BERRY ISLAND: Whale Cay, *Britton & Millspaugh 2183* (F, NY); Goat Cay, *Britton & Millspaugh 2288* (F, NY); Anderson Cay, Great Harbour Cay, *Correll 43687* (F, NY). BIMINI ISLANDS: South Bimini, *Correll 42174* (LL, NY); Bimini, Cat Cay, *Correll 45614* (NY); South Bimini, NE corner of Island, *Gillis 11295* (F). CAICOS ISLANDS: Long Cay, N end, *Millspaugh & Millspaugh 9235* (F, CAS, NY); Long Cay, S end, *Millspaugh & Millspaugh 9274* (F, NY, US); South Caicos, *Wilson 7690* (F, GH, K, NY). CAT ISLAND: Bennets Harbor, *Byrne 358* (A, WIS); Zonicle Hill, *Correll 16065* (NY). ELEUTHERA: Glass Window to Harbor Island, *Britton & Millspaugh 5393* (F, NY); North Eleuthera, near Watkins Hill, *Correll 41060* (MO); 6 mi. N of James Cistern, *Correll & Hill 45234* (NY). EXUMA CHAIN: Little Galiot Cay, *Britton & Millspaugh 2843* (F, GH, NY, US). INAGUA: Great Inagua, Rocky Point, *Correll 17171* (MO, NY). LONG ISLAND: Clarence Town, *Britton & Millspaugh 6291* (F, NY). NEW PROVIDENCE: near Nassau, *Curtis 83* (A, F, G, GH, MO, NY, US); Blue Hills, between Lake Cunningham and Lake Killarney (77°24.5′W, 25°03.5′N), *Webster et al. 10511A* (GH, US); Hog Island, *Wilson 8272* (F, NY). RAGGED ISLANDS: Great Ragged Island, *Wilson 7806* (F, NY). ROSE ISLAND: *Britton & Millspaugh 2149* (F, NY). CAYMAN ISLANDS: near Tibbett's Turn, *Proctor 29355* (LL); 0.8–1 km inland from Spot Bay, *Proctor 35189* (US). CUBA: CAMAGUEY: Cayo Sabinal, between Corte Ficote and El Fuerte, *Ekman 15539* (US); La Gloria, near Laguna Grande, *Shafer 602* (GH, NY, US); Santa Lucia, *Shafer 974* (GH, NY, US); Cayos Canal Nuevo, Cayo Lagua, *Shafer 2668* (F, NY, US); Cayo Guajaba, hills NW end, *Shafer 2855* (F, GH, NY, US); vicinity of Tiffini, *Shafer 2901* (F, NY, US). ORIENTE: Punta Piedra, Nipe Bay, *Britton et al. 12471* (NY, US); Río del Medio, Jauco region, *León 12426* (GH, US); Loma de Tabaco, Manatí Bay, *León & Alain 18937* (GH, US); Holguin to Myabe, *Shafer 1410* (NY, US); northward of Raimon, Nipe Bay, *Shafer 1792* (NY). PINAR DEL RÍO: Pan de Guajaibón, La Mulata, *Barker 18513* (NY); Pan de Guajaibón, *Alain & Acuña 2995* (NY); Sierra de Nipe, Río Piloto, *Ekman 5780* (G); Banes, prope Puerto Rico, *Ekman 6607* (NY). HAITI: Ile de Nord-Ouest, Port de Paix, *Ekman 2846* (NY, US); E of La Vallée, Tortue Island, *Leonard & Leonard 11312* (A, GH, NY, US). CULTIVATED: U.S.A. FLORIDA: Miami, Fairchild Tropical Garden, *Gillis 8672* (MO).

Zapoteca formosa subsp. *gracilis* is relatively uniform morphologically compared with the other subspecies of *Z. formosa*. It is related to subsp. *formosa*, from which it is distinguished by having elliptic to elliptic-oblong leaflets and narrowly triangular stipules and by being glabrous (Table 14). The seeds of subsp. *gracilis* differ from those of the remaining subspecies of *Z. formosa* by having semiregular, instead of irregular, pleurograms. Subspecies *gracilis* and subsp. *formosa* are essentially allopatric, although there are a few collections of both from Oriente Province, Cuba. Their relationship is discussed further under *Z. formosa* subsp. *formosa*.

Although leaflet morphology is quite constant among populations of *Z. formosa* subsp. *gracilis*, a few plants from the Bahamas (e.g., *Correll & Correll 45614*, *Curtis 82*, *Gillis 11295*, *Hill 3003*) have unusually narrow leaflets. These plants could be confused with *Z. portoricensis* but can be readily distinguished by their smaller and narrower stipules and relatively thicker leaflets (also see Table 14). In addition, *Z. formosa* and *Z. portoricensis* are strongly segregated geographically in the West Indies.

12d. Zapoteca formosa subsp. **rosei** (Wiggins) H. Hern., comb. nov. *Calliandra rosei* Wiggins, Contr. Dudley Herb. 4: 17. 1950. *Calliandra schottii* subsp. *rosei* (Wiggins) Felger & Lowe, J. Ariz. Acad. Sci. 6: 83. 1970. *Acacia gracilis* M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 10: 311. 1843. *Anneslia gracilis* (M. Martens & Galeotti) Britton & Rose, N. Amer. Fl. 23: 68. 1928. *Calliandra gracilis* (M. Martens & Galeotti) Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 309. 1929, non Griseb., 1861, nec Klotzsch, 1871, nec Renvoize, 1981. H.

S. Gentry, Publ. Carnegie Inst. Wash. 527: 122. 1942 TYPE: Mexico. Oaxaca: bord del l'Océan Pacifique, Oct. 1840, *Galeotti 3190* (holotype, BR (not seen); isotypes, G, K, LE).

Calliandra socorrensis I. M. Johnston, Contr. Gray Herb. 70: 71. 1924. *Anneslia socorrensis* (I. M. Johnston) Britton & Rose, N. Amer. Fl. 23: 64. 1928. TYPE: Mexico. Colima: Isla Socorro, Mar. June 1897, *A. W. Anthony s.n.* (holotype, UC no. 83534). In a later note, Johnston (Proc. Calif. Acad. Sci. 20: 62. 1931.) pointed out that Anthony made two unnumbered collections on Socorro Island. Since he implied that they were made from different localities, the second collection, also at UC (no. 89257), should not be considered an isotype.

Anneslia delicata Britton & Rose, N. Amer. Fl. 23: 67. 1928. TYPE: Mexico. Baja California Sur: San José del Cabo, 23 Sep. 1890, *T. S. Brandegee 196* (lectotype, NY, here designated; isolectotypes, A, GH, NY, UC (2), US).

Anneslia interior Britton & Rose, N. Amer. Fl. 23: 66. 1928. TYPE: Mexico. Durango: mountains of southern Durango, 15 Aug. 1897, *Rose 2317* (lectotype US no. 301227, here designated; isolectotype, NY).

Shrubs to 3(–4) m tall; stems usually slender, erect or drooping. Pinnae 1–3-jugate; petioles 1–4.2(–5) cm long; rachis 0.3–3.4 cm long; rachillae 1.9–6.5(–11.3) cm long; leaflets (3–)4–12(–17) pairs per pinna, distal leaflets oblong-obovate to oblong–very widely obovate, rarely oblong, the proximal ones sometimes becoming elliptic, the distal leaflets oblique at base sometimes becoming acute proximally, rounded to acute at apex, usually mucronate, 8 31 × 3 21 mm, usually becoming smaller proximally, glabrous to villous; stipules lanceolate to ovate-lanceolate, to 9 mm long, glabrous to villous. Capitula axillary, sometimes in simple pseudopanicles to 13.5 cm long; peduncles 1 4.7 (–5.8) cm long at anthesis. Calyx 1.5 2 mm long, glabrous, the teeth triangular to oblong-lanceolate; corolla 3–5 mm long, glabrous; filaments red-purple, or white in the basal half and red-purple or pink in the distal half. Pods to 9 × 0.9 cm at maturity, glabrous. Seeds rhomboid-ovoid to widely rhomboid-ovoid, 4–5 × 4 mm, brown or gray, the areola lighter usually; pleurogram irregular. Somatic chromosome number $2n = 26$.

Distribution (Fig. 44). This subspecies occurs along the Pacific slope of Mexico, from northern Sonora south and southeast to the Isthmus of Tehuantepec. It has also been collected in southern Baja California and on the Revillagigedo Islands (Isla Socorro and Isla Clarión). A number of collections have been made from the districts of Yautepec and Tlacolula, Oaxaca, and from a number of localities in the Balsas Basin. It is relatively common in disturbed or undisturbed habitats of tropical thorn woodlands and tropical deciduous or tropical semievergreen forests. It is found on steep calcareous slopes, on volcanic rock, or along the margins of seasonal streams at 0–1,430 m.

Common names. Huaje de caballo (Oaxaca), tosapolo (Sonora).

Additional specimens examined. MEXICO: BAJA CALIFORNIA SUR: 6 10 mi. SE of Todos Santos Cabo San Lucas hwy., on small road to Rancho La Burrera, *Breedlove & Axelrod 43213* (CAS, MEXU). CHIAPAS: Mpio. of Arriaga, along Mex. hwy. 195 near Monte Bonito, *Ton 3405* (CAS, MO, US). CHIHUAHUA: Mpio. de Batopilas, E of La Bufa, near Arroyo La Bufa, *Bye 7726* (MEXU); SW Chihuahua, *Palmer 297* (BM, GH, K, MEXU, NY, UC, US); La Junta, 13 km NE de Batopilas, *Tenorio & Torres 4445* (MEXU). COLIMA: Socorro Island, *Anthony s.n.* (UC); Revillagigedo Islands, Clarión Island, above Sulphur Bay, *Howell 8371* (CAS, GH); Revillagigedo Islands, Clarión Island, *Mason 1566* (CAS, GH); Revillagigedo Islands, *Mason 1661* (CAS); above Río Salado, 5 mi. S of Colima, *McVaugh & Koelz 1090* (MICH); hacia cumbre Everman, Isla Socorro, *Miranda 8732* (MEXU); Ventanas, *Miranda 8775* (MEXU); Manzanillo, *Palmer 896* (GH, K, MICH, NY, UC, US); 19 km al SW de Colima, carr. a Manzanillo, *Soto & Cortés 2571* (MEXU); along Colima side of Río Tuxpan below hwy. 110 bridge, *Stevens & Fairhurst 1834* (CAS, GH, MICH, MO, TEX). GUERRERO: Pie de la Cuesta, near Acapulco, *Carlson 3061* (F, US); 14.7 mi. N of Chilpancingo, *Dunn et al. 20519* (ENCB, MO); Distr. of Coyuca, Pungarabato, *Hinton et al. 6466* (A, BM, F, GH, LL, MO, NY, US); Distr. Galeana, Tecpan, *Hinton 10894* (BM, F, G, GH, K, LL, MEXU, MO, NY, US); Distr. Galeana, Atoyac, *Hinton 11605* (GH, LL, NY, US); Mpio. de la Unión, carr. Ixtapa Playa Azul, 3 km al SSE de la desv. a la Unión, *Ladd et al. 279* (MEXU, MO); La Corréa, *Langlassé 388* (G, GH, K, MEXU, P, US); Iguala Canyon, *Pringle 10057* (CAS, F, GH, LL, MICH, UC, US, WIS); Achotla, *Reko 4946* (NY, US); Mpio. de Zumpango del Río, Casa Verde, cerca de Xochipala, *Rzedowski 16087* (CAS, TEX); 10 km al NW de Petatlán, por el camino al Camalote, *Soto et al. 5967* (WIS); Bahía de Zihuatanejo, *Sousa 6159* (CAS, MEXU, MO, NY); 45 mi. S of Iguala, *Webster et al. 17M721* (BM, MEXU, NY, TEX, US). JALISCO: 3 km de la Boca de Tomatlán, cerca de Puerto Vallarta, *Delgado et al. 139* (CAS, MEXU, MO, TEX); Mpio. La Huerta, Estación Chamela, *H. Hernández & Lott 230* (MEXU, MO); hills between Barra de Navidad and La Manzanilla on Bahía Tenacatita, *McVaugh 20988* (MICH); cerros al N de San Patricio, *Pérez & Pérez 1256* (MEXU); carretera al Coastecomate, *Puga 2* (ENCB); Corcovado Canyon, 11 mi. NE of Autlán toward Guadalajara, *Wilbur & Wilbur 2385* (MEXU, MICH). MÉXICO: Distr. of Temascaltepec, Tenayac, *Hinton 4433* (GH, K, US); Distr. of Temascaltepec, Acatitlán, *Hinton 6545* (F, G, GH, K, LL, MICH, NY, UC, US); Distr. of Temascaltepec, Platanal, *Hinton 7094* (A, F, MICH, MO, UC, US). MICHOACÁN: Aquila, 3 km al W de la Cruz de Cachán, *Guerrero et al. 1012* (XAL); Mpio. Jungapeo, entre Agua Blanca y Lázaro Cárdenas, *H. Hernández & Chacón 185* (MEXU, MO); Distr. Coalcomán, Villa Victoria, *Hinton 12558* (BM, CAS, F, GH, MEXU, NY, UC, US); Distr. Zitácuaro, San José Purúa, *Hinton 13053* (BM, BR, CAS, F, G, GH, K, MEXU, MICH, NY, TEX,

UC, US); Barranca of Río Cancita at the bridge 9 mi. SE of Apatzingán, *McVaugh 17974* (MICH); entre El Quedable y Arturo Benítez, Tuzantla, *Medrano et al. 5083* (MEXU); Mpio. Tiquicheo, Agua de los Coyotes, entre La Crucecita y el Guayabo, *Soto 197* (CAS, MEXU); Mpio. de Arteaga, en cerros aledaños a Infiernillo, *Soto & Silva 1636* (MO); carr. Cuatro Caminos–Playa Azul, 4 km al S de Arteaga, *Soto & Silva 1699* (MEXU, TEX, WIS); 7 km al S de Arteaga, *Sousa & Soto 8033* (CAS, MEXU); Mpio. de Huetamo, Puerto de los Cirianes, 6 km al E de Huetamo, carr. Huetamo–Zitácuaro, *Tenorio et al. 1548* (MO). MORELOS: 10 km N de Teuixtla, *Gómez-Pompa 1068* (MEXU); Cerro Acatlipa, *Vázquez 2046* (MEXU). OAXACA: Distr. de Jamiltepec, de Río Verde a Jamiltepec, *Conzatti 4394* (US); Ixtepec, *Fisher 35491* (F, MO, NY, US); Mpio. Totolapan, 9 km E Totolapan por carr. a Tehuantepec, *H. Hernández & Torres 207* (MEXU, MO); Mpio. San Matéo de Mar, 13.3 km NW San Mateo del Mar, *H. Hernández & Torres 209* (MEXU, MO); Distr. Yautepec, 17 km NW La Reforma por carr. a El Camarón, *H. Hernández & Torres 210* (MEXU, MO); Mpio. Nejapa, 3 km S Nejapa de Madero por camino que desemboca en carr. Oaxaca–Tehuantepec, *H. Hernández & Torres 212* (MEXU, MO); Distr. Tlacolula, entre San José de Gracia y Totolapan, *H. Hernández & Torres 215* (MEXU, MO); Distr. Tlacolula, enfrente de la Virgen Juovila a 12 km E de Tatolapan, *H. Hernández & Torres 217* (MEXU, MO); Distr. Juchitán, 3.3 km E de La Ventosa por carr. Tapanatepec, *H. Hernández & Torres 337* (MEXU, MO); Distr. Tehuantepec, al pie del Cerro Guingola, vertiente E, en la entrada a las Ruinas Arqueológicas, *H. Hernández & Ramírez 918* (MEXU); Distr. Yautepec, 2.6 km de la desviación a San Bartolo Yautepec (Portillo de San Bartolo Yautepec) de la carr. Oaxaca Tehuantepec, *H. Hernández & Ramírez 930* (MEXU); 29 km de San José de Gracia, sobre carr. Oaxaca–Tehuantepec, entre San José de Gracia y San Juan Guegoyache, *H. Hernández & Ramírez 932* (MEXU); Distr. Tlacolula, 9 km NW de Totolapan por carr. a Oaxaca, *H. Hernández & Ramírez 943* (MEXU); Zipolite por el camino al arroyo, *Shapiro 336* (CAS, MEXU, US); Distr. Cuicatlán, Tomellín, *Sousa et al. 6146* (MO); Distr. Juquila, 7 km al NW de Río Grande, *Sousa et al. 7079* (BM, CAS, MEXU, MO); Distr. Juquila, 7 km al WNW de Pto. Escondido, *Sousa et al. 8408* (CAS, MEXU, MICH); Distr. Juchitán, Mpio. de San Miguel Chimalapa, Vista Hermosa, 3 km al NE de El Porvenir, *Sousa 8687* (CAS, MEXU, NY); 2 km al SW de San José de Garcia, cerca de Los Cantiles, carr. Oaxaca–Tehuantepec, *Téllez & Magallanes 113* (CAS, MEXU); 1 km al SW de El Chacal, o a 21 km al NE de El Camarón, *Téllez & Magallanes 253* (MEXU); Cerro Tres Cruces, al S de El Limón, el cual está a 11.1 km al SW del entronque de carr. Tehuantepec Oaxaca Buenos Aires, *Torres 1262* (MEXU, MO). SINALOA: Bahía Topolobampo, in the Sierra Navachiste, *Gentry 11460* (LL, MEXU, MICH); cerros del Fuerte 18–24 mi. N of Los Mochis, *Gentry 14427* (LL, MEXU, US); Mazatlán, *Ortega 7305* (CAS, G, K, MEXU, US); El Quelite, 34 mi. S of Elota, *Skorepa 82* (MO); Mpio. de Rosario, camino de Herradura El Alamo Cerro Yauco, 6 km al NE del Ejido de los de Ponce, *Tenorio et al. 2816* (MO). SONORA: Cañón de Nacapules, ca. 6 km NE Bahía San Carlos, *Felger et al. 84-124* (MEXU); Ensenada Grande (San Pedro Bay), 0.5 mi. E from S end of Bay, *Felger et al. 11579* (MEXU); San Bernardo, Río Mayo, *Gentry 1630* (A, F, K, LL, MEXU, MO, NY, UC, US); Cerro del Viejo SW of Caborca, *Gentry 14459* (US); Sierra Bojihuacame SE of Cd. Obregón, *Gentry 14488* (LL, US); San Bernardo and vicinity, Arroyo Gochico, *Gentry et al. 19286* (US); Hacienda de San Miguel, near Batopilas, *Palmer 16* (BM, GH, K, MEXU, NY, US).

This polymorphic, highly variable subspecies, along with *Z. formosa* subsp. *formosa*, represents the phylogenetic core within the species. Leaflet size is highly variable within and between populations, and a clinal variation pattern is evident, especially in the northern portion of its range, possibly a reflection of decreasing precipitation from south to north. There is some variation in filament color within *Z. formosa* subsp. *rosei*, although this character is consistent at the populational level. The distribution of the different color morphs is not known with precision. The following generalizations can, however, be drawn: the most widespread pattern of filament color is the white/red-purple pattern, which occurs from southern Oaxaca to Sonora and Chihuahua. The populations from the Isthmus of Tehuantepec, at the eastern distributional limit (e.g., *H. Hernández & Ramírez 918*, *Sousa & Téllez 8687*), and a few populations from Michoacán (e.g., *H. Hernández & Chacón 185*, *Soto 1636*) have entirely red-purple filaments. Populations from the districts of Tlacolula and Yautepec, Oaxaca, have white/pink filaments (e.g., *H. Hernández & Ramírez 930, 943*).

Zapoteca formosa subsp. *rosei* is closely related to subsp. *formosa* and to subsp. *mollicula* and subsp. *schottii*. It can be distinguished from subsp. *formosa* by the color of its filaments and by its usually smaller leaflets. However, plants of these two subspecies sometimes resemble each other closely. In some localities of Guerrero, the two subspecies become sympatric and apparently intergrade morphologically. These collections are not assigned to a particular subspecies; they have been listed separately under subsp. *formosa* (and see discussion under this subspecies).

As will be discussed below under the respective subspecies, patterns of morphological variation, especially in leaflet size, are essentially continuous between *Z. formosa* subsp. *rosei* on the one hand and subsp. *mollicula* and subsp. *schottii* on the other. Although each of these is relatively easily identifiable, their integrity breaks down because of the existence of morphological intermediates. *Zapoteca formosa* subsp. *rosei* can be distinguished from subsp. *mollicula* by having more-developed leaf parts (e.g., longer petioles and rachillae, usually more numerous and larger leaflets, and usually larger stipules (Table 14)). Similarly, subsp. *rosei* can be distinguished from subsp. *schottii* primarily

by having more numerous and larger leaflets (Table 14). Nevertheless, the differences between these two subspecies are less marked than those separating subsp. *rosei* and subsp. *mollicula*. Geographically, subsp. *mollicula* and subsp. *schottii* are peripheral to but contiguous with subsp. *rosei*. This fact, along with their close morphological affinities, suggests that subsp. *mollicula* and subsp. *schottii* were derived from subsp. *rosei*. Further discussion of the presumed relationships of these three taxa is provided under the respective subspecies.

12e. Zapoteca formosa subsp. **mollicula** (M. Martens & Galeotti) H. Hern., stat. et comb. nov. *Acacia mollicula* M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 10: 313. 1843. *Anneslia mollicula* (M. Martens & Galeotti) Britton & Rose, N. Amer. Fl. 23: 64. 1928. *Calliandra mollicula* (M. Martens & Galeotti) Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 309. 1929. TYPE: Mexico. Puebla: Plaine de Tehuacán, 5,500 ft., *H. Galeotti 3216* (lectotype here designated, BR).

Calliandra unijuga Rose, Contr. U.S. Natl. Herb. 5: 193. 1899. *Anneslia unijuga* (Rose) Britton & Rose, N. Amer. Fl. 23: 64. 1928. TYPE: Mexico. Oaxaca: Cuicatlán, 1,800 ft., 24 Sep. 1894, *L. C. Smith 203* (lectotype here designated, GH; isolectotypes, US 2 fragments).

Calliandra unijuga var. *pueblensis* J. F. Macbr., Contr. Gray Herb. 59: 4. 1919. TYPE: Mexico. Puebla: vicinity of San Luis Tultitlanapa, near Oaxaca, Barranca de Tlacuilosto, June 1908, *C. A. Purpus 3185* (lectotype, F, here designated; isotypes, BM, GH, NY, MO, UC, US (2)).

Erect shrubs to 2(–2.5) m tall; stems slender, sometimes with exfoliating bark; branchlets pilose in the younger parts, glabrate, sometimes glabrous throughout. Pinnae 1(2)-jugate; petioles 3 11 mm long; rachis 4–8 mm long; rachillae 6–18 mm long; leaflets (2–)3–5(–6) pairs per pinna, oblong-obovate to widely obovate, rarely elliptic, the distal ones oblique at base, 4–14 × 2–9 mm, the proximal ones smaller, becoming rounded or acute, rounded or rarely retuse at apex, usually mucronate, all membranous, finely pilose or villous to totally glabrous; stipules lanceolate to ovate-lanceolate, sometimes narrowly triangular, to 3 mm long, finely pilose to glabrous, usually ciliate. Capitula axillary; peduncles (1.2–)2.3–4.5 cm long at anthesis. Calyx ca. 2 mm long, the teeth triangular, glabrous; corolla ca. 5 mm long; filaments white in the basal half, red-purple in the distal half. Pods to 7.5 × 0.8 cm at maturity, glabrous. Seeds ovoid, ca. 5 × 4 mm, brown; pleurogram irregular.

Distribution (Fig. 44). Endemic to the Tehuacán and Cuicatlán valleys in the states of Puebla and Oaxaca, where it primarily occurs on dry, calcareous slopes, in arid scrub and tropical dry forests at 550–1,450 m.

Common name. Huajillo (Puebla).

Additional specimens examined. MEXICO. PUEBLA: lado W de Axusco, *Chiang et al. 2469* (MEXU); Coxcatlán, *Delgado 545* (CAS, MEXU); Tehuacán, *Rose et al. 9885* (NY, US); Zapotitlán, al SE de Zapotitlán de las Salinas (18°20′N, 97°26′W), *Zavala 129* (XAL). OAXACA: Tecomavaca, *Conzatti 4041* (MEXU, US); Coixtlahuaca, La Huerta, 29 km al NE de Tepelmeme de Morelos, *Cruz 2563* (ENCB, MEXU); Distr. Cuicatlán, Tomellín, *H. Hernández & Torres 218* (MEXU, MO); Distr. Cuicatlán, Tomellín por carr. a Santa María, *H. Hernández & Torres 221* (MEXU, MO); 7 km N Cuicatlán por carr. a Teotitlán del Camino, *H. Hernández & Torres 226* (MEXU, MO); Distr. Teotitlán, 8 km NW Tecomavaca por carr. a Teotitlán, *H. Hernández & Torres 227* (MEX, MO); Distr. Teotitlán, 5 km S de Tecomavaca por carr. a Cuicatlán, *H. Hernández & Ramírez 874* (MEXU); Distr. Teotitlán, 1 km Tomellín por el camino a la carr. Cuicatlán Teotitlán, *H. Hernández & Ramírez 876* (MEXU); Distr. Teotitlán, en el desemboque del camino viejo a Tomellín, sobre la carr. Cuicatlán Oaxaca, *H. Hernández & Ramírez 877* (MEXU); laderas al SE de Cuicatlán, *Miranda 4577* (MEXU); Cuicatlán, *Nelson 1648* (US); Tomellín Canyon, *Rose & Hough 4671* (US); Distr. Cuicatlán, 15 km S de Dominguillo, *Rzedowski 34957* (ENCB); Cañon de Tomellín, *Sousa et al. 6905* (BM, MEXU, MO).

Zapoteca formosa subsp. *mollicula* represents an extreme of morphological variation within the species in petiole length, number of pairs of pinnae, and number and size of leaflets. It is distinguished from the other subspecies by its 1-, rarely 2-jugate pinnae with fewer and smaller leaflets and by its somewhat shorter internodes. Leaflet size, however, is extremely variable in this subspecies, both at an intra- and interpopulational level (e.g., *Cruz Cisneros 2563, H. Hernández & Torres 218, Rose & Hough 4671, Sousa et al. 6904, 6905*). Similarly, vestiture is highly variable, and does not display any coherent pattern.

Zapoteca formosa subsp. *mollicula* clearly is closely related to the highly variable subsp. *rosei*. Perhaps the most taxonomically meaningful characters separating these taxa are the usually more reduced leaves of subsp. *mollicula*. However, variation in leaf characters (e.g., petiole length, number of pinnae, number of leaflets, size of leaflets) is essentially continuous, especially when plants of subsp. *rosei* from the districts of Tlacolula and Yautepec, Oaxaca (e.g., *Delgado et al. 724, H. Hernández & Torres 207, 210, 212, 215, 217, Hernández & Ramírez 930, 932, 943, Magallanes et al. 199, Sousa et al. 6549*) are compared

with some plants of subsp. *mollicula* (e.g., *Cruz Cisneros 2563*, *Hernández & Torres 218*, *Hernández & Ramirez 874*, *876*, *877*, *Rose & Hough 4671*, *Sousa et al. 6904*, *6905*).

12f. Zapoteca formosa subsp. **schottii** (Torrey ex S. Watson) H. Hern., comb. nov. *Calliandra schottii* Torrey ex S. Watson, Proc. Amer. Acad. Arts 20: 364. 1885. "*Calliandra portoricensis* Benth. var." Torrey, Emory Rep. 2: 61. 1859; Isely, Madroño 21: 280. 1972. This species was doubtfully referred to in Torrey's *Botany of the United States and Mexican Boundary Survey* (loc. cit.) as "*Calliandra* (*portoricensis* Benth. var.)." Subsequently, S. Watson based his *Calliandra schottii* on the description provided by Torrey, citing a Pringle collection (*272*). *Anneslia schottii* (Torrey ex S. Watson) Britton & Rose, N. Amer. Fl. 23: 67. 1928. *Calliandra schottii* subsp. *schottii* (Torrey ex S. Watson) Felger & Lowe, J. Ariz. Acad. Sci. 6: 83. 1970. TYPE: Mexico. Sonora: Pimeria Alta, Sierra Verde, Arroyo de los Samotas, 20 Aug. 1855, *Schott s.n.* (lectotype designated by Isely (Madroño 21: 280. 1972), GH; isolectotypes, NY (2), US (fragment)).

Erect shrubs to 1.5(2) mm tall; stems slender, densely branched; branchlets glabrous to finely pilose. Pinnae 1–2-jugate; petioles 1.2–3.5 cm long; rachis 0.4- 1.7 cm long; rachillae 1.9–4.5 cm long. Leaflets (3–)4–6(7) pairs per pinna, oblong-obovate, 4–12(–14) × 2–6(–7) mm, oblique at base, rounded to acute at apex, usually mucronate, membranous, glabrous to finely pubescent; stipules narrowly triangular to lanceolate, sometimes slightly curved, to 5 mm long, glabrous to finely pubescent. Capitula axillary; peduncles 1.8–4.5(–6) cm long at anthesis. Calyx ca. 1.5–2 mm long, glabrous, the teeth triangular-lanceolate; corolla ca. 3 mm long; filaments white in basal half, pink in distal half. Pods to 7 × 0.6 cm at maturity, glabrous, rarely very sparsely and minutely pilose. Seeds rhomboid-ovoid, 5–8 × 3.5–5 mm, brown, the areola lighter; pleurogram irregular.

Distribution (Fig. 44). Endemic to rocky, arid slopes in a few localities of the northern portion of the Sonoran Desert in Pima County, Arizona (e.g., Baboquivari Mts., Santa Catalina Mts.) and northern Sonora at 1,100–1,400 m. This subspecies occupies the northernmost part of the distribution of the species.

Additional specimens examined. U.S.A. ARIZONA: Pima Co. W of Tucson, Robles Pass, *Bartram 409* (US); Coyote Mountains, *Goodding 24-57* (CAS); Moristo Canyon, Baboquivari Mountains, *Goodding 247-45* (NY); Baboquivari Canyon, Baboquivari Mountains, *Gould & Haskell 3253b* (CAS, F, GH, MO, NY); Catalina Mountains, Sabino Canyon, *Jones s.n.* (CAS, F, GH, MO, NY, UC, US); Toro Canyon, Baboquivari Mountains, *Kearney & Peebles 10397* (CAS, MICH); South Canyon, *Kearney & Peebles 14960* (CAS, GH, NY, US); 5 mi. below Federal Prison Camp Headquarters, Santa Catalina Mts., *Parker et al. 5861* (GH, NY, UC). MEXICO: SONORA: Sierra Jojoba, *Gentry & Webber 21985* (A, US); northwestern Mts., *Pringle 272* (US); 17.7 mi. SE of Magdalena, *Starr & Birgy 169* (MEXU); Cañón de Agua Amarga, *White 3609* (MICH?, GH).

Zapoteca formosa subsp. *schottii* is closely related to and was probably derived from subsp. *rosei*. The former has generally smaller stature, less numerous, smaller leaflets, and smaller pods (Table 14). These two taxa show geographically contiguous distributions (Fig. 44), and there is clinal variation in leaflet size, with subsp. *schottii* occupying the extreme position. Although the patterns of morphological variation are apparently continuous between the two taxa, subsp. *schottii* is relatively easily recognizable as a separate taxonomic unit with a somewhat arbitrary boundary. In the Baboquivari Mountains and in northern Sonora and Chihuahua, a number of difficultly placed intermediate specimens have been collected.

Zapoteca formosa subsp. *schottii* could be confused with subsp. *mollicula*, since they have leaflets of comparable size. However, subsp. *schottii* can be readily distinguished by the longer internodes and more elongate petioles and rachillae (Table 14). Further, although vestiture is highly variable in subsp. *mollicula*, most of its individuals have denser vestiture than do plants of subsp. *schottii*.

13. Zapoteca scutellifera (Benth.) H. Hern., comb. nov. *Calliandra scutellifera* Benth., J. Bot. (Hooker) 2: 139. 1840; Benth., London J. Bot. 3:98. 1844; Benth., Trans. Linn. Soc. London 30: 542. 1875; Benth. in C. Martius, Fl. Bras. 15(2): 112. 1876. *Feuilleea scutellifera* (Benth.) Kuntze, Revis. Gen. Pl. 189. 1891. TYPE: Brazil. Territory of Rondônia: Rio Madeira, Ribeirão, in siccis arenosis, May 1828, *Riedel 1334* (lectotype, K, here designated; isolectotypes, A, K, LE (3), NY—fragm., P, US).

Scandent shrubs; branchlets terete or subangulate, the surface costate under magnification, glabrous to finely puberulent, usually villous on the younger parts. Leaves glandular, the pinnae 2 3-

jugate; petioles terete with a conspicuous adaxial channel, 3.5 8 cm long, glabrous to sparsely villous, villous in the area of the channel; rachis 1 5 cm long; rachillae 5–7 cm long; glands close to the base of the petioles, at the points of insertion of the pinnae, and sometimes between the distal pairs of leaflets, scutelliform, the larger ones on the petioles to 2 mm diam., glabrous to puberulent abaxially; leaflets 6–11 pairs per pinna, oblong-obovate, falcate or subfalcate, oblique at the base, rounded to subacute at the apex, mucronate, the median ones 15–20 × 5–7 mm, the proximal ones smaller, membranous, glabrous, sometimes ciliate; primary and secondary leaflet veins conspicuous abaxially; stipules leafy, linear-triangular, to 4 mm long, glabrous to villous. Capitula axillary; peduncles solitary or fasciculate at distant nodes, glabrous to sparsely villous, ca. 6.5 cm long at anthesis. Flowers pentamerous; calyx cup-shaped, 1–1.5 mm long, finely ciliate, the teeth triangular, acute; corolla campanulate, 4–5 mm long, glabrous, the lobes lanceolate; filaments ca. 2.5 cm long, white in the basal half, pink at the distal half, the staminal tube ca. 1 mm long; ovary ca. 1 mm long, glabrous. Pods acute, rostrate, ca. 9 × 0.7 cm, thickly membranous, finely puberulent, especially at the margins.

Distribution (Fig. 44). Endemic to the Amazon Basin where it has been collected at scattered localities. In Brazil known from the states of Amazonas and Pará, and from the territory of Rondônia, also in Bolivia from the departments of El Beni and Santa Cruz. It usually occurs in open sandy sites.

Additional specimens examined. BRAZIL: AMAZONAS: Amazonum ad ostium flum. Solimões, *Spruce 1586* (BM, G, F, GH, K, NY, P). PARÁ: Mun. de Itaituba, estrada Santarém–Cuiabá, BR 163. Km 1011 com uma penetracão de 3 km dentro da mata, margem direita do Rio Jamaxim sul do Pará, 70°40′S, 55°15′W, *Amaral et al. 1231* (MO, NY). BOLIVIA. EL BENI: prov. Vaca Diez, Guayaramerin, 10°49′S, 65°22′W, *Krapovickas & Schinini 35129* (MO). SANTA CRUZ: prov. Sará, Buenavista, 450 m, *Steinbach 7047* (A, BM, F, G, GH, K, NY, MO).

This morphologically uniform species is closely related to *Z. formosa* but differs by having scutelliform extrafloral glands, scandent habit, and usually smaller, linear-triangular stipules. Moreover, it can be distinguished from *Z. formosa* subsp. *formosa* by its white/pink, rather than white, filaments. The scutelliform glands, which are constant throughout the known populations of *Z. scutellifera*, are an excellent diagnostic feature, as they occur only in this species of *Zapoteca*. They are fully developed at the earliest stages of leaf development, which probably reflects their defensive function.

14. Zapoteca tehuana H. Hern., sp. nov. TYPE: cultivated at MO, Jan. 1, 1986, *H. Hernández 950* (holotype, MEXU; isotype, MO). (Original source: Mexico. Oaxaca: Distr. Tehauntepec, El Manguito, SW El Limón, a 11.1 km SW de la entrada a Buenos Aires, 800 m, *R. Torres 1167* (MEXU)). Additional isotypes to be distributed. Figure 45.

Frutices, caulibus gracilibus. Pinnae (1)2(3)-jugae, foliolis 10–21-jugis in utraque pinna, oblongo-lanceolatis vel ovato-lanceolatis, membranaceis vel sub-chartaceis, ordinatione venarum evidenter brochidodroma; stipulae foliosae ca. 2 mm longae. Numerus chromosomatum somaticus $2n = 26$.

Shrubs ca. 1 1.8 m high; stems slender, ca. 5 10 mm diam. at base, the bark smooth except for small exfoliations; branchlets terete, fissured under magnification, glabrous. Pinnae (1–)2(3)-jugate. Petioles eglandular, terete, with a conspicuous adaxial channel, 0.5 3 cm long, glabrous, sometimes sparsely villous; rachis 0.7 1.8 cm long in 2-jugate pinnae, to 3.8 cm long in 3-jugate pinnae; rachillae to 7 cm long; leaflets 10–21 pairs per pinna, oblong-lanceolate to ovate-lanceolate, the distal pairs sometimes obovate, at base oblique, at apex acute to subacute, sometimes mucronulate, the median ones 9–15 × 2 4 mm, the proximal and distal pairs smaller, the anterior proximal leaflet reduced in size, rarely lacking, all membranous to thinly chartaceous, usually drying light green, usually glabrous throughout, occasionally pilose and ciliate, with conspicuous brochidodromous venation; stipules leafy, triangular, ca. 2 mm long, glabrous, rarely pilose. Capitula axillary; peduncles fasciculate at distant nodes, filiform, (2–)7–10 cm long at anthesis. Flowers pentamerous, or rarely tetramerous; calyx ca. 2–2.5 mm long, glabrous or pilose, usually ciliate, each tooth with a central vein, triangular, ca. 1 mm long; corolla campanulate, ca. 5–5.5 mm long, glabrous, the lobes ovate-lanceolate, acute; filaments (20)24 25 mm long, white in the basal half and pink in the distal half or white throughout, the staminal tube ca. 2 mm long; ovary ca. 1.5 mm long, very shortly (< 0.3 mm) stipitate. Pods linear, at apex subacute, rostellate, to 12 cm long when mature, thickly membranous, glabrous, reticulate-veined. Seeds widely ovoid to widely rhomboid, flattened, 5 6 × 4 mm, gray, the areola light gray; pleurogram irregular, demarcated by a dark line. Somatic chromosome number $2n = 26$.

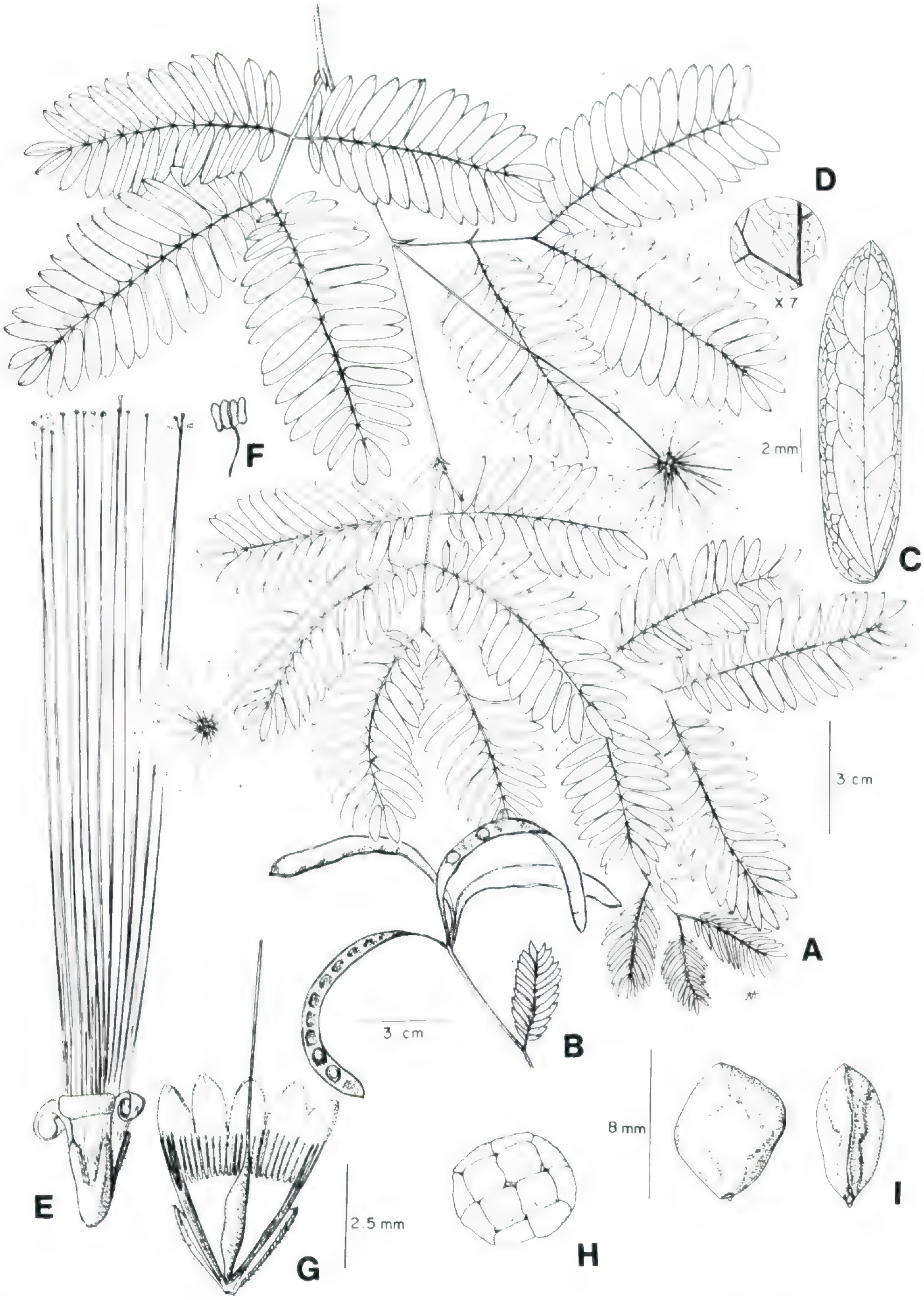


FIGURE 45. *Zapoteca tehuana.* A. Branchlet with inflorescences at anthesis. —B. Branchlet with dehisced pods. C. Leaflet. —D. Detail of venation in cleared leaflet. —E. Flower. —F. Anther. —G. Dissected flower. —H. Polyad. —I. Seeds. (Drawn from living plant, *H. Hernández 950* (MEXU, MO); pods from *R. Torres 4167* (MEXU).)

Distribution (Fig. 34). This species is endemic to a restricted area southwest of the Isthmus of Tehuantepec in Oaxaca, Mexico, where it grows in secondary vegetation derived from tropical deciduous forest mixed with probably relictual elements of temperate deciduous forests.

Additional specimens examined. MEXICO. OAXACA: Distr. Tehuantepec, cañada en el Arroyo de las Minas 2 km al SW de El Limón y 14 km al NW de Tehuantepec, *García & Torres 1679* (MEXU, MO); Distr. Tehuantepec, El Limón, arriba de El Chicozapote, SW de Tehuantepec, entrando por camino a Buenos Aires, *H. Hernández & Torres 303* (MEXU, MO); Distr. Tehuantepec,

El Manguito, al SW de El Limón el cual está a 11.1 km al SW de la entrada a Buenos Aires, *Torres 4167* (MEXU, MO); Distr. Tehuantepec, 15 km SW de Buenos Aires hacia Tenango, entrando por Hierba Santa, *Torres & Martínez 7375* (MEXU); subida al Cerro Guingola por ladera S, *L. Torres et al. 708* (MEXU).

Zapoteca tehuana is a narrowly endemic species probably not closely related to species of subg. *Zapoteca*, and further knowledge on this species could provide evidence for its placement in a separate subgenus. It differs from the remaining species of subg. *Zapoteca* primarily by having conspicuous brochidodromous leaflet venation and relatively thick leaflets. It might be confused with some of the species with oblong or ovate-lanceolate leaflets of comparable size (e.g., *Z. portoricensis* and *Z. lambertiana*) but differs by having leaves usually having fewer pairs of pinnae, smaller stipules, white or white/pink filaments, and shorter stature. The relationship between *Z. tehuana* and *Z. aculeata* are discussed under the latter.

III. Zapoteca subg. **Aculeata** H. Hern., subg. nov. TYPE: *Zapoteca aculeata* (Spruce ex Benth.) H. Hern.

Pinnae 1-, raro 2-jugae, folia sine nectariis, glabra vel fere glabra, foliolis 3–7-jugis in utraque pinna, mediocribus chartaceis vel coriaceis, ordinatione venarum conspicua; stipulae spinescentes. Capitula axillaria. Pollinia tumoribus lenticularibus praedita. Legumina coriacea glabra.

Leaves glabrous or nearly so, the pinnae 1-, rarely 2-jugate, the petiole without nectaries, leaflets 3–7 pairs per pinna, moderately large, chartaceous to coriaceous, with a very conspicuous venation; stipules spinescent. Capitula axillary. Polyads with lens-shaped thickenings. Pods coriaceous, glabrous.

This subgenus comprises a single species, *Z. aculeata*, characterized by medium size, chartaceous to coriaceous leaflets, and spinescent stipules.

15. Zapoteca aculeata (Spruce ex Benth.) H. Hern., comb. nov. *Calliandra aculeata* Spruce ex Benth., Trans. Linn. Soc. London 30: 541. 1875. TYPE: Ecuador, ad pedes m. Tungurahua, Sep. 1857, *Spruce 5054* (lectotype, K, here designated; isolectotypes, BM, F, G, (2), GH, K (2), LE, NY, P, S, (2)). The isolectotypes are dated as follows: BM, 1857–9; F, 1857–9; G, 1857–9, 1861; GH, 1857–9; K, Aug. 1857; LE, 1857–9; NY, 1857–9; P, 1857–9, 1861; S, 1857–9. Figure 46.

Trees to ca. 10 m tall; branchlets terete, costate, glabrous. Pinnae 1-, rarely 2-jugate; petioles eglandular, terete, with a conspicuous adaxial channel, 4–25 mm long, villous, rarely glabrate; rachis 3–5 cm long when pinnae 2-jugate; rachillae 1–12.5 cm long; leaflets (3–)4–6(–7) pairs per pinna, the proximal anterior one usually reduced or lacking, all ovate-lanceolate, at base oblique, at apex acute to acuminate, the distal ones 1.5–6.3 × 0.4–2.3 cm, the proximal ones smaller, all chartaceous to coriaceous, glabrous, the base sometimes villous; leaflet venation conspicuous; stipules spinescent, rigid, adpressed to the branchlets, sometimes becoming divaricate, linear-lanceolate, sometimes conical, beaked, 2–10 mm long, glabrous. Capitula axillary; peduncles usually fasciculate at distant nodes, rarely solitary, (2.5–)5–9 cm long at anthesis. Calyx shortly, sometimes irregularly dentate, ca. 2.5 mm long, glabrous, the teeth sometimes more than 5, shallowly triangular to deltate; corolla campanulate, 5–6 mm long, glabrous, the lobes ovate-lanceolate, acute; filaments ca. 2.5 cm long, red-purple, the staminal tube ca. 2 mm long; ovary ca. 1–1.5 mm long, glabrous. Pods about 10–12.5 × 0.9–1.1 cm, subacute to rounded at apex, sometimes rostellate, coriaceous, glabrous, the surface reticulate-veined.

Distribution (Fig. 47). *Zapoteca aculeata* has been collected from natural populations at the foot of the Mount Tungurahua in the Ecuadorian Andes (Province of Ambato) and from cultivated individuals at public gardens in Ambato, Baños, and Quito. Collections come from elevations of 1,900–2,850 m.

Additional specimens examined. ECUADOR. TUNGURAHUA: mountain side to S of Baños, *Penland & Summers 104* (F, GH, US). CULTIVATED. ECUADOR. PICHINCHA: Quito, *Acosta Solís 13599* (F). TUNGURAHUA: Ambato, *Acosta Solís 9488, 9523* (F); *Rose & Rose 22365* (GH, NY, US).

Zapoteca aculeata represents by itself a subgenus of *Zaboteca*. It is a poorly known, unmistakable species characterized by spinescent stipules, medium size, and coriaceous, ovate-lanceolate leaflets, which are usually larger than the essentially membranous leaflets of subg. *Zapoteca*. It is not obviously closely related to any other species of the genus; however, as shown in the chapter on morphology, an analysis of its leaflet architecture revealed outstanding similarities to that of *Z. tehuana*. *Zapoteca aculeata* is known from only a few collections made in a restricted area of the Ecuadorian Andes and from cultivated individuals

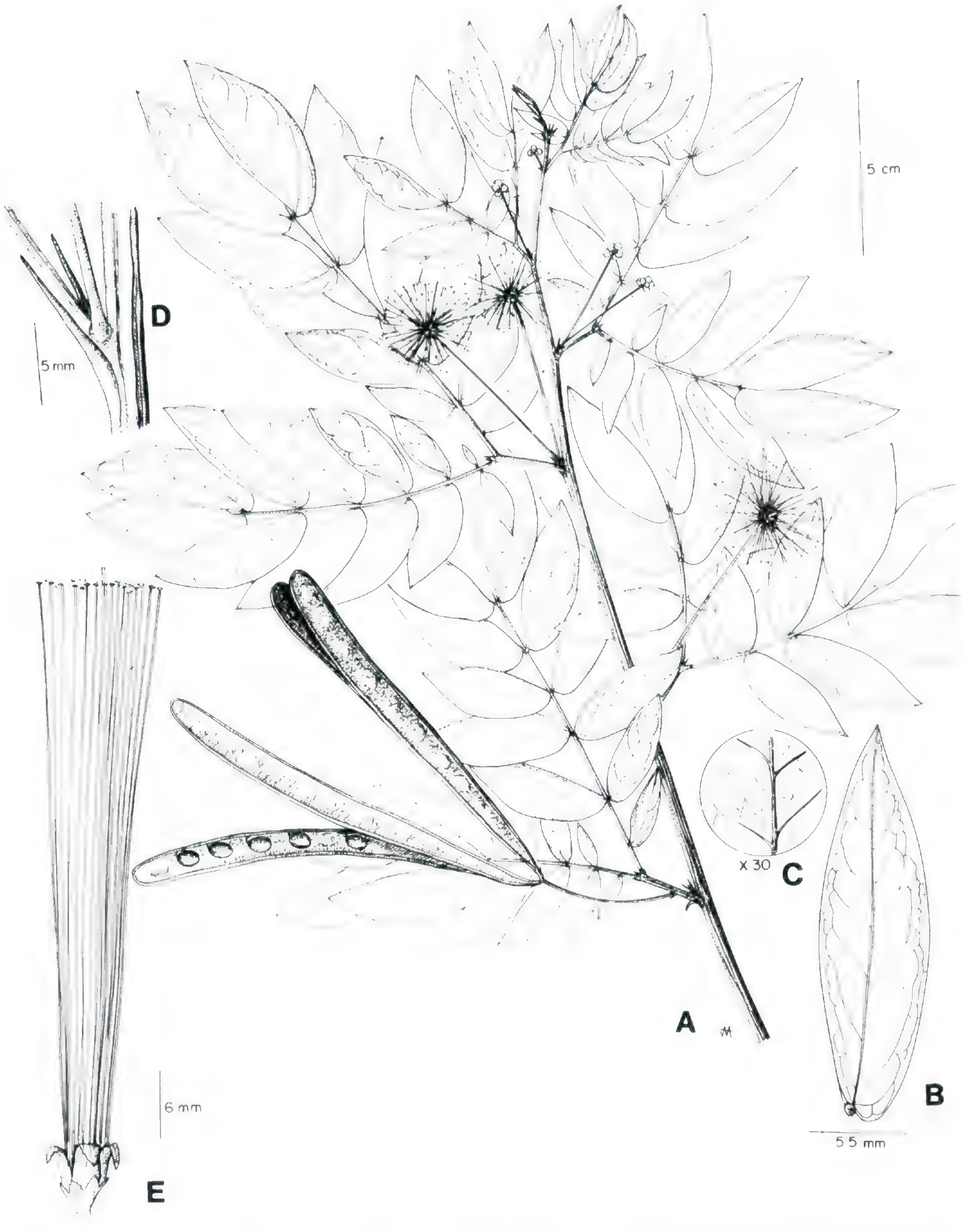


FIGURE 46. *Zapoteca aculeata.* – A. Branchlet with inflorescences at anthesis, and dehisced pods. — B. Leaflet. C. Detail of venation in cleared leaflet. D. Spinescent stipules. E. Flower. (From *Rose & Rose 22365* (US); leaflet from *Acosta 13599* (MO); pods from *Penland & Summers 104* (US).)

at Ambato, Baños, and Quito; it has not been collected for more than 40 years.

IV. Zapoteca subg. **Amazonica** H. Hern., subg. nov. TYPE: *Zapoteca amazonica* (Benth.) H. Hern.

Folia sine nectariis, glabra vel fere glabra, pinnis unijugis, foliolis 1 1½-jugis in utraque pinna, chartaceis vel coriaceis, ordinatione venarum forte conspicua; stipulae foliosae. Capitula in pseudopaniculis elongatis simplicibus vel compositis disposita. Pollinia tumoribus lenticularibus praedita. Legumina coriacea glabra. Semina sine pleurogramate.

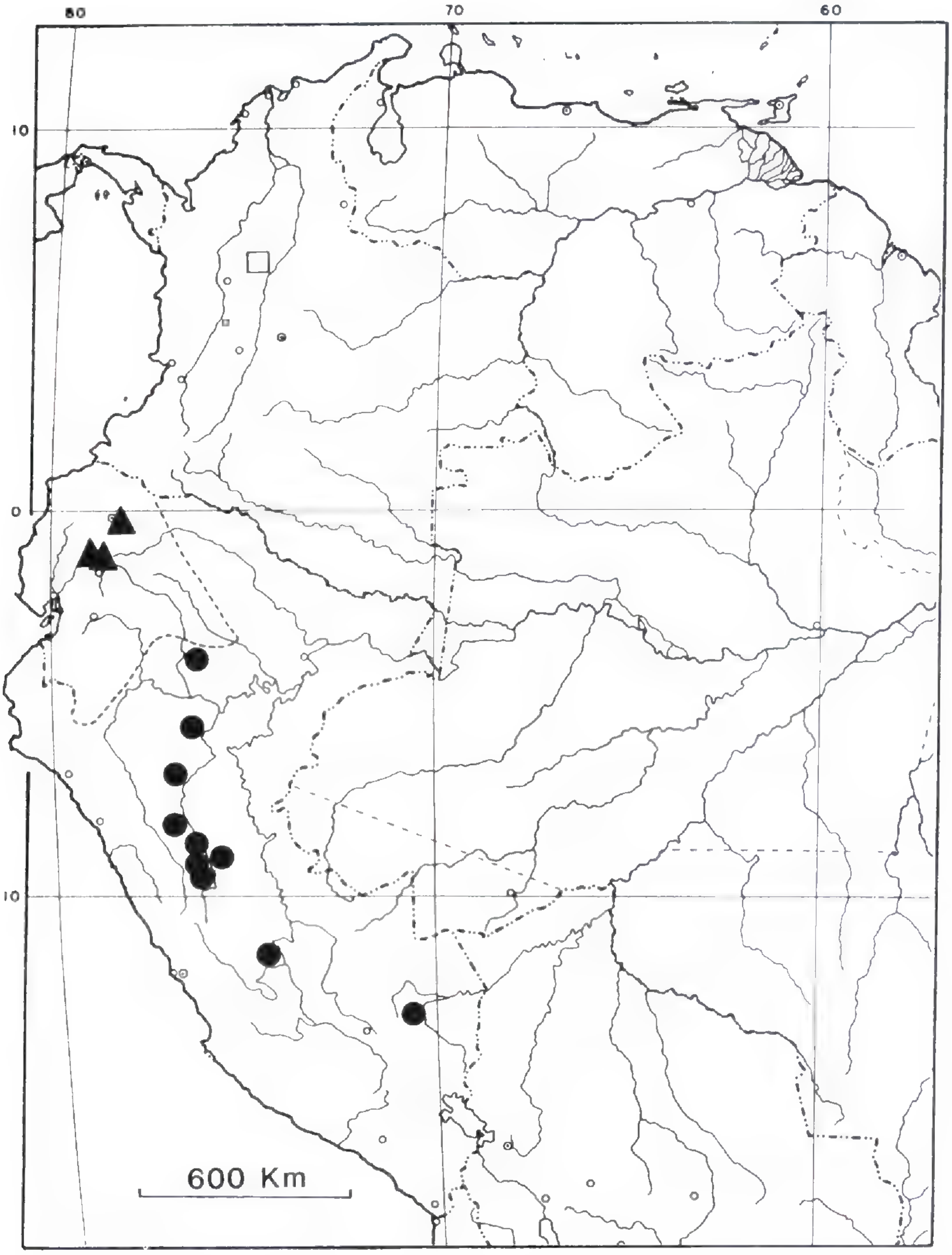


FIGURE 47. Distribution of *Zapoteca aculeata* (triangles), *Z. microcephala* (open square), and *Z. amazonica* (dots).

Leaves without nectaries, glabrous or nearly so, the pinnae 1-jugate; leaflets 1–1½ pairs per pinna, chartaceous to coriaceous; leaflet venation conspicuous; stipules leafy. Capitula in long, simple or compound pseudopanicles. Polyads with lens-shaped thickenings. Pods coriaceous, glabrous. Seeds without pleurogram.

This subgenus comprises two relatively specialized species, *Z. microcephala* and *Z. amazonica*, which are characterized by a set of characteristics that are highly advanced in *Zapoteca*: leaves reduced to one pair of pinnae, with 1–1½ pairs of large, chartaceous to coriaceous leaflets; capitula organized in long, simple or compound pseudopanicles.

16. Zapoteca microcephala (Britton & Killip) H. Hern., comb. nov. *Calliandra microcephala* Britton & Killip, Ann. New York Acad. Sci. 35: 134. 1936. TYPE: Colombia: 1760–1808, *Mutis 107* (holotype, US no. 1561096; isotypes, MA (4) not seen; photos at MEXU, MO).

Shrubs: branches terete, the surface smooth, glabrous. Pinnae 1-jugate; petioles eglandular, slender, with a pair of channels running longitudinally in the adaxial surface, (30–)40–70 mm long, glabrous abaxially, usually scabrous between the channels; rachillae 13–19 mm long; leaflets 1½ pairs per pinna, the proximal anterior leaflet lacking, all falcately lanceolate, at base strongly

TABLE 15. Comparison of *Zapoteca microcephala* with *Z. amazonica*.

	Z. microcephala	*Z. amazonica*
Distribution	Magdalena River Valley, Colombia	Amazonian Peru
Habit	erect shrubs	scandent shrubs
Pairs of leaflets per pinna	1½	1
Petiole length	(30)40 70 mm	20–42 mm
Leaflet pubescence	ciliate	glabrous
Pseudopanicles		
Form	simple	compound
Length	20–30 cm	up to 40 cm
Stipule length	1 2 mm	7–22 mm
Filament color	white	white/red-purple

oblique, sharply long-acuminate at apex, the distal leaflets 7.5–10.5 × 2.5–4.5 cm, the proximal one smaller, all chartaceous, glabrous, usually ciliate; leaflet venation conspicuous, with 2 primary and at least 1 secondary veins prominent; stipules leafy, triangular to narrowly triangular, ca. 1–2 mm long, glabrous. Capitula in terminal, elongate, simple pseudopanicles, ca. 20 30 cm long; peduncles fasciculate, rarely solitary, filiform, ca. 4.5 cm long at anthesis. Calyx ca. 2 mm long, the teeth triangular, < 1 mm long; corolla campanulate, ca. 3–4 mm long, the lobes ovate-lanceolate; stamens white, the staminal tube ca. 2 mm long. Pods to 15 × 1.1 cm when mature, at apex acute or retuse, coriaceous, glabrous, the valves reticulate-veined.

Distribution (Fig. 47). Endemic to a restricted area of the Median Valley of the Magdalena River in Colombia.

Additional specimens examined. COLOMBIA. SANTANDER: vicinity of Puerto Berrio, between Cararé and Magdalena rivers, *Haught 1711* (F, K, US), *Haught 1734* (US); without locality, *Mutis 3800* (MA, US).

This narrowly endemic species is clearly allied to *Z. amazonica*, from which it is geographically isolated (Fig. 47). *Zapoteca microcephala* can be readily distinguished from that species by 1½ pairs of smaller leaflets per pinna, simple (nonramified), shorter pseudopanicles, smaller stipules, and white filaments. Table 15 provides an account of the main comparative characters distinguishing these closely related species. *Zapoteca microcephala* is known from only four collections, and has not been collected since Haught (*1711*, *1734*) found it in 1935 in the floristically rich area of the Magdalena River Valley, Colombia.

17. Zapoteca amazonica (Benth.) H. Hern., comb. nov. *Calliandra amazonica* Benth., London J. Bot. 3: 94. 1844; Benth., London J. Bot. 5: 101. 1846; Benth., Trans. Linn. Soc. London 30: 538. 1875; J. F. Macbr., Fieldiana, Bot. 13: 67. 1943. *Inga bauhiniifolia* "*bauhiniaefolia*" Poeppig, Nov. Gen. Sp. Pl. 3: 80, t. 290. 1845. (The epithet is presumably also based on *Poeppig 2070* used by Bentham in the description of *Calliandra amazonica*.) TYPE of *Z. amazonica*: Peru. Loreto: in sylvis provinciae Maynas circum Yurimaguas, 1834, *Poeppig 2070* (lectotype, G, here designated; isolectotypes, F, G, LE pro parte, NY, P). The specimens at G and P are dated 1834, whereas those at F and NY are dated 1831. Figure 48.

Scandent shrubs 3–5(–8) m tall; stems slender, ca. 15 mm diam., the bark smooth; branchlets spreading, terete, glabrous. Pinnae 1-jugate; petioles eglandular, 20–42 mm long, usually glabrous; rachilla ± corrugate, with a conspicuous adaxial channel, 10–21 mm long (excluding the pulvini), usually glabrous, but occasionally sparsely villous in the extremes; leaflets 1 pair per pinna, falcately lanceolate-ovate, 7–22 × 2.8–9.2 cm, strongly oblique basally, acuminate to caudate, chartaceous to coriaceous, usually drying lighter green abaxially, ± lustrous adaxially, glabrous or rarely glabrate; leaflet venation conspicuous, with 2 primary and at least 1 secondary vein prominent; stipules leafy, ovate-lanceolate, acuminate to acute at apex, 7–22 × 3–8 mm, glabrous. Capitula arranged in terminal, elongate, compound pseudopanicles to 40 cm long or more, the peduncles fasciculate, rarely solitary, 0.8–7 cm long at anthesis. Calyx dentate, ca. 2.2 mm long, the teeth shallowly triangular or deltate, ca. 0.7 mm long, glabrous, rarely ciliate; corolla campanulate, ca. 4–5 mm long, glabrous, the lobes lanceolate; filaments white in the basal half and purple-red in the distal half, the tube ca. 2.5 mm long; ovary about 2 mm long, glabrous.

FIGURE 48. *Zapoteca amazonica*. A. Branchlet with compound pseudopanicle.—B. Primary stem showing smooth bark. C. Leaflet.—D. Detail of venation in a cleared leaflet. –E. Flower.—F. Pod.—G. Seed. (From *Plowman & Schunke 1115* (F) and *Schunke 1197* (G); stem from *Schunke 3371* (US); seed from *Schunke 1737* (US).)

Pods to 24 × 1 cm when mature, acute at apex, coriaceous, glabrous, the valves reticulate-veined. Seeds narrowly rhomboid to narrowly ellipsoid, flattened, ca. 14 × 5 mm, dark brown, without pleurogram.

Distribution (Fig. 47). This species has been collected primarily in shady sites of undisturbed tropical lowland forests of Amazonian Peru, from Río Alto Madre de Dios to Coronel Portillo (Río Pastaza) in the Departamento of Loreto, especially

along Río Huallaga. Collections come from 350–900 m.

Additional specimens examined. PERU. JUNÍN: Sanibeni ad Satipo, *Woytkowski 5943* (F, GH, LL, MO, NY, US). HUÁNUCO: above Río Huallaga at Tingo María, *Croat 21102* (MO); Tingo María, km 138, trocha lote del Aguila, *Ferreyra 932* (US); Pachitea, Puerto Inca, just N of town (9°18′S, 74°58′W), *Foster 8832* (MO); Pachitea, Codo de Pozuzo (9°40′S, 75°28′W), *Foster 9209* (MO); along Río Huallaga, near riachuela Chontalagua, *Mexia 8295* (BM, F, G, GH, MO, NY, S, UC, US); Leoncio Prado, Rupa Rupa, Tingo María (9°18′S, 75°59′W), *Plowman et al. 11249* (F, US); Tingo María, *Stork & Horton 9477* (F, G, UC). LORETO: Coronel Portillo, 4–5 horas arriba del caserío Abujao, sobre al Río Abujao, *Díaz 861* (MO, NY). MADRE DE DIOS: Pantiacolla, serranía across Río Alto Madre de Dios from Shintuya, *Gentry et al. 27293* (MO). SAN MARTÍN: Mariscal Cáceres, Tocache Nuevo, Cerro Sinsin, 15 km W Tocache Nuevo along road to Puerto Pizana (8°09′S, 76°34′W), *Plowman & Schunke 11445* (F); Mariscal Cáceres, Depto. Tocache, 2 km de Tocache Nuevo, Fundo la Campiña, *Schunke 3371* (F, G, NY, US); Mariscal Cáceres, Depto. Tocache Nuevo, Canato, margen izquierdo Río Huallaga, *Schunke 4497* (F, G, NY, US); Mariscal Cáceres, Depto. Tocache Nuevo, Malpaso de Balsa, Probana, 1 km abajo desembocadura Río Mishollo, *Schunke 4737* (F, GH, MO, US); Mariscal Cáceres, Depto. Tocache Nuevo, Quebrada de Santiago, E Puerto Pizana, *Schunke 6483* (MO, NY); Mariscal Cáceres, Puerto Pizana (margen derecho del Río Huallaga), *Schunke 6913* (MO); Mariscal Cáceres, Depto. Tocache Nuevo, Quebrada de Huaquisha (margen Río Huallaga), *Schunke 8053* (MO, NY); Tarapoto, *Spruce 4494* (BM, BR, F, G, GH, K, P, NY); Alto Río Huallaga, Tarapoto, *Williams 6548* (F, US).

Zapoteca amazonica and *Z. microcephala* represent a distinct evolutionary line within the genus; these closely related species probably differentiated from a common ancestor after becoming separated from the rest of the genus. *Zapoteca amazonica*, which is remarkably uniform morphologically, can be readily distinguished from *Z. microcephala* by its scandent habit, one pair of larger leaflets per pinna, larger stipules, elongate pseudopanicles, and white/purple-red filaments. The differences between the two species were discussed further under *Z. microcephala* (see also Table 15).

Zapoteca amazonica probably is the most specialized species in the genus, presenting a combination of derived characters: scandent habit; extreme reduction of leaflet number concomitant with an increase in size; relatively complex leaflet venation patterns; capitula organized in complex, terminal, compound pseudopanicles. The specialized nature of this species was discussed in the section on morphology.

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POLLEN MORPHOLOGY OF THE MELANTHIACEAE AND ITS SYSTEMATIC IMPLICATIONS[1]

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ABSTRACT

Pollen grains of several selected genera of Melanthiaceae were observed with scanning and transmission electron microscopes. *Helonias* and *Ypsilandra* have the distinctive feature of the exine composed of an amorphous layer and spinules, which agrees well with *Heloniopsis*. *Chionographis* and *Chamaelirium* both have distinctive four-porate pollen grains with clavate exines. *Japonolirion*, endemic to Japan, has monosulcate grains with gemmate exines, clearly different from *Tofieldia*, which is characterized by disulcate grains with reticulate exines. *Aletris* shows a wide range of infrageneric variation in exine sculpture, perforate-foveolate, reticulate, and gemmate. *Xerophyllum* and *Narthecium* have monosulcate grains with reticulate exines; the two genera are distinguished by the size of the muri. Pollen of *Metanarthecium* has distinctive reticulate exine sculpture characterized by verrucate protrusions within lumina. The palynological data indicate that the Melanthiaceae consist of at least three heterogenous groups, among which *Helonias*, *Heloniopsis*, and *Ypsilandra* represent one group, and *Chamaelirium* and *Chionographis* another distinct group.

The Melanthiaceae comprise ca. 24 genera distributed in North America, Japan, and China (Dahlgren & Clifford, 1982). These genera are *Aletris*, *Amianthium*, *Chamaelirium*, *Chionographis*, *Helonias*, *Heloniopsis*, *Metanarthecium*, *Narthecium*, *Nietneria*, *Oceanoros*, *Petrosavia*, *Pleea*, *Protolirion*, *Schoenocaulon* (= *Sabadilla*), *Stenanthella*, *Stenanthium*, *Tofieldia*, *Toxicoscordion*, *Tracyanthus*, *Veratrum*, *Ypsilandra*, *Xerophyllum*, and *Zigadenus* (Dahlgren & Clifford, 1982). Krause (1930) recognized the tribe Tofieldieae (Liliaceae Melanthioideae), in which *Tofieldia* (Temperate-Arctic Northern Hemisphere), *Pleea* (eastern North America), *Narthecium* (Northern Hemisphere), and *Nietneria* (Guinea) were included. However, in his treatment, *Aletris* was placed in the different subfamily, Alectroideae. Hutchinson (1934, 1959) grouped these genera into two tribes, Heloniadeae and Narthecieae. The Heloniadeae, characterized by the absence of bracts, consist of *Helonias*, *Chamaelirium*, *Ypsilandra*, and *Chionographis*, and the tribe Narthecieae, characterized by the presence of bracts, comprise *Pleea*, *Tofieldia*, *Hewardia*, *Xerophyllum*, *Heloniopsis*, *Clara*, *Narthecium*, *Metanarthecium*, *Aletris*, and *Nietneria*. Hutchinson (1934, 1959) regarded the Heloniadeae as the most primitive tribe in the Liliaceae, and that the tribe is closely related to the Narthecieae. Dahlgren et al. (1985) placed these genera in the family Melanthiaceae and recognized six tribes, Petrosavieae, Melanthieae, Narthecieae, Tofieldieae, Chionographideae, and Xerophylleae. They included *Lophiola* in the tribe Narthecieae.

Although many brief notes on pollen morphology of these genera using light microscopy have been given by Beug (1961), Erdtman (1952), Faegri et al. (1964), Huang (1970, 1972), Huynh (1976), Ikuse (1956), Kuprianova (1948), Radurescu (1973), Schultze (1978), Shimakura (1973), Thanikaimoni (1970), Ting-Su (1949), Utech (1979), Wunderlich (1936), and Van der Hammen (1956), a comprehensive pollen morphological study has not been made for these genera with electron microscopy.

Although Schultze (1978) classified *Chionographis*, *Chamaelirium*, *Heloniopsis*, *Ypsilandra*, and *Helonias* in the tribe Heloniadeae, the different pollen types and exine structure suggest that the treatment is inappropriate. Recently, Tak-

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TABLE 1. List of voucher specimens and pollen sizes.

Species	Collection Data	Pollen Sizes (μm)
Helonias bullata	U.S.A. Maryland: Anne Arundel Co., 27 Apr. 1941, *M. B. Waste* (NA)	28.5 ± 1.6 × 19.3 ± 2.2
H. bullata	U.S.A. New Jersey: Burlington Co., 3 May 1928, *O. M. & G. G. Freeman, s.n.* (NA)	27.7 ± 1.3 × 20.0 ± 2.0
Ypsilandra yunnanensis	China. Yunnan: 19 June 1930, *T. T. Yu 19036* (KUN)	30.1 ± 1.8 × 21.0 ± 2.3
Chamaelirium luteum	U.S.A. South Carolina: Lancaster Co., 1 May 1980, *H. Koyama et al. 6257* (NA)	16.2 ± 1.2 × 16.0 ± 1.0
C. luteum	U.S.A. West Virginia: Mineral Co., 19 June 1938, *O. M. Freeman s.n.* (NA)	19.0 ± 1.5 × 18.1 ± 1.3
C. luteum	U.S.A. Florida: Duval Co., Apr., *A. H. Curtiss 2903* (NA)	16.2 ± 1.7 × 16.0 ± 1.1
C. luteum	U.S.A. Pennsylvania: Vernango Co., 19 June 1930, *O. M. Freeman s.n.* (NA)	18.4 ± 1.7 × 18.1 ± 1.3
Chionographis japonica	Japan. Oomi: 13 May 1954, *M. Togashi s.n.* (KYO)	14.0 ± 1.1 × 13.3 ± 1.1
C. japonica	Japan. Hyougo: Awaji-shima, 1 June 1978, *N. Fukuoka & N. Kurosawa 1586* (KYO)	13.2 ± 0.9 × 13.3 ± 1.0
C. koidzumiana	Japan. Kii: Mt. Nachi, 11 Nov. 1974, *G. Murata 5715* (KYO)	16.2 ± 1.2 × 16.2 ± 1.8
C. koidzumiana	Japan. Yakushima: May 1927, *S. Sugimoto 7462* (KYO)	15.8 ± 1.4 × 14.4 ± 1.3
Tofieldia calyculata	Poland: July 1952, *Wisniewska et al. s.n.* (NA)	19.1 ± 1.4 × 14.2 ± 0.9
T. calyculata	Italy. Pralongia: 18 July 1879, *Larsen 35105* (NA)	17.3 ± 2.2 × 13.4 ± 0.9
T. coccinea	Japan. Shikotan Ins.: Matakotan, 19 July 1931, *J. Ohwi s.n.* (KYO)	18.2 ± 1.0 × 14.5 ± 1.4
T. coccinea	Japan. Hokkaido: Kushiro, 13 June 1982, *K. Takita 999* (KYO)	17.1 ± 1.3 × 13.7 ± 1.1
T. coccinea	Japan. Kyusyu: Hiuga, 28 July T 2, *M. Ogata s.n.* (KYO)	16.7 ± 0.9 × 13.5 ± 0.9
T. coccinea	Japan. Hoki: Mt. Daisen, 15 Sep. 1914, *N. Kinashi s.n.* (KYO)	16.8 ± 0.9 × 13.0 ± 0.5
T. coccinea	U.S.A. Alaska: 22 July 1948, *J. A. Calder s.n.* (KYO)	19.3 ± 1.9 × 14.8 ± 1.5
T. glabra	U.S.A. Washington: Garfield Co., 18 Oct. 1930, *O. M. Freeman s.n.* (NA)	18.3 ± 0.9 × 14.2 ± 0.7
T. glutinosa	U.S.A. Minnesota: Polk Co., 12 July 1939, *O. A. Stevens 432* (NA)	20.7 ± 1.3 × 15.2 ± 1.3
T. glutinosa	Canada. British Columbia: 26 June 1971, *J. Pojar 110* (KYO)	23.9 ± 1.6 × 16.8 ± 1.2
T. intermedia	U.S.A. Washington: Yakima Co., 15 July 1940, *J. W. Thompson 15079* (NA)	23.6 ± 1.4 × 18.8 ± 1.4
T. japonica	Japan. Akita Pref.: 1 Aug. 1978, *Fujita 807* (KYO)	25.2 ± 2.1 × 17.4 ± 1.1
T. japonica	Japan. Niigata: 5 Aug. 1978, *Terao 972* (KYO)	22.9 ± 1.6 × 18.9 ± 1.1
T. japonica	Japan. Shiga Pref.: 29 Sep. 1974, *G. Murata 22326* (KYO)	23.2 ± 1.4 × 12.1 ± 1.0
T. nuda	Japan. Bizen: Kurokami-yama, 6 July 1919, *Z. Tashiro s.n.* (KYO)	15.0 ± 0.8 × 10.9 ± 0.8
T. nuda	Japan. Shiga Pref.: 30 May 1962, *Fukuoka 4754* (KYO)	17.0 ± 1.4 × 12.1 ± 1.0
T. occidentalis	U.S.A. California: Del Norte Co., 10 Aug. 1937, *C. B. Wold s.n.* (NA)	21.9 ± 1.7 × 16.2 ± 0.9
T. occidentalis	U.S.A. California: Trinity Co., 7 July 1949, *E. K. Balls 13885* (NA)	20.6 ± 1.2 × 16.0 ± 0.9

TABLE 1. Continued.

Species	Collection Data	Pollen Sizes (μm)
T. okuboi	Japan. Aomori Pref.: 13 July 1962, *H. Ohashi 68772* (KYO)	19.1 ± 0.9 × 15.0 ± 1.1
T. palustris	Canada: Mckenzie, 16 July 1940, *J. J. Lynch & C. E. Gillham 1597* (NA)	17.7 ± 1.4 × 14.7 ± 1.1
T. palustris	Sweden: Torne Lapmark, 21 July 1935, *C. G. Alm s.n.* (KYO)	18.1 ± 1.6 × 13.7 ± 1.0
T. palustris	U.S.A. Alaska: Carlisle Island, 1 July 1940, *I. V. Gabrielson s.n.* (NA)	17.3 ± 0.8 × 14.4 ± 1.2
T. pusilla	Greenland. Blomsterdalen, 13 July 1966, *F. J. A. Daniels et al. 163* (KYO)	18.1 ± 0.8 × 15.5 ± 0.7
T. pusilla	Sweden: Jämtland, 18 June 1963, *Folkeson s.n.* (KYO)	18.1 ± 1.2 × 15.2 ± 1.2
T. racemosa	U.S.A. Louisiana: 15 July 1978, *S. Parwin & E. Sunmdel 592* (KYO)	21.4 ± 2.0 × 16.3 ± 2.5
T. racemosa	U.S.A. Mississippi: Hancock Co., 25 June 1938, *D. S. & H. B. Correll 9107* (NA)	20.2 ± 1.3 × 15.3 ± 1.8
T. racemosa	U.S.A. North Carolina: Onslow Co., 30 June 1950, *W. B. Fox & S. G. Boyce 3721* (NA)	19.3 ± 0.9 × 15.1 ± 1.3
Pleea tenuifolia	U.S.A. North Carolina: Aug. 1884, *G. M. Carthy 4* (NA)	20.8 ± 1.8 × 15.8 ± 1.3
P. tenuifolia	U.S.A. North Carolina: Onslow Co., 26 Aug. 1949, *W. B. Fox 3228* (NA)	20.0 ± 1.5 × 15.8 ± 1.3
P. tenuifolia	U.S.A. Florida: Walton Co., *A. H. Curtiss 2904* (NA)	22.7 ± 1.3 × 17.9 ± 1.2
Japonolirion ozense	Japan, Tochigi Pref.: *M. Shibutu & M. Takahashi s.n.* (TUS)	19.2 ± 2.0 × 15.6 ± 1.8
Xerophyllum asphodeloides	U.S.A. New Jersey: Newfield Aug. 1877, *C. Martindale s.n.* (NA)	22.6 ± 1.5 × 14.9 ± 1.4
X. asphodeloides	U.S.A. New Jersey: Burlington Co., 23 May 1963, *C. F. Parker s.n.* (NA)	23.9 ± 1.1 × 16.4 ± 1.6
X. asphodeloides	U.S.A. North Carolina: 23 May 1963, *Freeman, s.n.* (NA)	24.4 ± 1.5 × 17.4 ± 1.2
X. asphodeloides	U.S.A. New Jersey: Pomona, 12 June 1892, *F. L. Lewton s.n.* (NA)	23.8 ± 2.8 × 17.2 ± 1.9
X. asphodeloides	U.S.A. North Carolina: Burke Co., 2 July 1891, *J. K. Small & A. A. Heller s.n.* (NA)	24.4 ± 1.1 × 17.1 ± 1.5
X. tenax	U.S.A. Oregon: 22 Aug. 1975, *W. Hesse 3633* (NA)	29.0 ± 3.2 × 19.9 ± 1.3
X. tenax	U.S.A. Oregon: Clackamas Co., 20 June 1939, *C. L. Hitchcock & J. S. Martin 4786* (NA)	24.1 ± 1.4 × 17.8 ± 1.0
X. tenax	U.S.A. Idaho: Idaho Co., 5 Aug. 1950, *Q. Jones 355* (NA)	25.4 ± 1.5 × 18.3 ± 2.1
Narthecium americanum	U.S.A. New Jersey: Bridgeton City, 31 Aug. 1879, *Unknown collector s.n.* (NA)	19.9 ± 1.4 × 11.9 ± 1.2
N. americanum	U.S.A. New Jersey: Bassto, July 1877, *I. C. Martindale s.n.* (NA)	17.7 ± 1.3 × 12.1 ± 1.5
N. americanum	U.S.A. New Jersey: Burlington Co., 18 June 1933, *F. J. Hermann 4460* (NA)	17.8 ± 1.5 × 12.2 ± 1.2
N. americanum	U.S.A. New Jersey: 23 June 1932, *Hermann 3315* (NA)	19.1 ± 1.3 × 13.5 ± 1.2
N. californicum	U.S.A. California: Mount Dyer, 3 Aug. 1880, *R. M. Austin s.n.* (NA)	20.6 ± 1.5 × 13.5 ± 1.2
N. californicum	U.S.A. California: Trinity Co., 7 July 1948, *E. K. Balls 13880* (NA)	18.0 ± 2.4 × 12.4 ± 1.5
N. californicum	U.S.A. Oregon: 12 June 1946, *P. L. Ricker 6180* (NA)	18.5 ± 1.3 × 12.2 ± 1.0

TABLE 1. Continued.

Species	Collection Data	Pollen Sizes (μm)
N. californicum	U.S.A. California: Del Norte Co., 16 June 1977, *L. Debuhr 2625* (KYO)	18.3 ± 1.4 × 13.2 ± 1.0
N. ossifragum	Sweden: Småland, 16 July 1957, *J. Christoffersson s.n.* (KYO)	19.8 ± 1.2 × 13.4 ± 1.4
V. ossifragum	Denmark. Raabjierg Mile, 31 July 1938, *Schjottz s.n.* (KYO)	19.0 ± 1.6 × 13.0 ± 1.1
Aletris aurea	U.S.A. Florida: Duval Co., May 1897, *A. H. Curtiss s.n.* (NA)	25.9 ± 1.6 × 17.1 ± 1.5
A. aurea	U.S.A. Texas: Tyler Co., 4 June 1968, *D. S. Correll 35835* (NA)	26.0 ± 1.7 × 16.8 ± 1.8
A. aurea	U.S.A. North Carolina: New Hanover Co., 19 May 1973, *D. E. Boufford 8877* (KYO)	23.9 ± 1.2 × 17.3 ± 1.7
A. bracteata	U.S.A. Florida: Monroe Co., 25 Mar. 1980, *W. C. Brumbach 9541* (NA)	24.8 ± 1.9 × 18.3 ± 1.6
A. bracteata	U.S.A. Florida: 4 11 May 1904, *J. K. Small & P. Wilson s.n.* (NA)	25.2 ± 1.1 × 17.3 ± 1.4
A. bracteata	U.S.A. Florida: Dade Co., 10 Feb. 1948, *O. M. Freeman s.n.* (NA)	24.3 ± 1.7 × 17.3 ± 2.0
A. farinosa	U.S.A. Florida: May–June 1875, *C. Reynolds s.n.* (NA)	26.9 ± 1.6 × 16.3 ± 1.9
A. farinosa	U.S.A. Virginia: Norfolk, June 1840, *F. Rugel s.n.* (NA)	23.4 ± 1.8 × 16.9 ± 2.2
A. farinosa	U.S.A. New Jersey: Burlington Co., 1 July 1932, *F. J. Hermann 3379* (NA)	25.7 ± 2.1 × 17.8 ± 2.0
A. farinosa	U.S.A. North Carolina: Transylvania Co., 13 July 1950, *W. B. Fox 3986* (NA)	21.8 ± 1.5 × 15.8 ± 1.4
A. foliata	Japan. Kai: 16 July 1962, *G. Murata 27002* (KYO)	27.5 ± 1.6 × 20.6 ± 1.8
A. foliata	Japan. Niigate Pref.: Aug. 1960, *Koyama 0581* (KYO)	27.6 ± 2.7 × 18.2 ± 2.1
A. lanuginosa	China. Szechuan: Sep. 1938, *Maclaren 23* (KYO)	22.8 ± 1.5 × 15.1 ± 1.4
A. lutea	U.S.A. Pennsylvania: Longwood Garden, 2 May 1962, *J. E. Peele 827* (NA)	24.0 ± 1.7 × 15.4 ± 1.8
A. lutea	U.S.A. Alabama: De Kalb Co., 9 June 1936, *C. Q. Erlauson 783* (NA)	22.9 ± 1.9 × 16.8 ± 1.7
A. lutea	U.S.A. Florida: Lake Co., 26 May 1966, *C. R. Gunn 3399* (NA)	21.8 ± 2.1 × 16.0 ± 1.8
A. lutea	U.S.A. Florida: Gulf Co., 4 May 1979, *D. E. Boufford 20670* (KYO)	23.8 ± 1.4 × 16.8 ± 1.0
A. obovata	U.S.A. Florida: Bradford Co., 17 May 1940, *R. F. Martin 1441* (NA)	22.7 ± 1.8 × 16.4 ± 1.7
A. obovata	U.S.A. Georgia: Folkston, 18 May 1930, *F. S. Blanton 6604* (NA)	25.5 ± 2.0 × 18.7 ± 1.7
A. obovata	U.S.A. Georgia: Liberty Co., 25 May 1943, *W. C. Jrimson s.n.* (KYO)	22.7 ± 1.6 × 14.6 ± 1.0
A. pauciflora	Nepal: between Mouma and Tip top 1a, alt. 4,400 m, 23 July 1962, *K. Nishida 681* (KYO)	32.4 ± 3.8 × 20.5 ± 3.2
A. sitimensis	Bhutan: Sela 1a, alt. 3,200 m, 27 July 1958, *S. Vakano 135* (KYO)	26.0 ± 1.7 × 14.0 ± 2.4
A. spicata	Japan. Kochi Pref.: May 1889, *T. Makino s.n.* (KYO)	24.2 ± 1.7 × 18.5 ± 2.0
A. spicata	Japan. Kagoshima Pref.: 1 May 1965, *F. Konta 5015* (KYO)	22.4 ± 2.0 × 17.2 ± 2.5

TABLE 1. Continued.

Species	Collection Data	Pollen Sizes (μm)
Metanarthecium luteo-viride	Japan. Nagano Pref.: 21 July 1973, *H. Takahashi 1617* (KYO)	18.0 ± 1.2 × 13.1 ± 1.4
M. luteo-viride	Japan. Bitchu: 31 July 1962, *G. Murata 27319* (KYO)	17.2 ± 1.3 × 11.6 ± 1.5
M. luteo-viride	Japan. Ehime Pref.: 27 July 1983, *G. Murata 44755* (KYO)	18.3 ± 1.1 × 13.5 ± 1.5
Lophiola americana	U.S.A. Alabama: 20 May 1979, *H. H. Iltis s.n.* (WIS)	18.5 ± 1.6 × 12.7 ± 1.8
Amianthium sp.	U.S.A. North Carolina: Macon Co., 28 June 1982. *F. H. Utech & M. Ohara 82-270* (CM)	23.2 ± 1.4 × 15.4 ± 1.2
Stenanthium occidentale	U.S.A. Washington: Whatcom Co., 11 July 1978, *F. H. Utech 78-287* (CM)	24.5 ± 1.8 × 16.8 ± 1.7
Schoenocaulon pringlei	Mexico. Federal District: Aug. 1960, *Unknown collector s.n.* (WIS)	25.2 ± 1.6 × 17.2 ± 1.4

ahashi (1982a) showed that *Heloniopsis orientalis* Tanaka is characterized by a peculiar exine structure without columellae. He also pointed out that palynological evidence on the related genera would be useful to reveal their systematic relationships.

In the present study, pollen grains of 92 samples of 40 species of 15 genera in the Melanthiaceae were studied in detail with transmission and scanning electron microscopes. The probable systematic relationships of these genera are proposed based on the palynological evidence thus obtained.

MATERIALS AND METHODS

Pollen grains were taken from specimens in the herbaria of Carnegie Museum of Natural History (CM), U.S. National Arboretum (NA), Kunming Institute of Botany (KUN), Kyoto University (KYO), and Tohoku University (TUS). Voucher specimens are listed in Table 1. Pollen grains from each specimen were observed using scanning electron and transmission electron microscopy. Preparation methods followed Takahashi (1982b). An image analyzing system IBAS-1 was used for measurements and calculations of pollen grains.

OBSERVATIONS

Helonias and *Ypsilandra* (Figs. 1–4)

Pollen grains monosulcate, 27.7 ± 1.3–28.5 ± 1.6 μm in major axis of ellipse and 19.3 ± 2.2–20.0 ± 2.0 μm in polar axis of *Helonias bullata*, and 30.0 ± 1.8 in major axis of ellipse and 21.0 ± 2.3 in polar axis of *Ypsilandra yunnanensis*, provided with a sulcus. Except for sulcus, exine ornamentation finely granulated with spinules (Figs. 2, 3), these ovate, 1 μm high, with acute tips. Exine (spinules excluded) 0.4–0.6 μm thick, consisting of an amorphous layer and spinules. Outer surface of exine granular and the inner layer lamellated (Fig. 4).

There is no difference in pollen type and exine structure between *Helonias* and *Ypsilandra*.

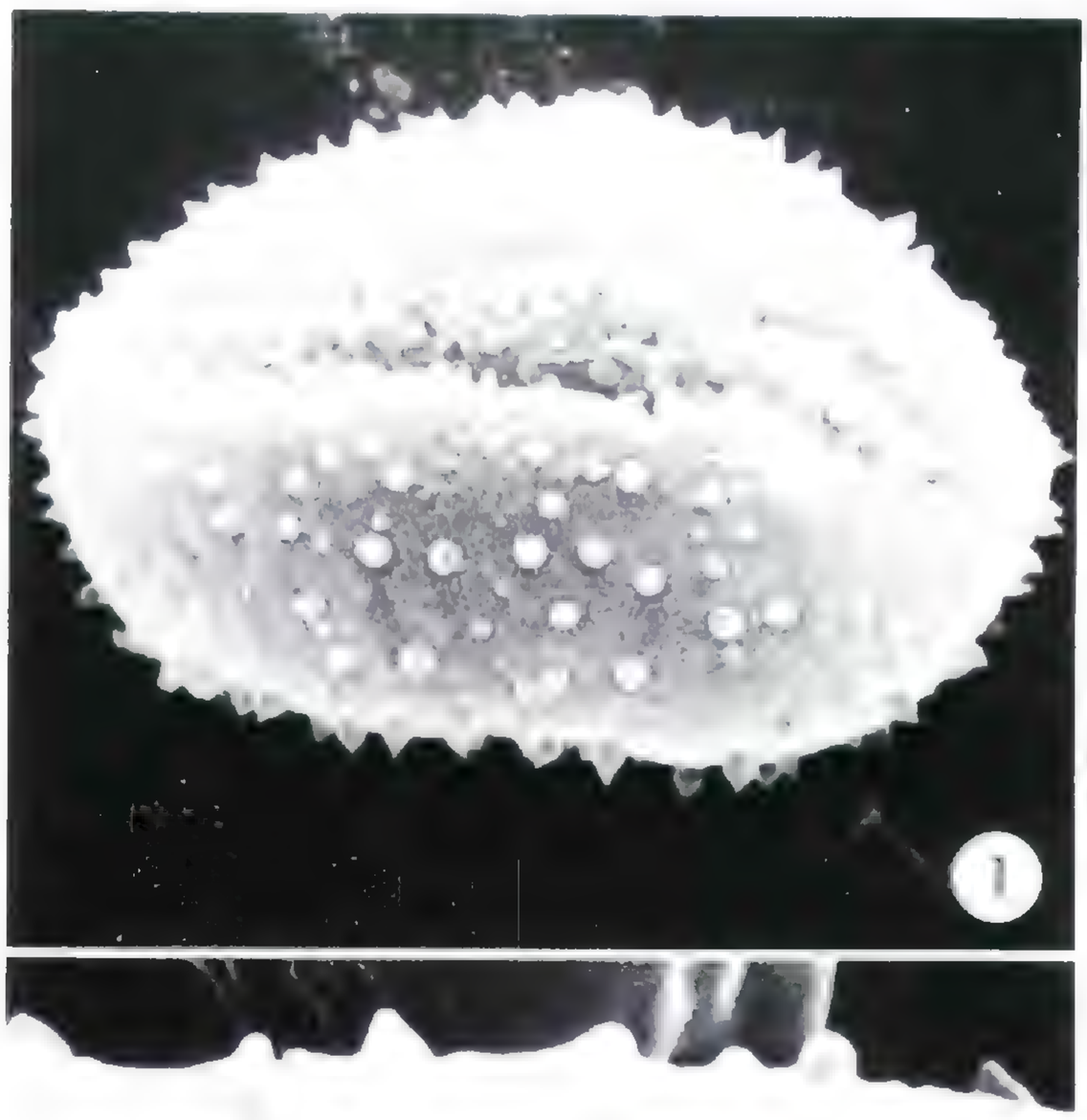
Chamaelirium and *Chionographis* (Figs. 5 9)

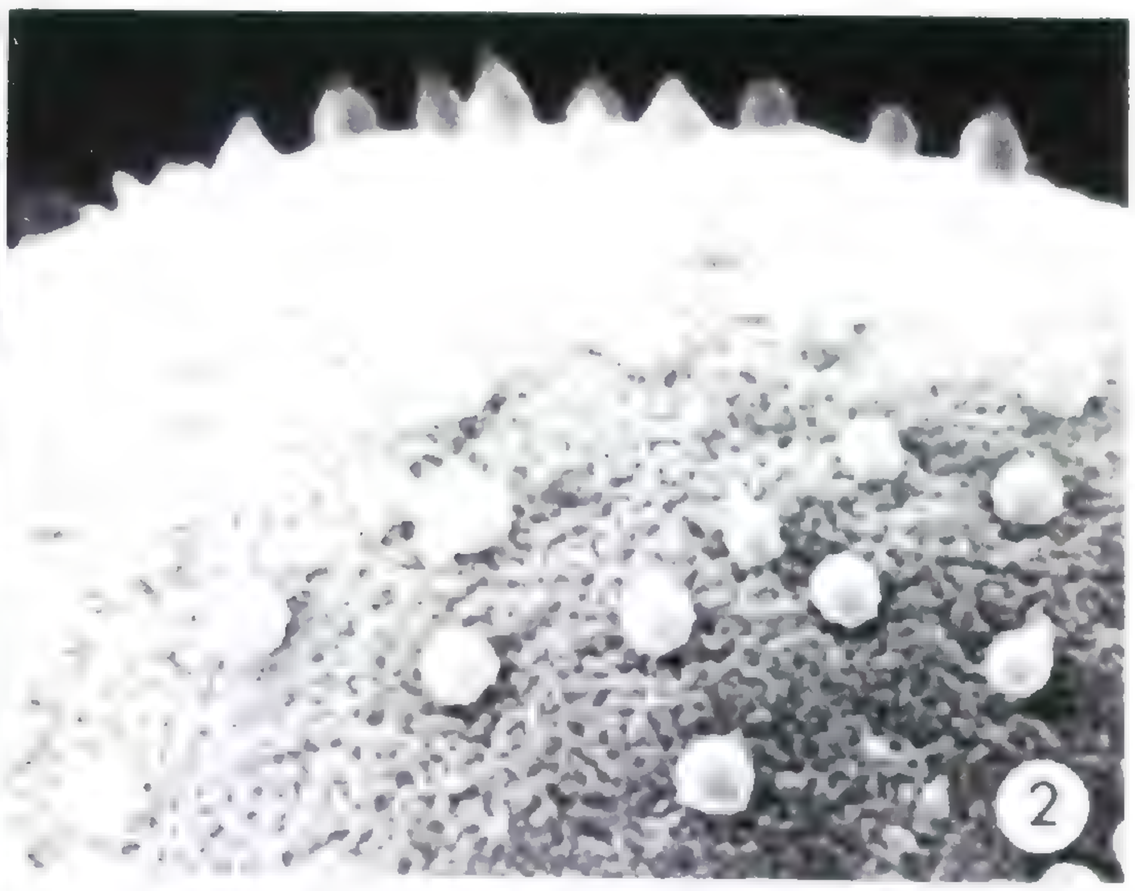
Pollen grains spherical, 4-porate (Figs. 5, 8), 16.2 ± 1.2–19.0 ± 1.5 μm in major axis of ellipse and 16.0 ± 1.0 18.1 ± 1.3 μm in polar axis of *Chamaelirium*, and 13.2 ± 0.9–16.2 ± 1.2 in major axis of ellipse and 16.2 ± 1.8 μm in polar axis of *Chionographis*. Porus with exinous gemmae. Except for the porus, exine sculpture clavate. Clavae with small projections on the head (Fig. 7). Exine structure intectate, consisting of 0.4 0.5-μm-high clavae and 0.4 0.4-μm-thick foot layer. Inner part of foot layer lamellated.

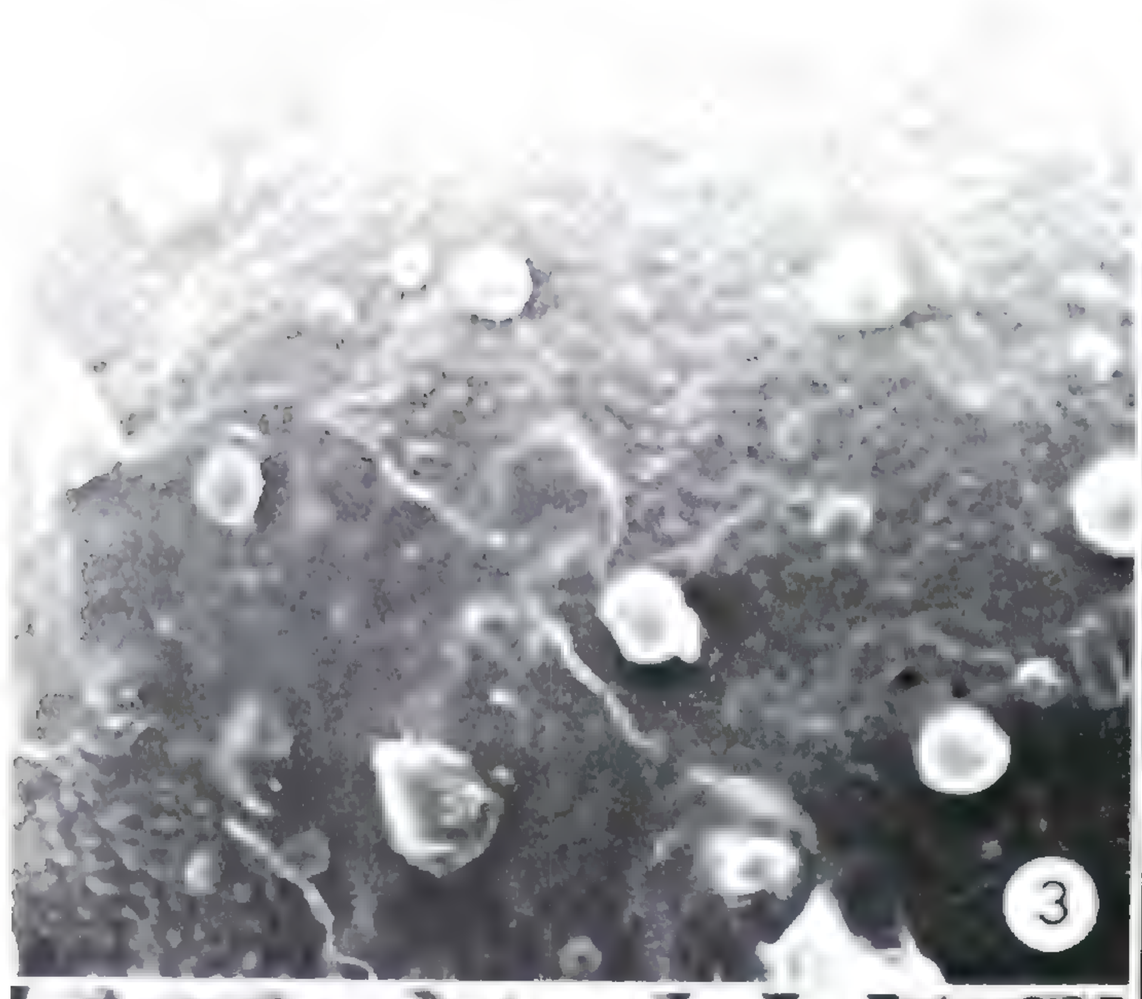
There is no difference in pollen type and exine structure between *Chamaelirium* and *Chionographis*.

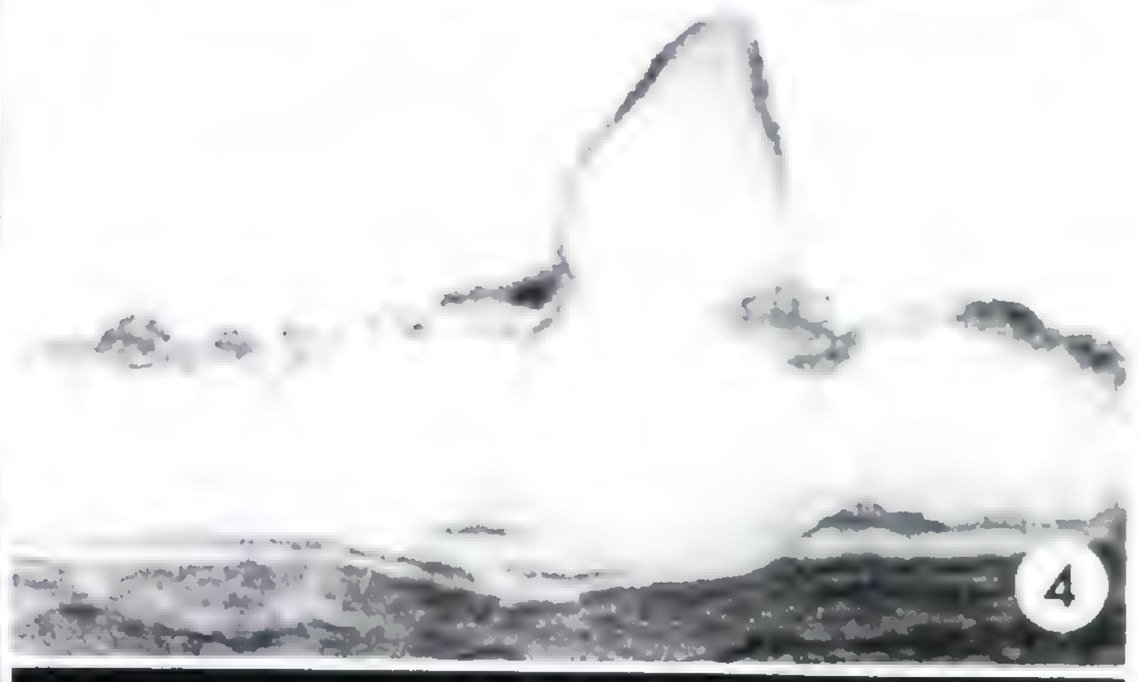
Tofieldia (Figs. 10–17)

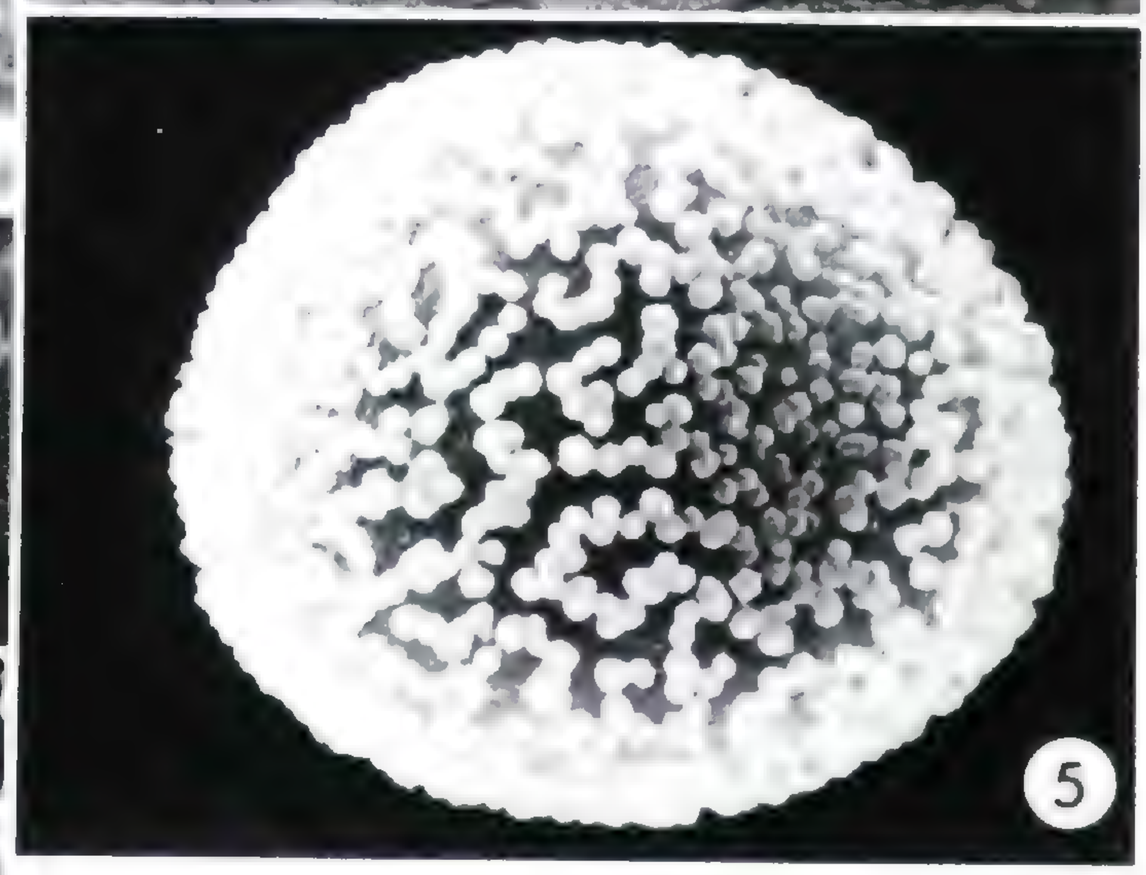
Pollen grains disulcate, 16.7 ± 0.9–25.2 ± 2.1 μm in major axis of ellipse and 10.9 ± 0.8 18.9 ± 1.4 μm in polar axis. Pollen size variable among species. Furrows extending near the ends of pollen grains. Except for the furrows, exine ornamentation reticulate, consisting of 0.5-μm-thick muri and

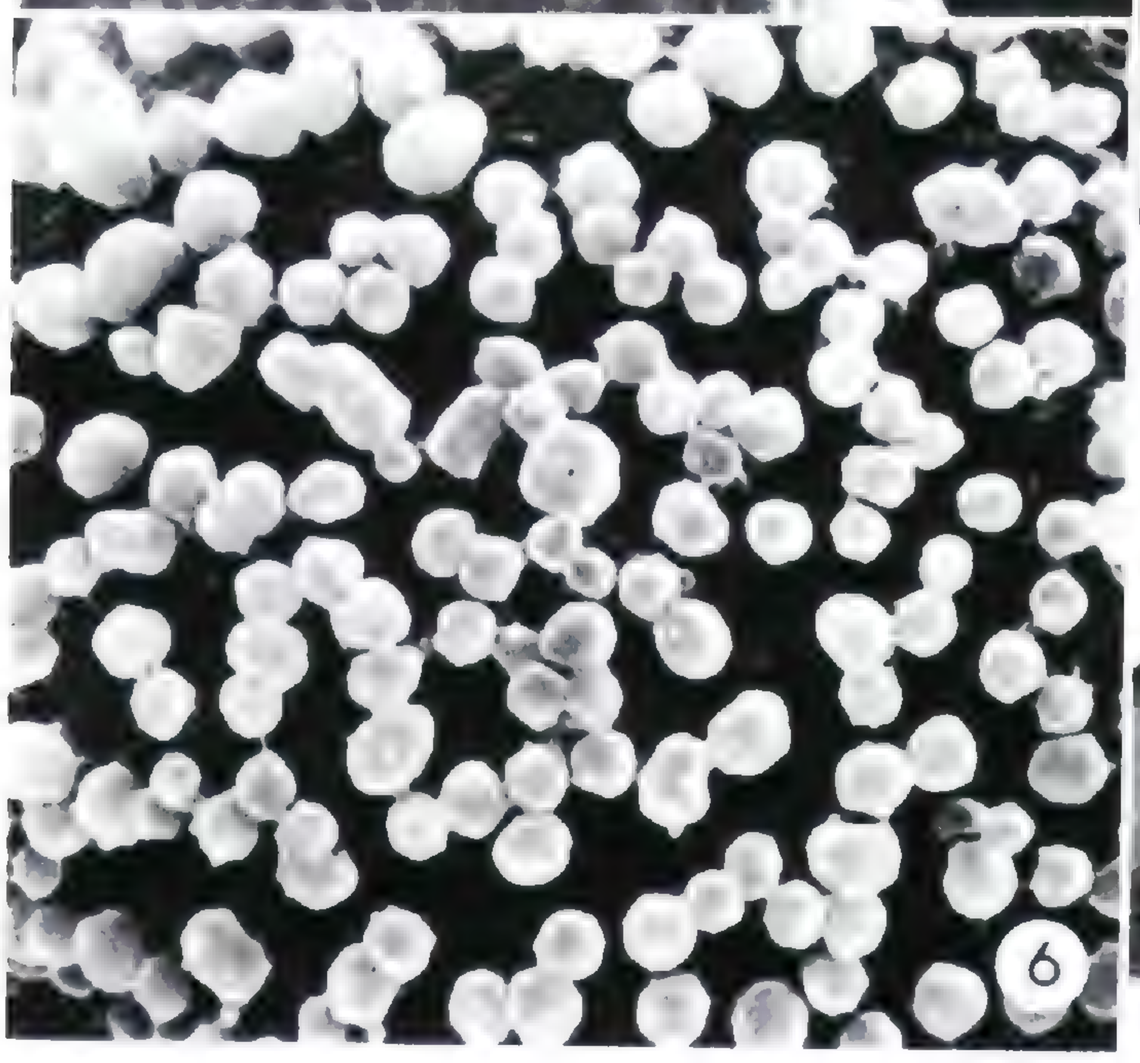




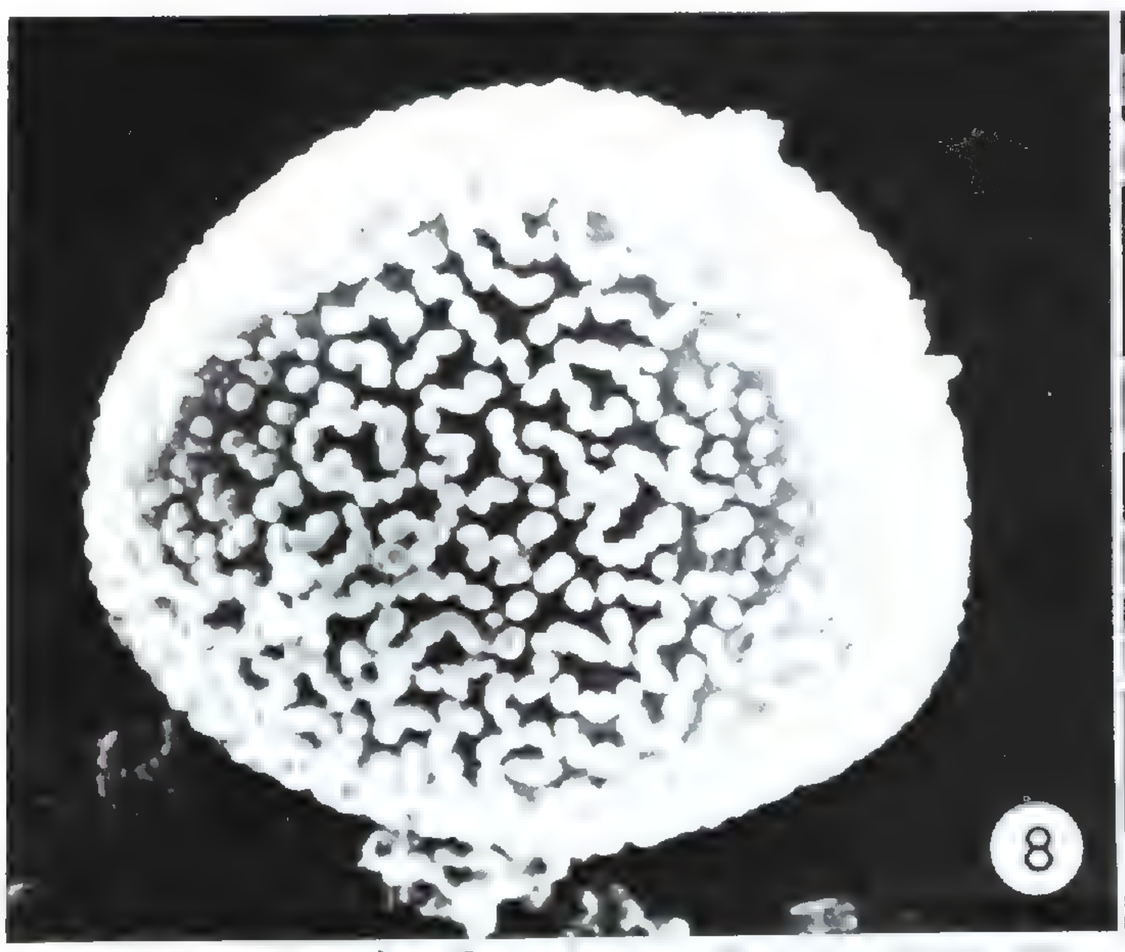


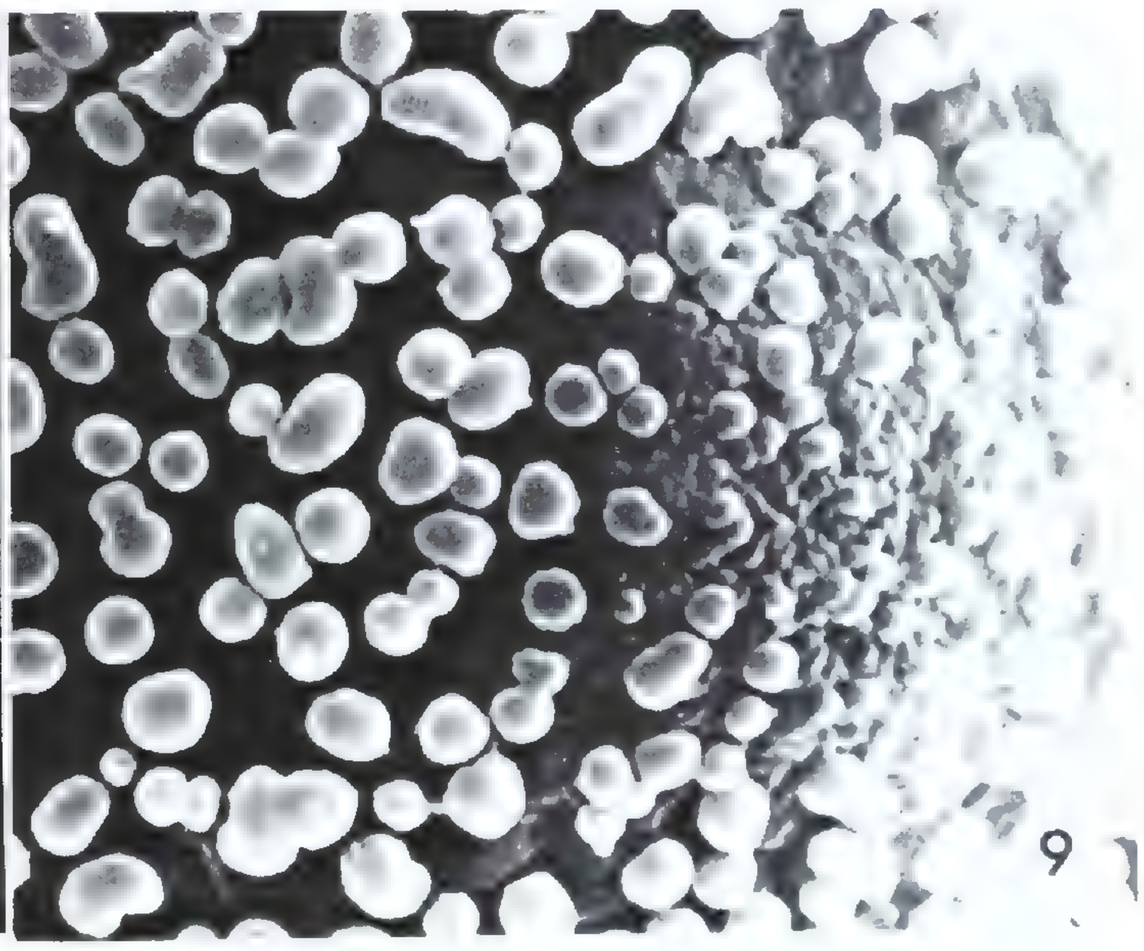


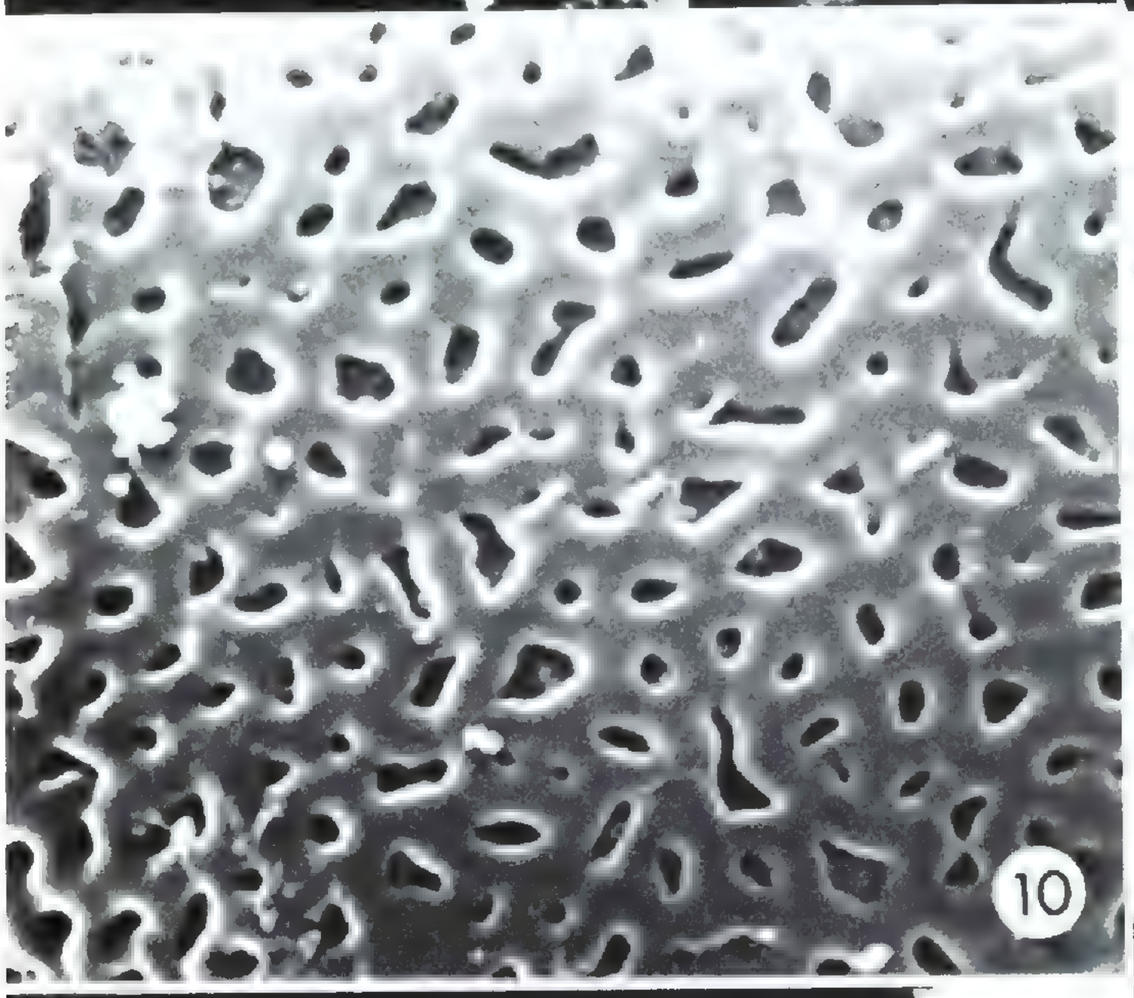


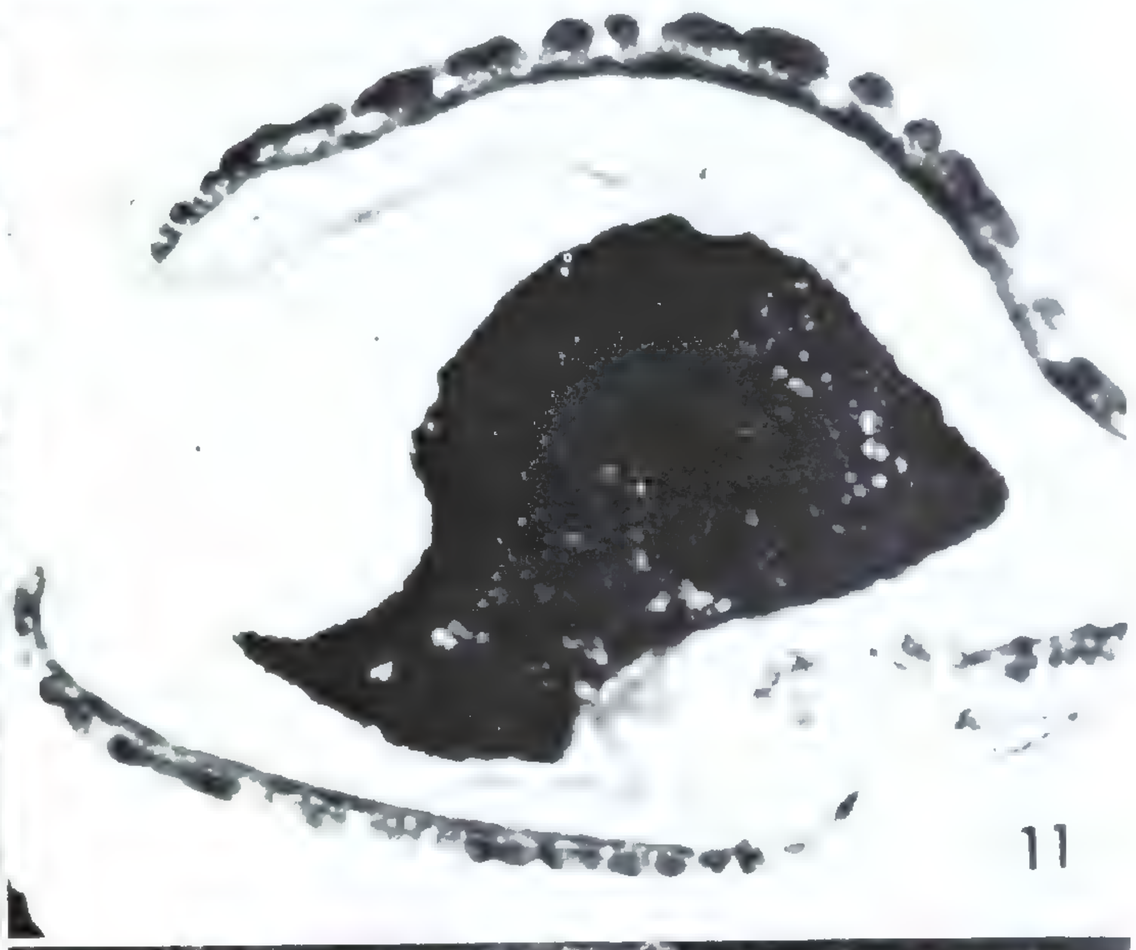


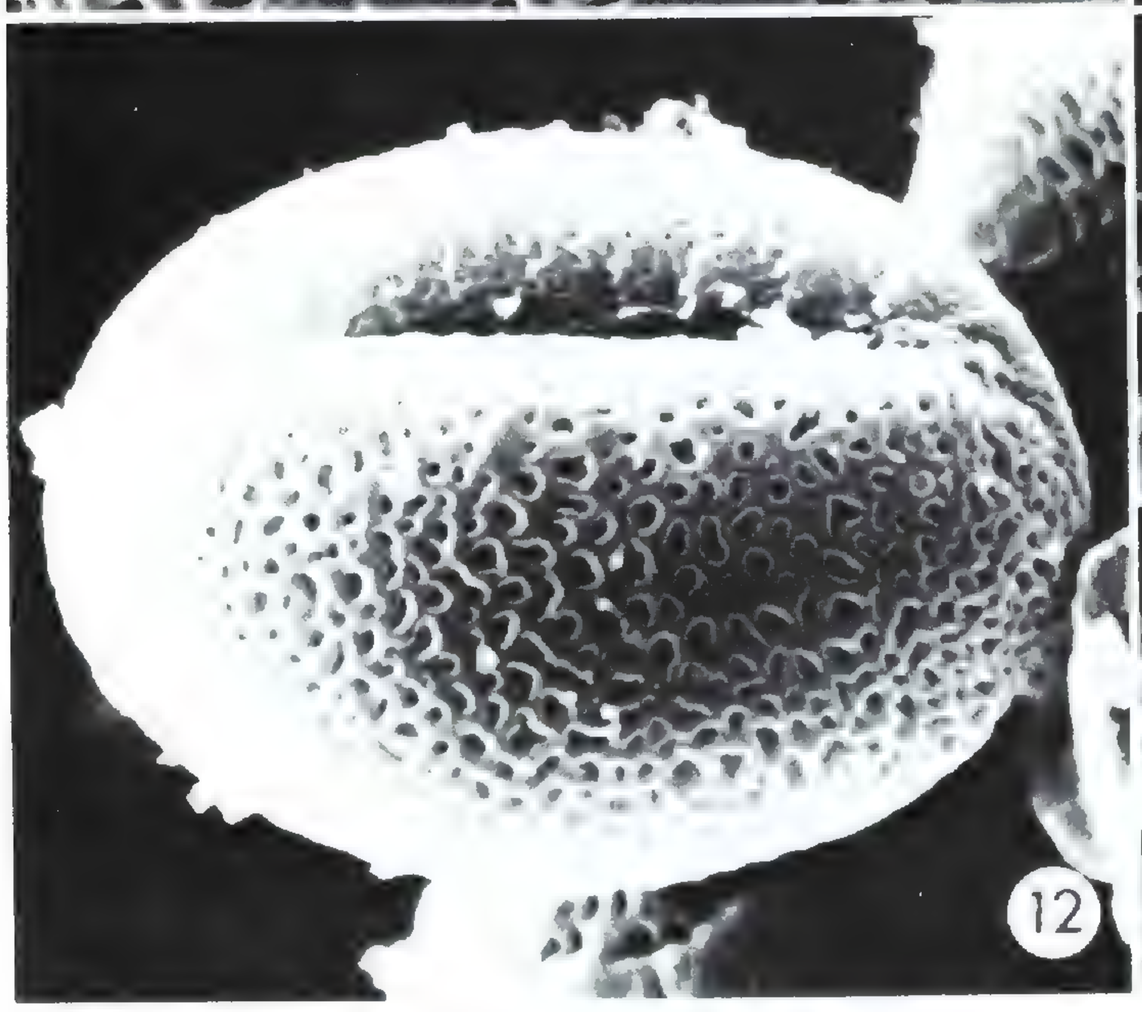
FIGURES 1–7.—1. Pollen grain of *Helonias bullata*, SEM ×2,600.—2. Exine sculpture of *Helonias bullata*, SEM ×6,000.—3. Exine sculpture of *Ypsilandra yunnanensis*, SEM ×6,000.—4. Exine structure of *Ypsilandra yunnanensis*, TEM ×34,000.—5. Pollen grain of *Chamaelirium luteum*, SEM ×6,000.—6. Gemmate exine sculpture of *Chamaelirium luteum*, SEM ×74,000.—7. Exine structure of *Chionographis koidzumiana*, TEM ×49,400.



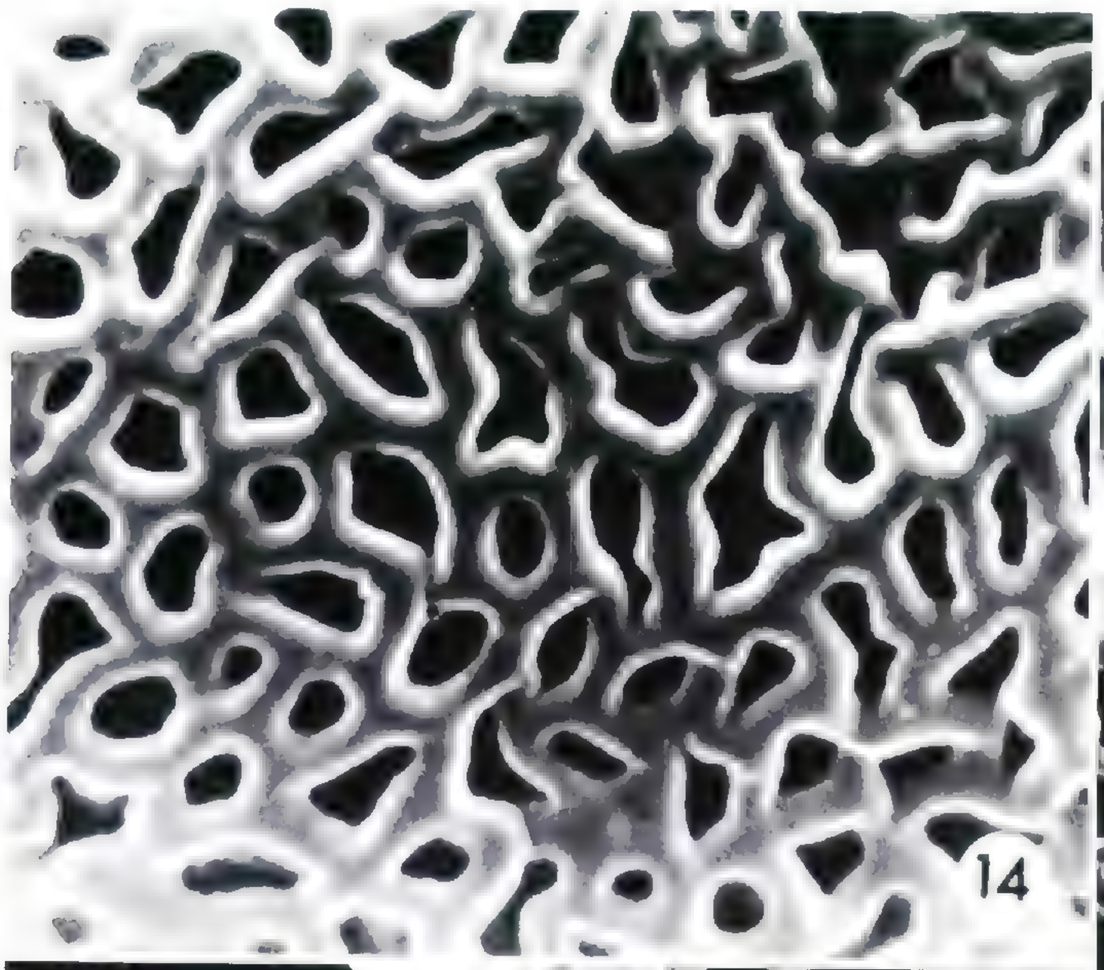


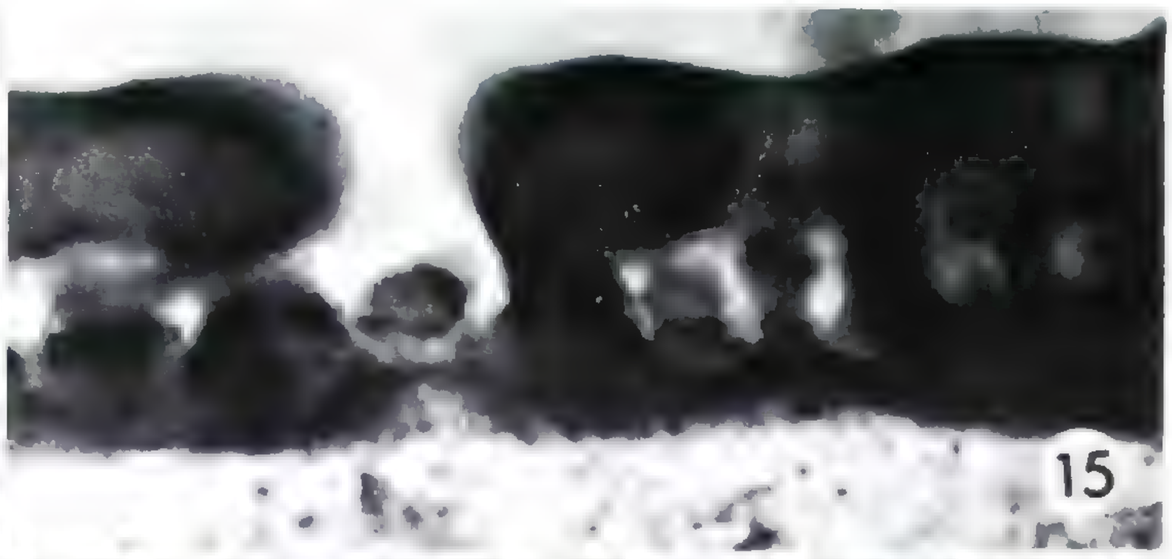


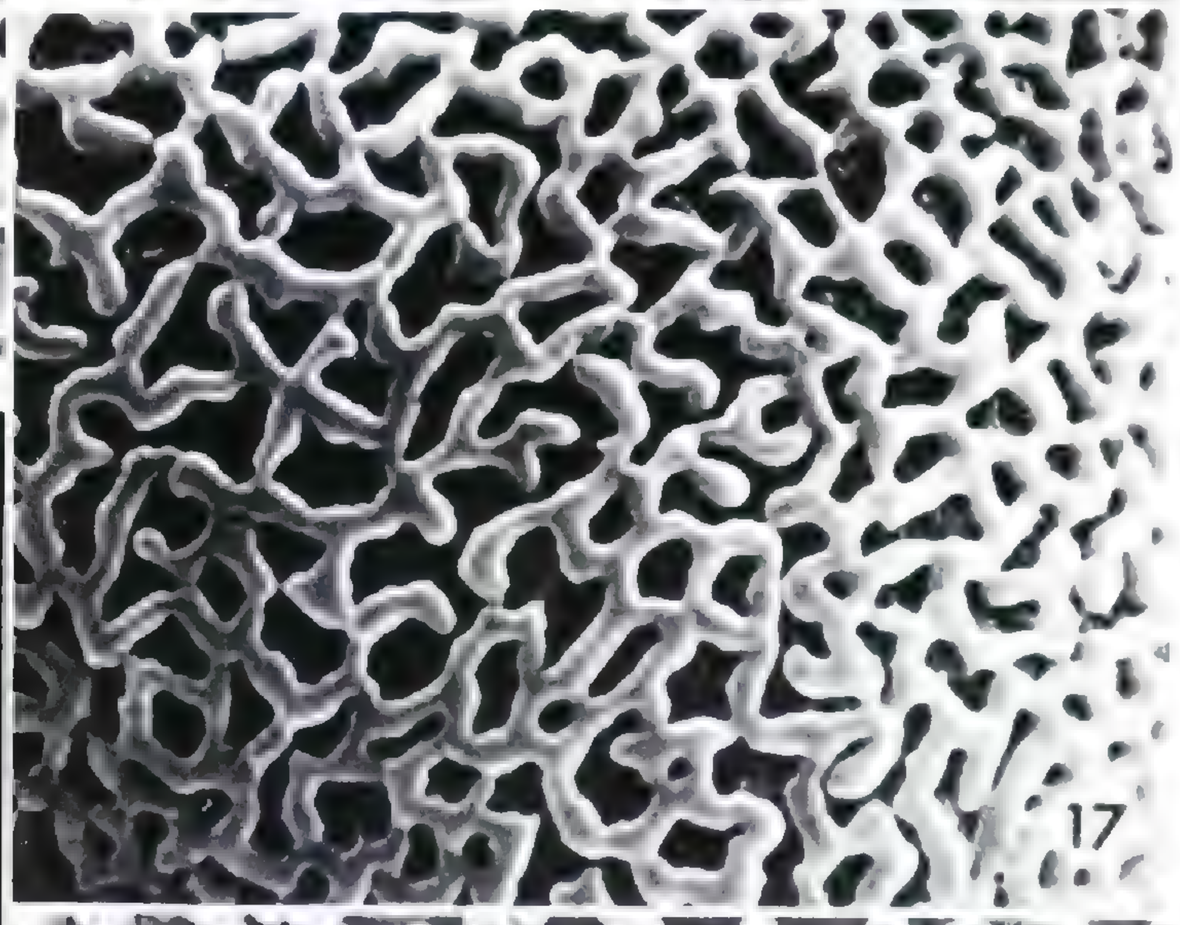


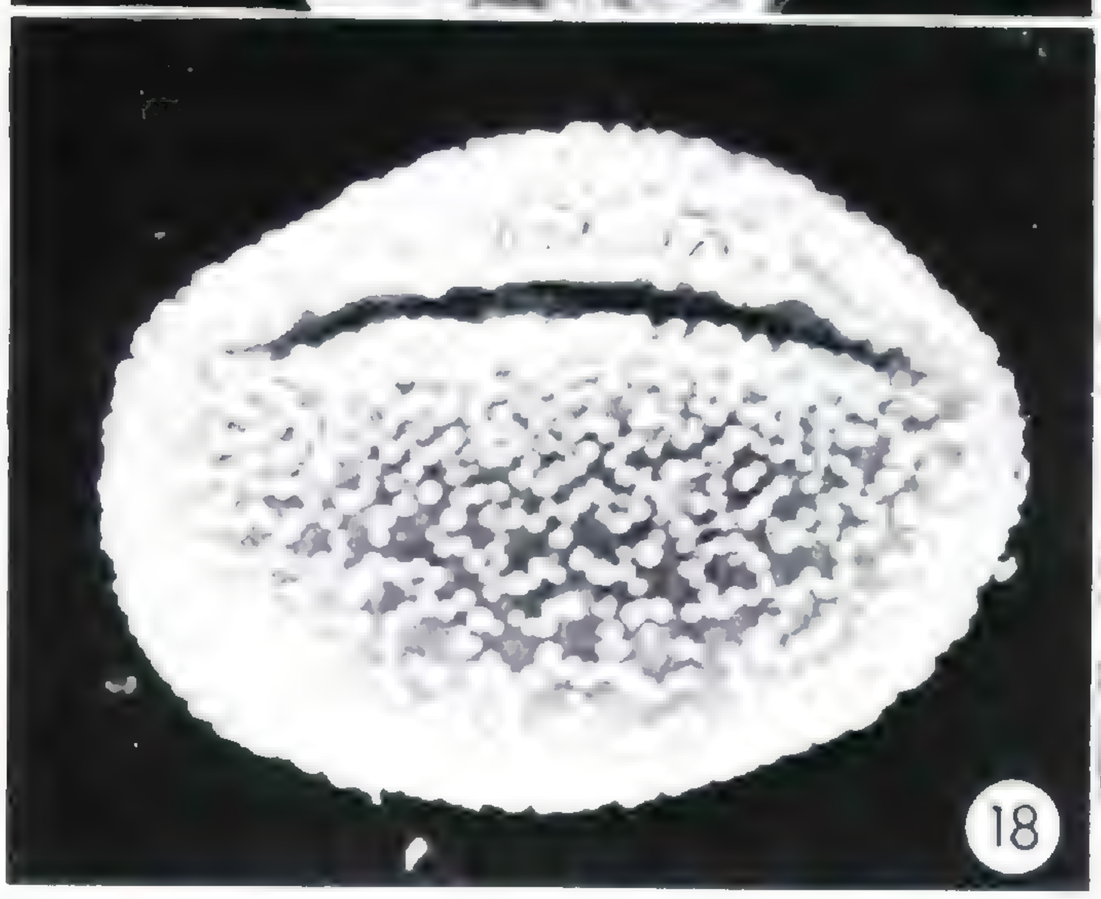


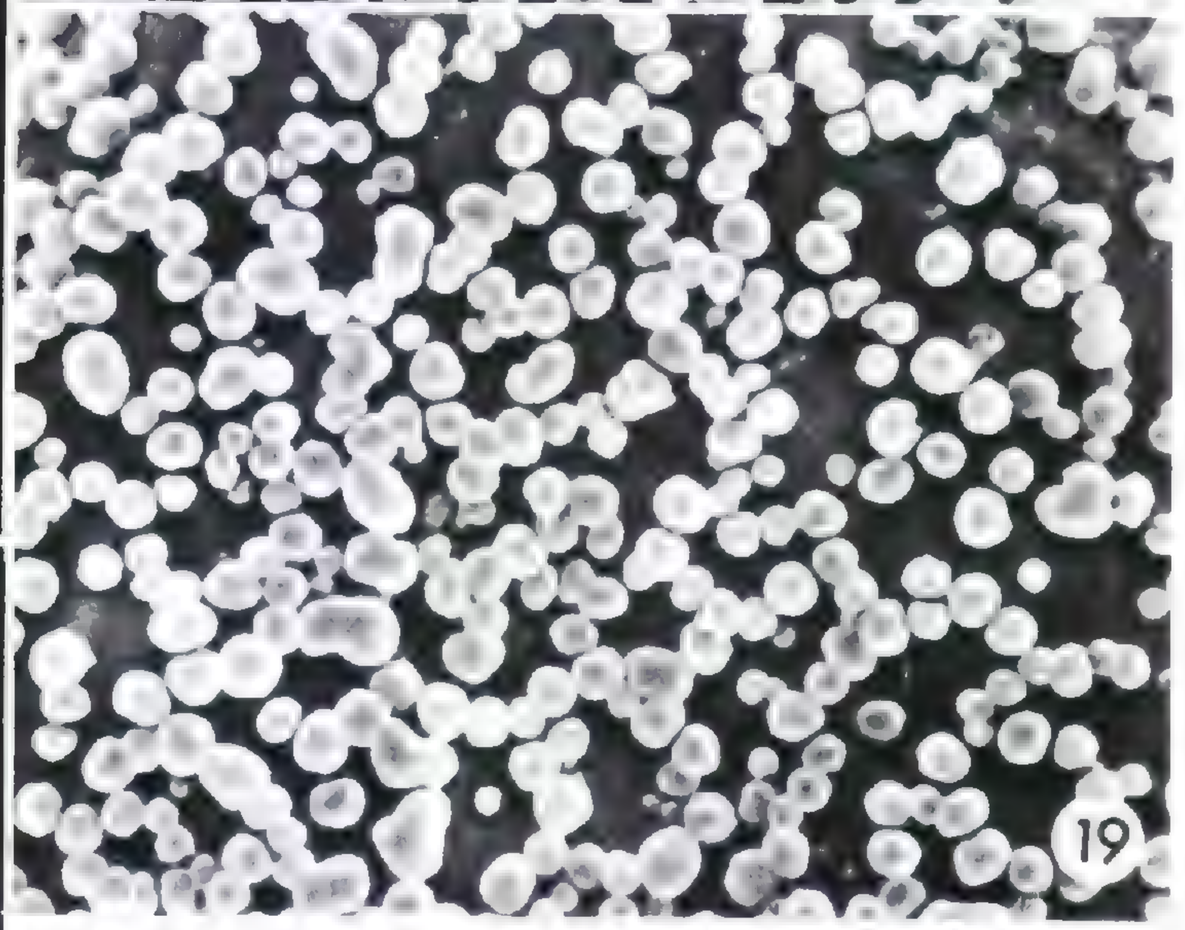
FIGURES 8–13.—8. Pollen grain of *Chionographis koidzumiana*, SEM ×3,000.—9. Gemmate exine sculpture of *Chionographis koidumiana*, SEM ×18,000.—10. Reticulate exine sculpture of *Tofieldia glutinosa*, SEM ×10,000.—11. Pollen grain of *T. glutinosa*, TEM ×4,100.—12, 13. Disulcate pollen grain of *T. occidentalis*, SEM ×3,200.











FIGURES 14–20. 14. Reticulate exine sculpture of *Tofieldia occidentalis*, SEM ×10,000.—15. Exine structure of *T. glutinosa*, TEM ×43,600.—16. Pollen grain of *T. pusilla*, SEM ×3,600.—17. Discontinuous reticulate exine sculpture of *T. pusilla*, SEM ×7,600.—18. Pollen grain of *Japonolirion ozense*, SEM ×3,000.—19. Gemmate exine sculpture of *J. ozense*, SEM ×7,400. 20. Exine structure of *J. ozense*, TEM ×2,400.

lumina 0.2–0.7 μm diam. with nonangulate margins. Exine structure semitectate, consisting of 0.3-μm-thick tectum, 0.1-μm high columellae, and 0.2–0.3 μm-thick foot layer.

The reticuloid exine sculpture of *T. pusilla*, which has discontinuous muri, is unique in the genus.

Pleea

Pollen grains disulcate, 20.0 ± 1.5 22.7 ± 1.3 μm in major axis of ellipse and 15.8 ± 1.3–17.9 ± 1.2 μm in polar axis. Furrows extending near the ends of pollen grains. Except for the furrow, exine ornamentation reticulate, consisting of muri and lumina 0.2–0.3 μm diam. with nonangulate margins. Exine 0.5 μm high, consisting of 0.2-μm-thick tectum, 0.1-μm-high columellae, and 0.2-μm-thick foot layer.

Japonolirion (Figs. 18–20)

Pollen grains monosulcate, 19.2 ± 2.0 μm in major axis of ellipse and 15.6 ± 1.8 μm in polar axis, provided with a furrow. This with no marginal thickening, exinous islet absent. Except for the sulcus, exine ornamentation gemmate. Gemmae 0.2–0.3 μm diam., spheroidal. Exine composed of foot layer 0.2–0.3 μm thick and gemmate protrusion 0.3–0.4 μm high.

Xerophyllum (Figs. 21 24)

Pollen grains monosulcate, 22.6 ± 1.5–29.0 ± 3.2 μm in major axis of ellipse and 14.9 ± 1.4–19.9 ± 1.3 μm in polar axis, provided with a furrow, this lacking exinous islets. Except for the furrow, exine ornamentation reticulate and characterized by narrow muri, these 0.1–0.2 μm thick, the angulate lumina 0.5–1.0 μm diam. Exine 1.0 μm thick, semitectate, consisting of 0.5–0.6-μm-thick tectum, 1.0-μm-high columellae, and 0.5–0.6-μm-thick foot layer.

There is no conspicuous difference in pollen morphology between *X. asphodeloides* and *X. tenax*.

Varthecium (Figs. 25–27)

Pollen grains monosulcate, 17.7 ± 1.3–20.6 ± 1.5 μm in major axis of ellipse and 11.9 ± 1.2–13.5 ± 1.2 μm in polar axis, provided with a furrow. Exine 0.5 μm thick, semitectate, consisting of 0.2-μm-thick tectum, 0.2-μm-high columellae, and 0.1-μm-thick foot layer, reticulate, the reticulum consisting of 0.3-μm-thick muri and lumina 0.1–0.5 μm diam.

No conspicuous interspecific variation was recognized in pollen size, pollen type, and exine sculpture within *Varthecium*.

Aletris (Figs. 28 32)

Pollen grains monosulcate, 21.8 ± 1.5–32.4 ± 3.8 μm in major axis of ellipse and 14.0 ± 2.4–20.5 ± 3.2 μm in polar axis, provided with a sulcus with exinous gemmae. This extended to the ends of grains.

The genus shows wide variation in exine sculpture, e.g., perforate-foveolate, reticulate, and gemmate. The perforate-foveolate type is shown in *A. aurea*, *A. bracteata*, *A. farinosa*, *A. obovata*, and *A. lutea*. The perforatum are 0.1–0.3 μm in diameter.

The reticulate type is represented by *A. folia*, *A. spicata*, and *A. ossifragum*. Here the lumina, 0.5–1.0 μm in diameter, are roudish rather than angulate. The foveolate or reticulate exine consists of tectum, columellae, and foot layer.

The gemmate type is observed in *A. pauciflora* and *A. lanuginosa*. The gemmate exine is composed of 0.6–0.8-μm-gemmae and 0.2–0.3-μm-foot layer.

Metanarthecium (Fig. 33)

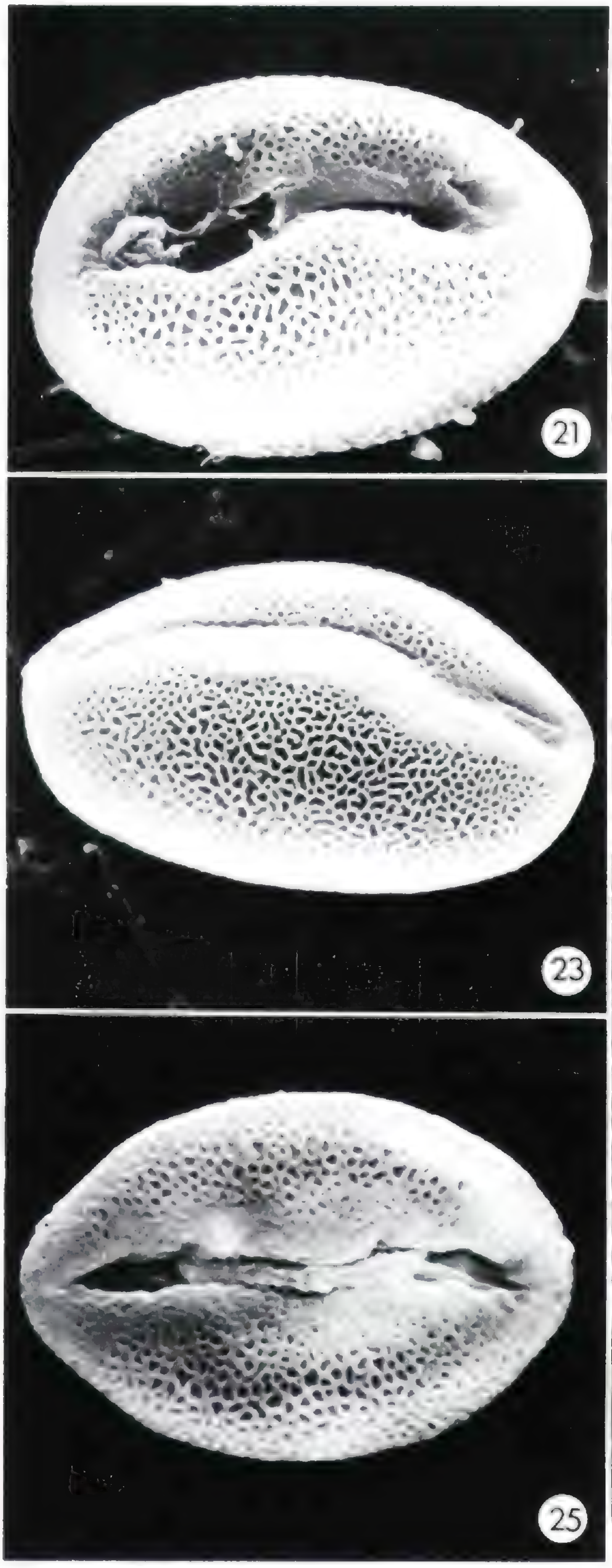
Pollen grains monosulcate, 17.2 ± 1.3 18.3 ± 1.0 μm in the longest axis of ellipse and 11.6 ± 1.5–13.5 ± 1.5 μm in polar axis, provided with a furrow having a membranous surface and no marginal thickening. Except for the furrow, exine sculpture reticulate, the reticulum characterized by small projection on lumina (Fig. 33). Lumina 1.0–1.5 μm diam., muri 0.2 0.3 μm thick. Exine composed of tectum, columellae, and foot layer.

Lophiola (Figs. 34 35)

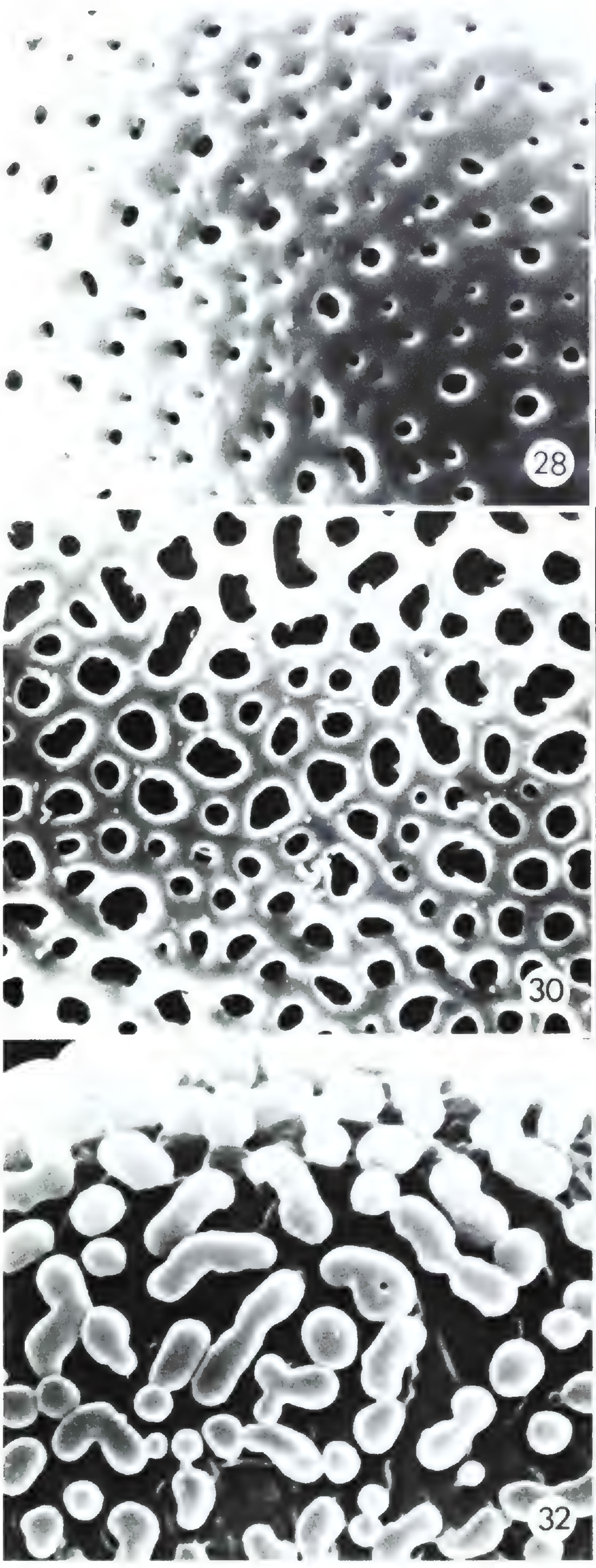
Pollen grains monosulcate, 18.5 ± 1.6 μm in the longest axis of ellipse and 12.7 ± 1.8 μm in polar axis, provided with a furrow. Exine sculpture reticulate, the reticulum composed of 0.1–0.3-μm-wide lumina and 0.1-μm-thick muri.

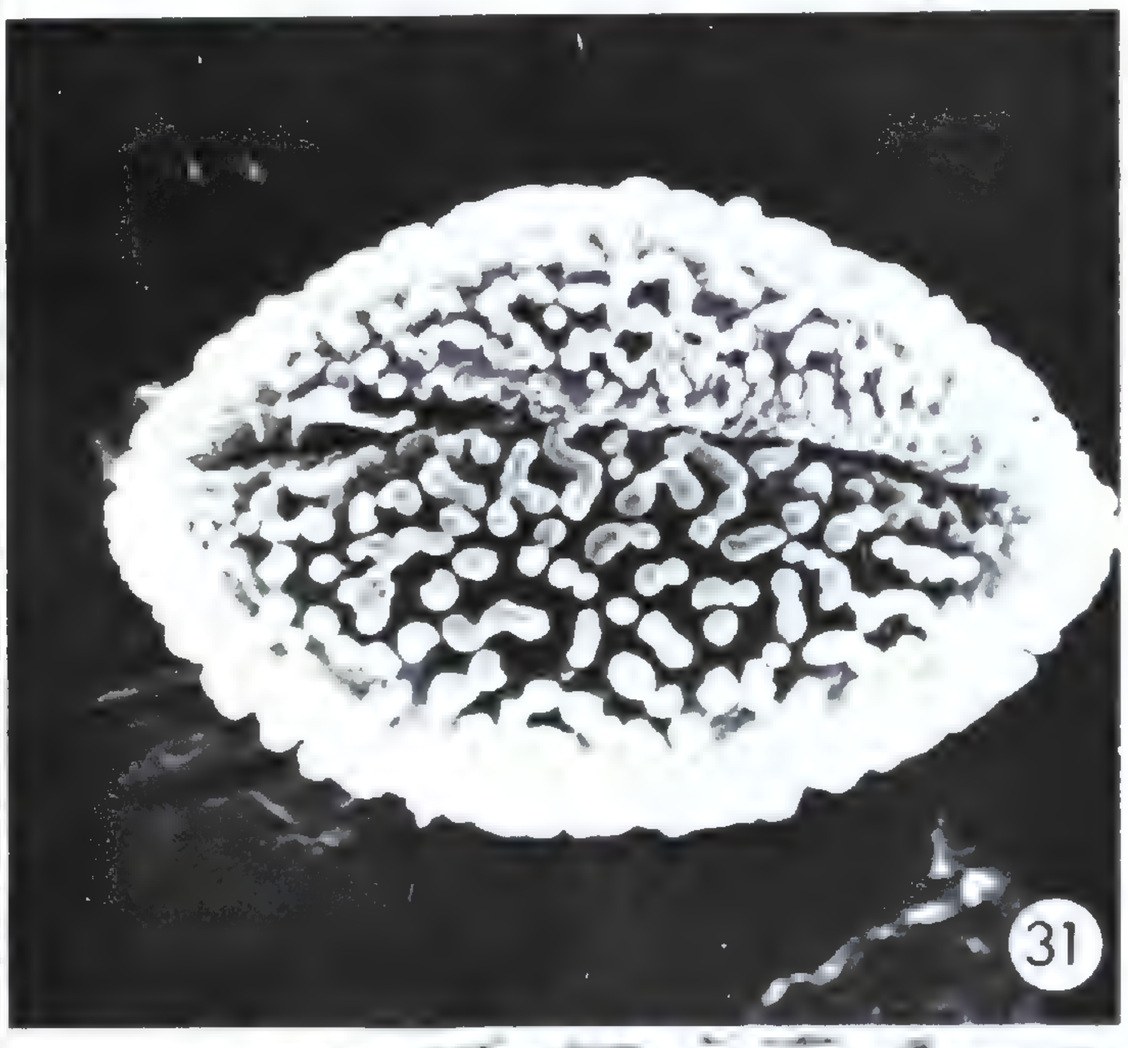
Amianthium, *Stenanthium*, and *Schoenocaulon* (Figs. 36 39)

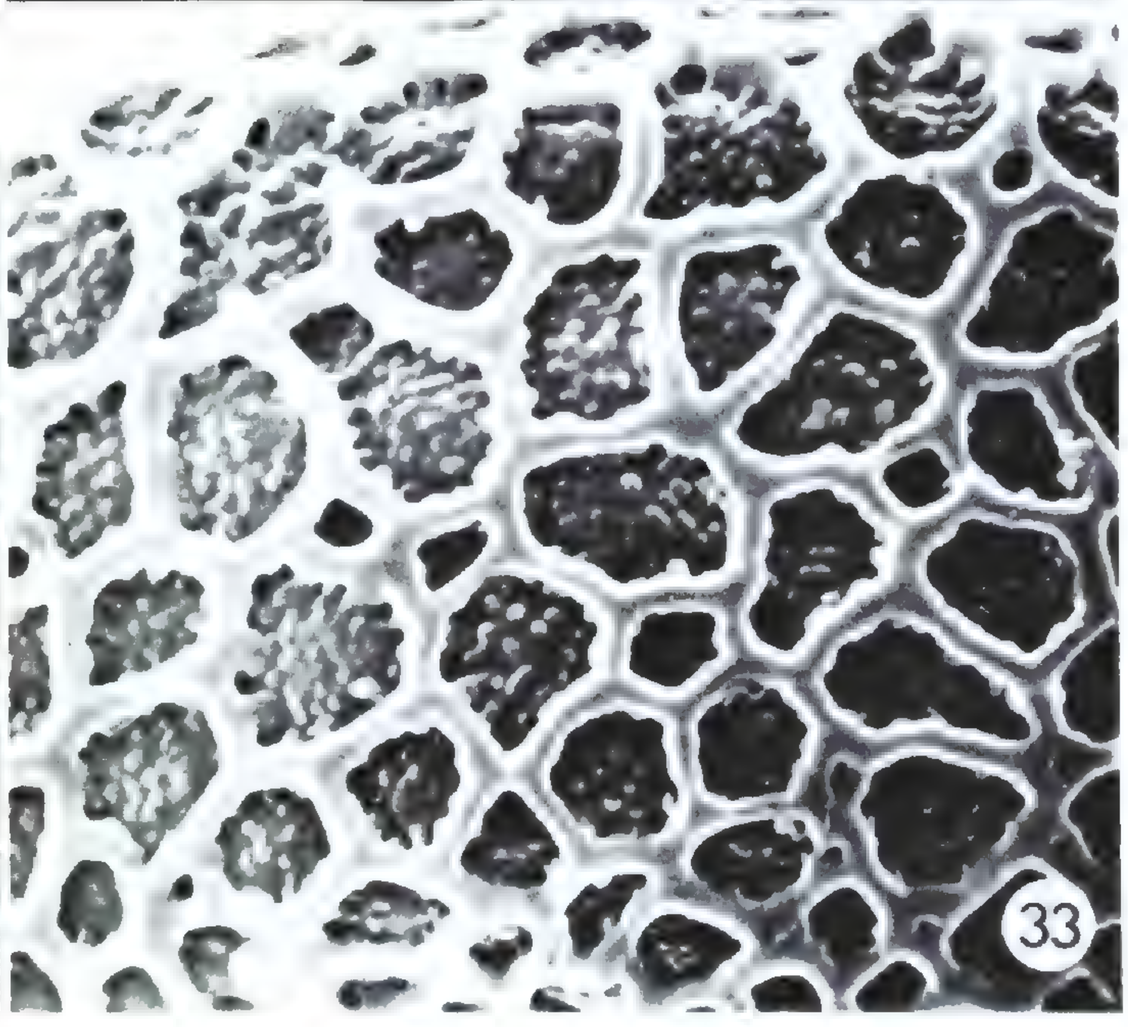
Pollen grains monosulcate, 23.2 ± 1.4 25.2 ± 1.6 μm in the longest axis of ellipse and 15.4 ± 1.2–17.2 ± 1.4 μm in polar axis, provided with



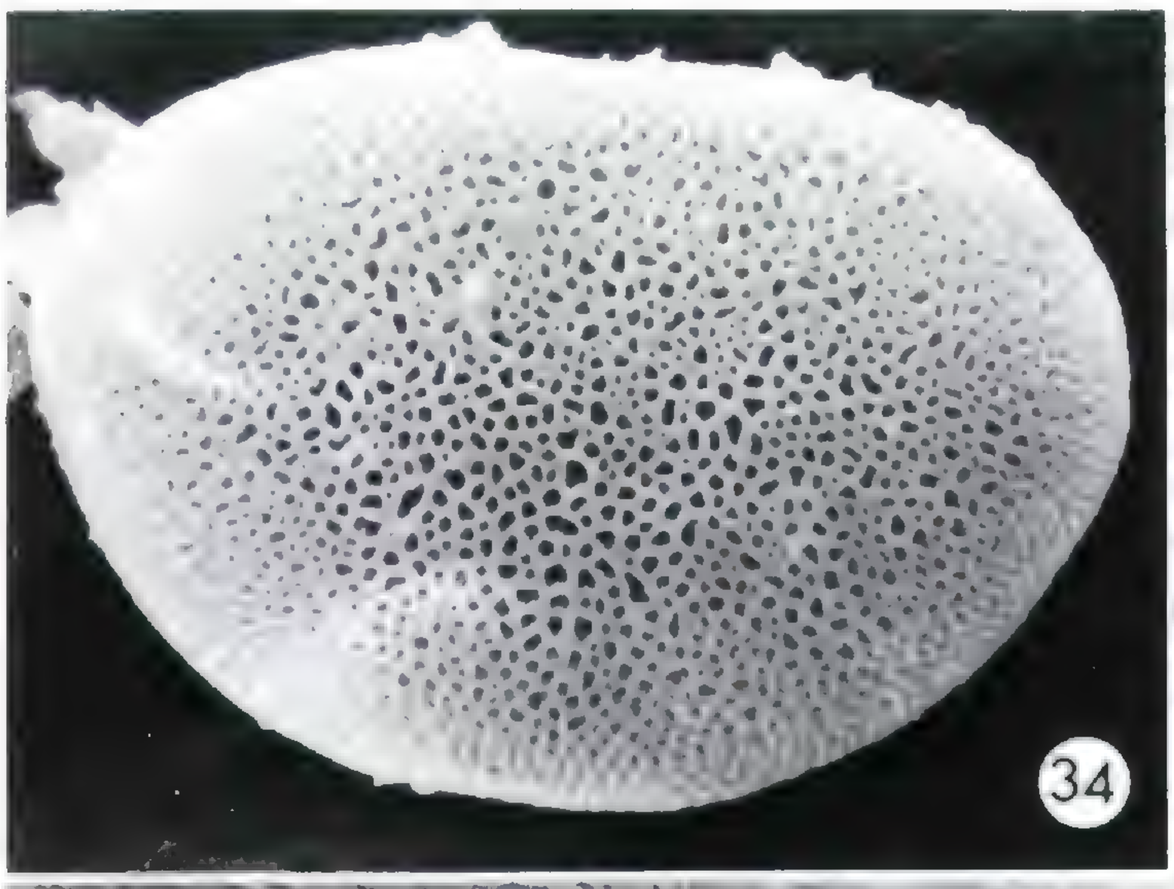
FIGURES 21–27.—21. Pollen grain of *Xerophyllum asphodeloides*, SEM ×3,000.—22. Reticulate exine sculpture of *X. asphodeloides*, SEM ×3,000.—23. Pollen grain of *X. setifolium*, SEM. ×2,600.—24. Exine structure of *X. asphodeloides*, TEM ×42,000.—25. Pollen grain of *Narthecium americanum*, SEM ×3,000.—26. Reticulate exine sculpture of *N. californicum*, SEM ×12,000.—27. Exine structure of *Narthecium*, TEM ×44,000.

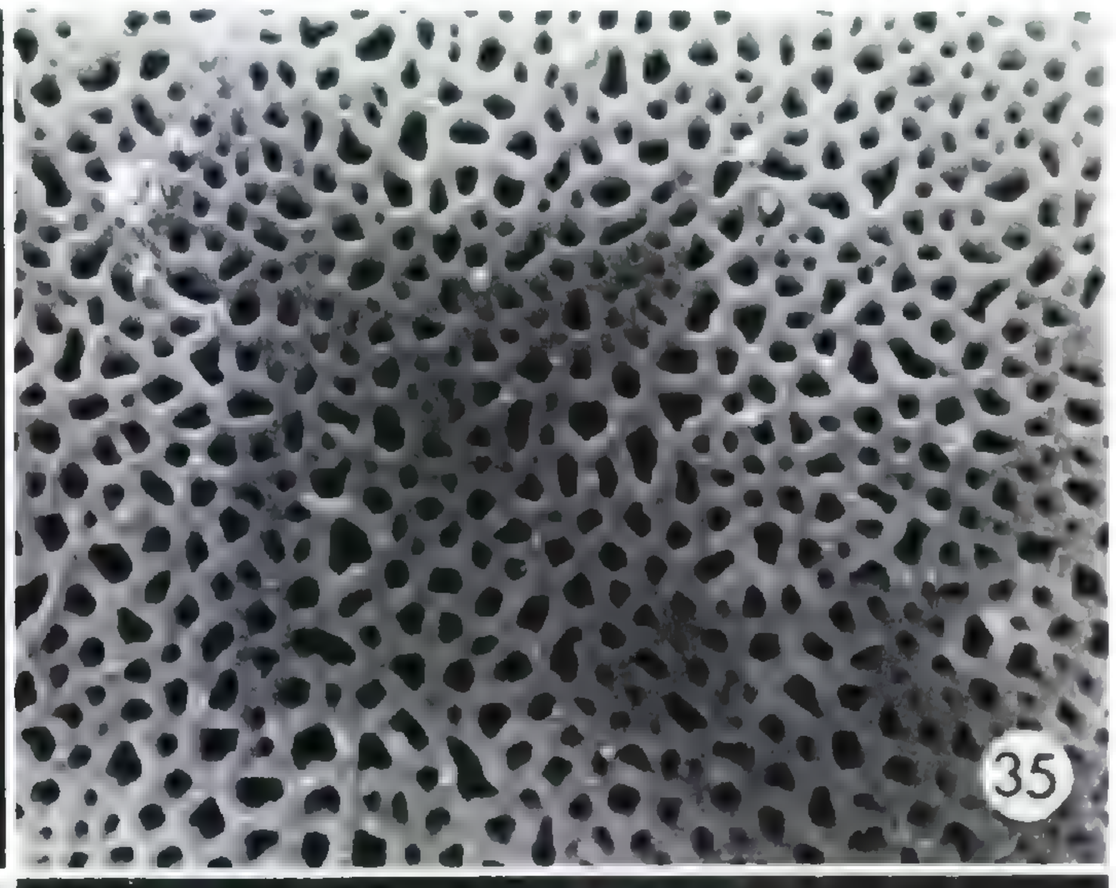


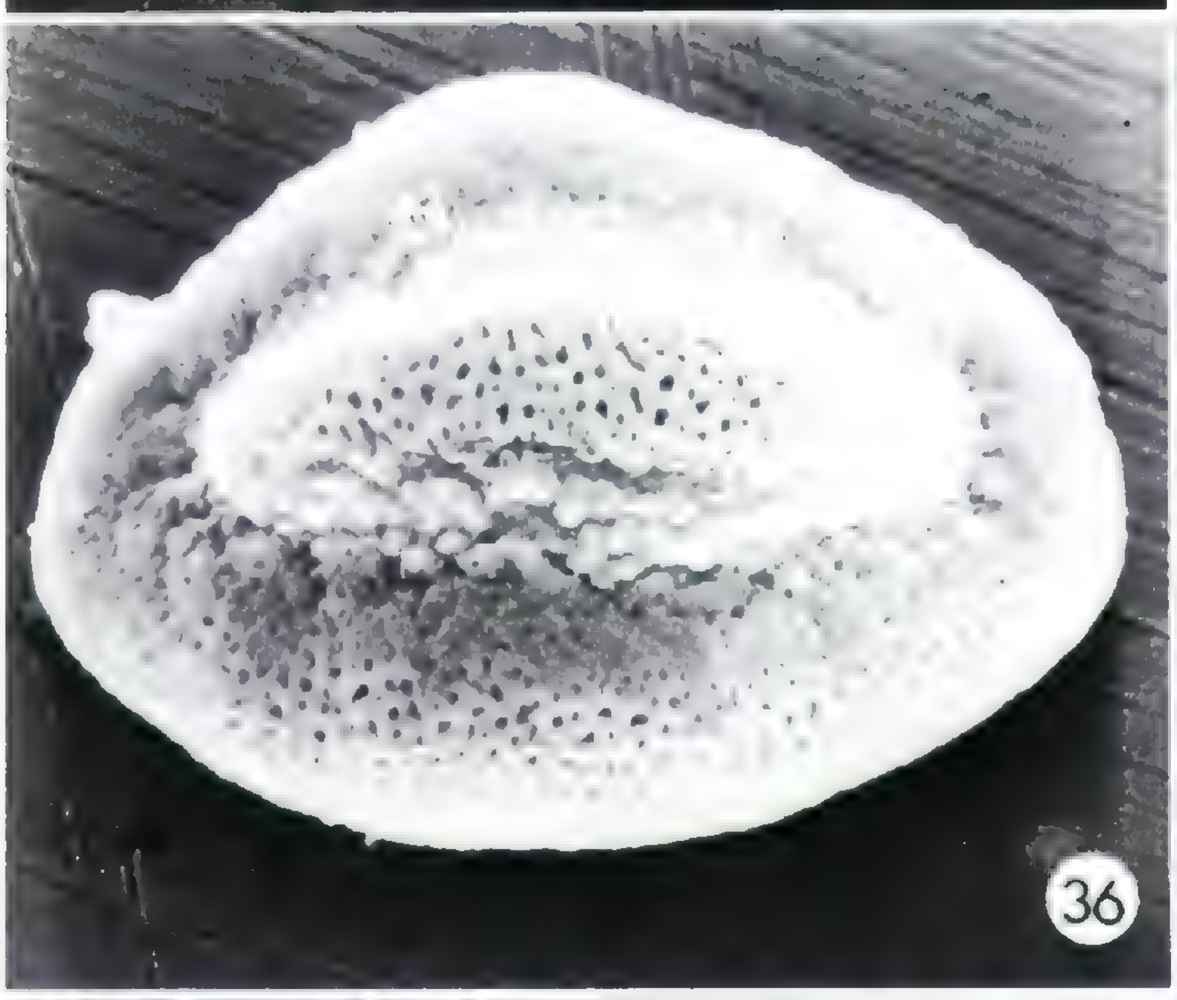


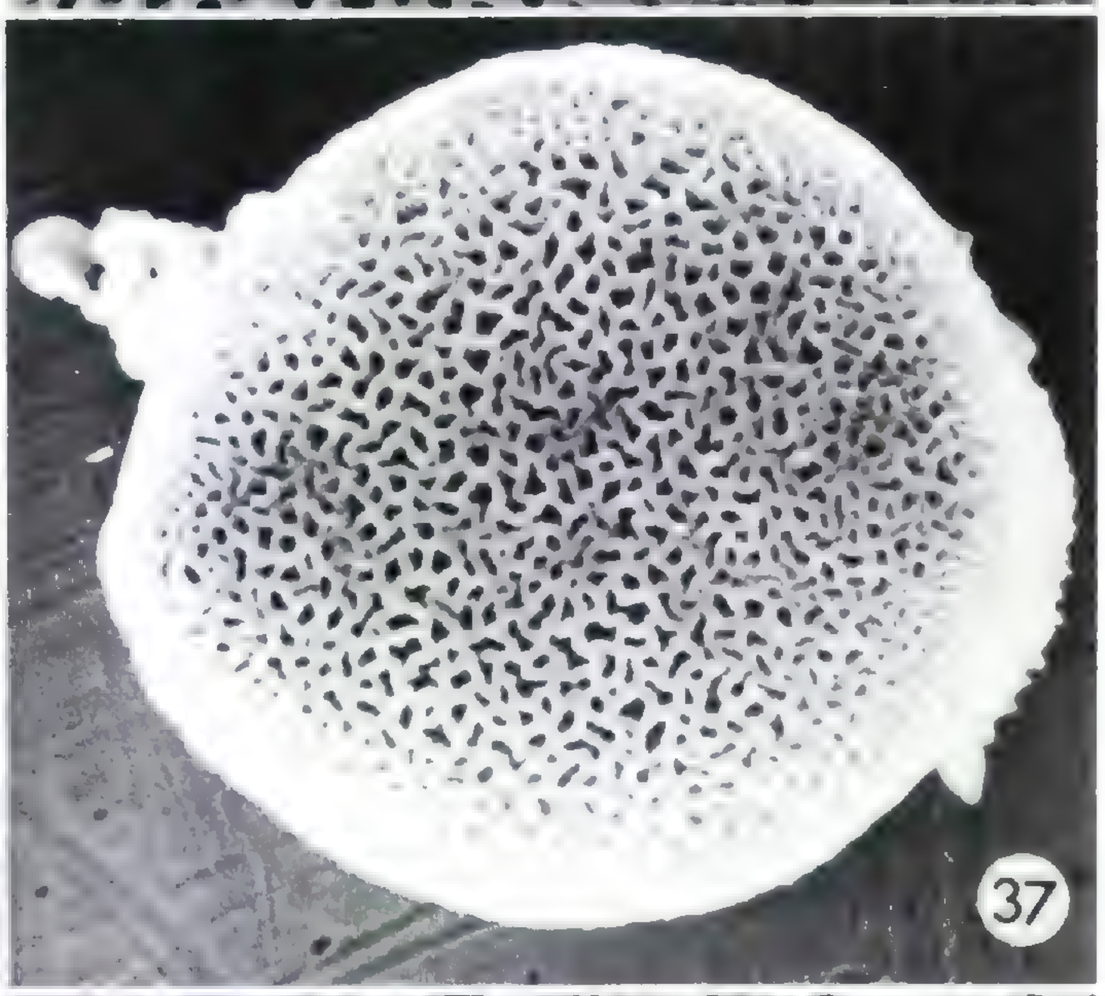


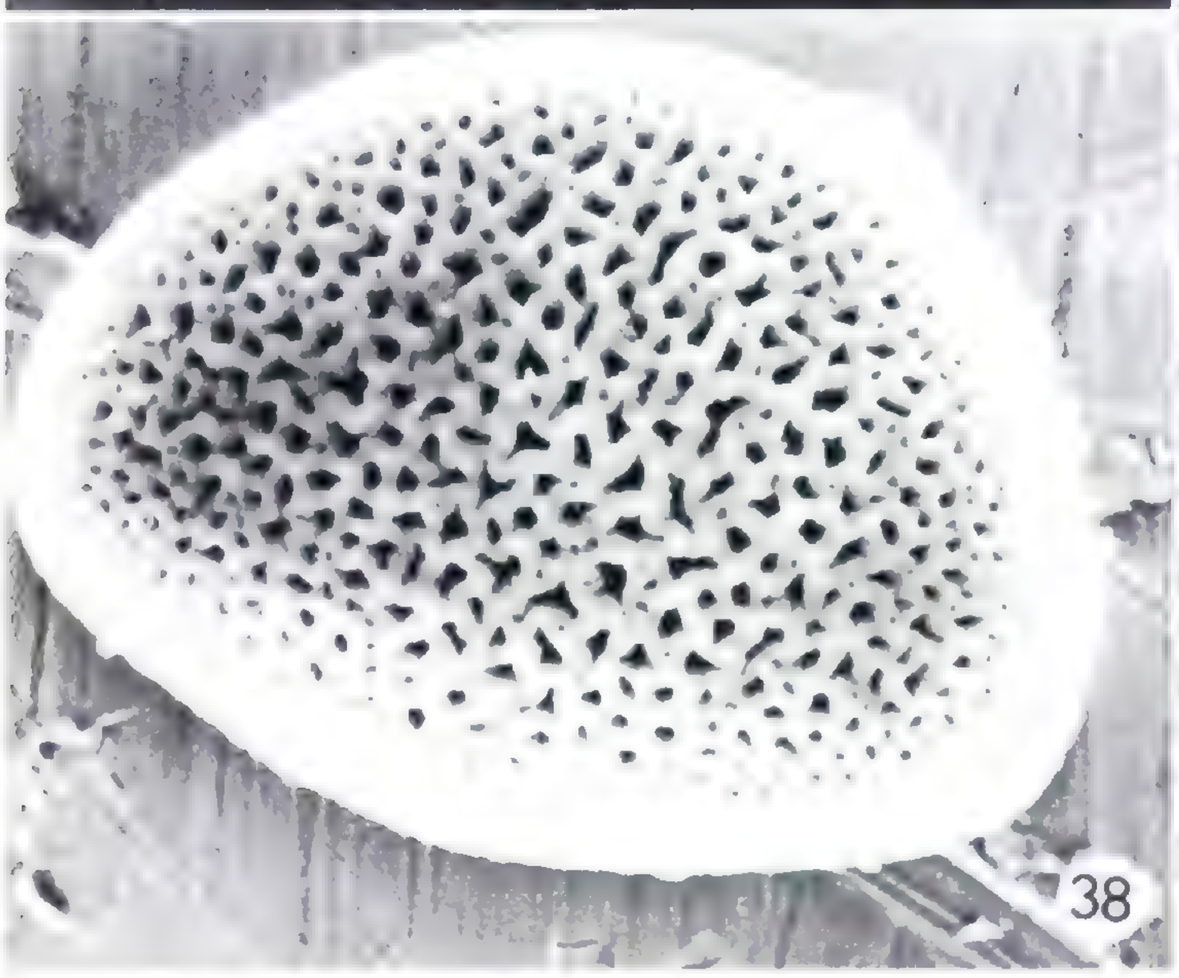
FIGURES 28-33.—28. Perforate exine sculpture of *Aletris aurea*, SEM ×7,400.—29. Exine structure of *A. aurea*, TEM ×40,000.—30. Reticulate exine sculpture of *A. farinosa*, SEM ×7,400. 31. Pollen grain of *A. lanuginosa*, SEM ×7,600. 32. Gemmate exine sculpture of *A. lanuginosa*, SEM ×7,600.—33. Reticulate exine sculpture of *Methanarthecium luteo-viride*, SEM ×7,200.

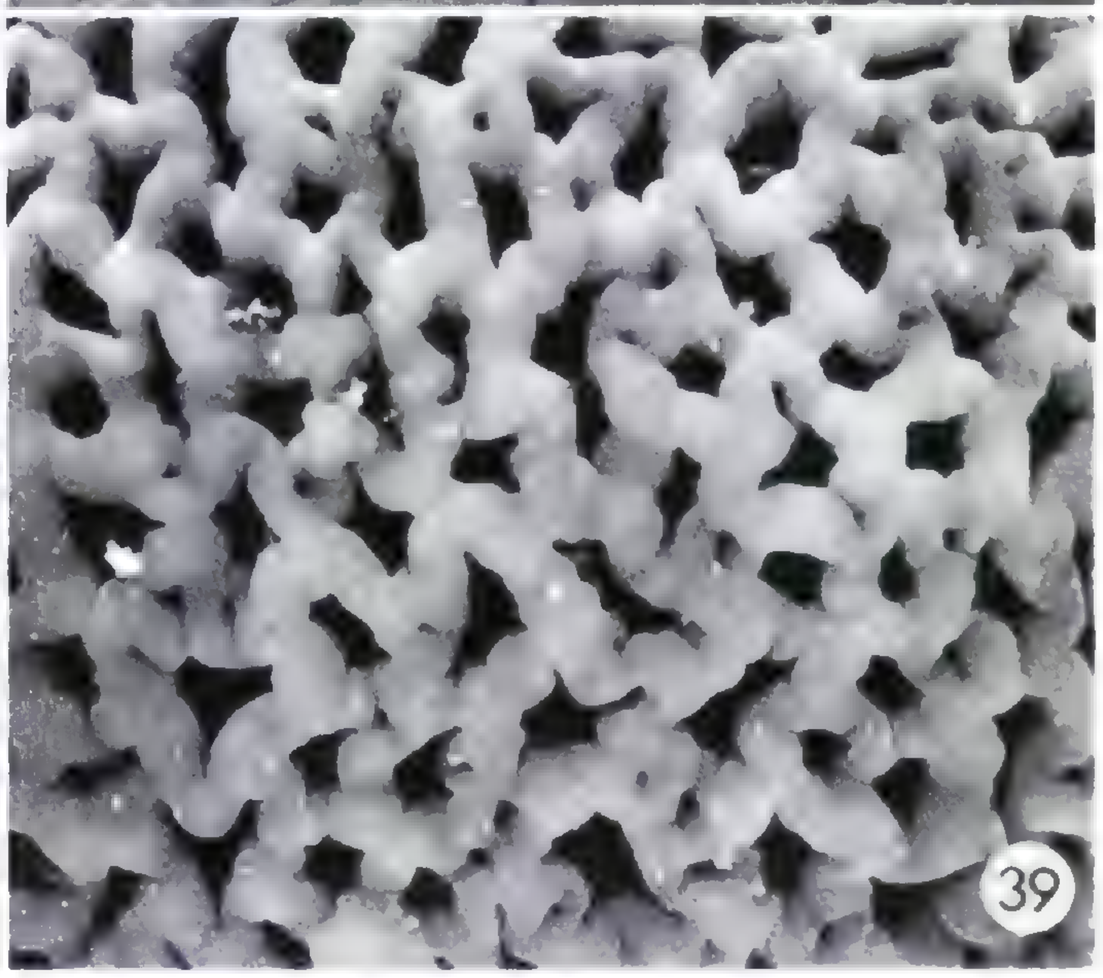












FIGURES 34–39. —34. Pollen grain of *Lophiola americana*, SEM ×3,800.—35. Reticulate exine sculpture of *Lophiola americana*, SEM ×7,600.—36. Pollen grain of *Amianthium* sp., SEM ×3,000.—37. Pollen grain of *Stenanthium occidentale*, SEM ×3,000.—38. Pollen grain of *Schoenocaulon pringlei*, SEM ×3,000.—39. Reticulate exine sculpture of *Schoenocaulon pringlei*, SEM ×7,600.

a furrow, the furrow with an operculum. Exine sculpture reticulate, the reticulum consisting of 0.3-μm-wide lumina and 0.3 0.6-μm-thick muri. The lumina angular.

DISCUSSION

Helonias and *Ypsilandra* are characterized by a distinctive exine structure that consists of an

amorphous layer and spinules, and the same exine structures were observed in *Heloniopsis* (Takahashi, 1982a). Utech (1978, 1980) and Utech & Kawano (1981) suggested that *Heloniopsis* and *Helonias* should be maintained in the same tribe based on floral vasculature and karyology despite Hutchinson's (1934, 1959) placement of *Helonias* in Heloniadeae apart from *Heloniopsis* in the Narthecieae. The present pollen morphological evidence supports the suggestion by Utech & Kawano (1981) and further indicates that *Ypsilandra* should be included in the same tribe with *Helonias* and *Heloniopsis*. The three genera are closely related to each other and are distinctive because of the amorphous exine structure with spinules. Dahlgren et al. (1985) included *Helonias* and *Heloniopsis* in the tribe Narthecieae, with *Methanarthecium*, *Vietneria*, *Narthecium*, and *Lophiola*. We now regard *Helonias*, *Heloniopsis*, and *Ypsilandra* as congeneric, and a more thorough taxonomic account of this controversial group is needed.

Chionographis from Japan has clavate exine sculpture and four-porate pollen grains. *Chamaelirium* from the eastern United States has the same pollen. This type of grain and exine structure are unique in the Melanthiaceae, and suggest that *Chamaelirium* and *Chionographis* are closely related to each other as an isolated group in the Melanthiaceae. The pollen morphology supports the treatment of Dahlgren et al. (1985), who distinguished the tribe Chionographideae as made up of *Chionographis* and *Chamaelirium*.

Japonolirion, which consists of only the Japanese endemic *J. ozense*, is sometimes included in *Tofieldia* (Willis, 1966; Hutchinson, 1934, 1959). The pollen grains of *Japonolirion* are monosulcate with gemmate exines, as opposed to those of *Tofieldia*, which are disulcate with reticulate exines. The pollen morphology of *Japonolirion* implies that the genus should not be included in *Tofieldia* but should be treated as a separate genus. The report of gemmate exine of *Tofieldia okuboi* (Ikuse, 1956) appears to be incorrect, as we have found reticulate exine in this species, conforming to other species of *Tofieldia*.

There is a wide range of variation in exine sculpture, perforate-foveolate, reticulate, and gemmate types in the genus *Aletris*. The species with gemmate exine are *A. lanuginosa* and *A. pauciflora*, which are distributed in China and Nepal. The other species of *Aletris* have reticulate exines. Similar variation in exine sculpture occurs in *Clintonia* (Takahashi & Sohma, 1982) and *Paris* (Takahashi, 1984). A parallel derivation from tectate-perforate to intectate exine appears to have taken place independently within these genera (Takahashi, 1984).

Ambrose (1985) transferred the genus *Lophiola* into the Narthecieae. The exine sculpture of the genus has a reticulum similar to that of genera in the Narthecieae; thus the palynological evidence supports Ambrose's taxonomic position of *Lophiola*. All the evidence available at present suggests that Heloniadeae and Narthecieae sensu Hutchinson (1959) consist of at least three or four heterogenous groups, and therefore the revision of the classificatory system of these groups is now in order.

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A NEW SUBGENUS AND FIVE NEW SPECIES IN *PASSIFLORA* (PASSIFLORACEAE) FROM SOUTH AMERICA[1]

Linda K. Escobar[2]

ABSTRACT

Five new species of *Passiflora* (Passifloraceae) are described: *Passiflora solomonii* from Bolivia; *P. caatingae* from Bahia, Brazil; *P. sierrae* from the Sierra Nevada de Santa Marta of northeastern Colombia, and *P. amazonica* and *P. pascoënsis* from Peru. *Passiflora sierrae* is placed in a new subgenus *Porphyropathanthus*. All are lianas or herbaceous climbers with axillary tendrils and simple leaves, found on roadsides or in recent clearings.

Passiflora amazonica L. Escobar, sp. nov. TYPE: Peru. Amazonas: Bongara Prov., km 385–365 Moyobamba Bagua road (77°45′W, 5°45′S), 2,000 1,800 m, 17 Feb. 1984, *D. N. Smith 6012* (holotype, MO). Figure 1.

In subg. *Tacsonia* juxta *P. mixtam* Linn. f. collocanda, ab hac foliis rugosis rigide coriaceis margine grosse dentatis diversa.

Liana. Plants pubescent with straight to curling yellowish, transparent trichomes 0.2 1.0 mm long. Stems subangular, striate. Leaf blades 3-lobed to ca. ½ their length, widely depressed ovate in outline, (8.5 -)11–11.7 cm long, (9.0–)14–15.2 cm wide, acute at lobe apices, deeply cordate at base, coarsely dentate at margins, stiff-coriaceous, rugose, scarcely pubescent (mostly on veins) on adaxial surface, densely pubescent on abaxial surface with curved trichomes ca. 0.5 mm long; leaf lobes ovate, lateral ones (6.0–)7.2–8.2 cm long, (3.6–)4.2–5.6 cm wide, divergent from mid-lobe ca. 75°, this (7.3–)9.3–9.7 cm long, (4.2)5.4–5.8 cm wide; petioles 2.3 2.6 cm long, with up to 10 elongated nectaries ca. 1 mm long scattered along adaxial surface; stipules auricular, ca. 1.5 cm long, ca. 0.7 cm wide, acuminate with arista 4.6 mm long at apex, lacerate at margins. Peduncles solitary, 5–6 cm long; bracts 3, connate ca. ¼ their length, forming a closely fitting tube around base of hypanthium, each bract lanceolate, 3–4 cm long, ca. 1.4 cm wide, acuminate at apex, densely pubescent with tightly curled trichomes on inner surface, moderately pubescent with slightly curved trichomes on outer surface; flower stipe ca. 4 mm long. Flowers salverform, 9.5–10.5 cm long, ca. 6.5 cm diam. at apex, probably pendent; hypanthium cylindrical, ca. 6.5 cm long, 1.0 1.2 cm wide (pressed), densely pubescent on outer surface with straight to slightly curved trichomes up to 1 mm long; sepals ovate-oblong, 4.0–4.3 cm long, 1.2–1.8 cm wide, acute at apex with subapical arista ca. 1 mm long, coriaceous, pink; petals subequal to sepals, up to 1.5 cm wide, rounded at apex, membranaceous, pink; corona reduced to an undulate, irregularly toothed band; operculum dependent, nonplicate; ovary pubescent with straight trichomes ca. 0.5 mm long. Fruit unknown.

Distribution. *Passiflora amazonica* is known only from montane forest at 1,800–2,000 m elevation in Amazonas Department in northern Peru.

Additional collections examined. PERU. AMAZONAS: Bongara. 40 43 km E of Pomacocha, near La Cumbre, km 376 of Carretera Marginal, 5°45′S, 77°45′W, 13 June 1986, *S. Knapp & P. Alcorn 7740* (MO).

Passiflora amazonica is placed in subg. *Tacsonia* near *P. mixta* L. f., a widespread Andean species (Escobar, 1980; Killip, 1938) from which it differs by the stiff-coriaceous, rugose leaves with coarsely dentate margins.

[1] The present study was initiated in November 1987 while on a leave of absence, and completed in 1988 while on a sabbatical leave supported by the University of Antioquia. I am grateful to the curators of the herbaria of the Missouri Botanical Garden, The New York Botanical Garden, and the Smithsonian Institution for help and use of the facilities during my stay at their institutions. Special thanks are due Dr. Rupert Barneby, who reviewed the manuscript and provided the Latin diagnoses, and to Dr. John MacDougal for criticism of the manuscript.

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№ 3433072

FIGURE 1. Holotype of *Passiflora amazonica* L. Escobar, deposited in the herbarium of the Missouri Botanical Garden (MO).

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HERBARIUM

№ 3110137

FIGURE 2. Holotype of *Passiflora caatingae* L. Escobar, deposited in the herbarium of the Missouri Botanical Garden (MO).

Passiflora caatingae L. Escobar, sp. nov. TYPE: Brazil. Bahia: 27 km NE of Cândido Sales, along Highway BR-116, caatinga, 890 m, 30 Mar. 1976, *G. Davidse, T. P. Ramamoorthy & D. M. Vital 11635A* (holotype, MO). Figure 2.

Subgeneris *Tacsonioidi* referenda, *P. mendoncae* Harms proxime accedens, sed ab hac stipulis lineari-lanceolatis bracteisque minoribus diversa.

Liana. Plants glabrous with terete, striate stems. Leaf blades 3-lobed to ca. ¾ their length, depressed ovate in outline, 3.6–6.9 cm long, 6.4–11.2 cm wide, acuminate at lobe apices, cordate at base, shallowly serrate at margins (glandular in sinuses of serrations on very young leaves), coriaceous, lustrous, yellow-green; leaf lobes elliptic to oblong, lateral lobes 3.8–5.5 cm long, 1.5–2.2 cm wide, divergent from mid-lobe ca. 85°, mid-lobes 4.0–6.8 cm long, 1.6–2.8 cm wide; petioles 0.9–2.4 cm long, with 2–4, paired, scarlike nectaries at or below mid-point on adaxial surface; stipules linear-lanceolate, soon deciduous, ca. 1 mm long, ca. 0.2 mm wide at base. Peduncles solitary, 2.0–2.5 cm long; bracts 3, free to base, verticillate, ovate, 1.0–1.5 cm long, 0.8–1.0 cm wide, borne 0.5–1.1 cm below base of hypanthium, acuminate at apex, with arista ca. 0.5 mm long, narrowed at base, minutely serrate at margins; flower stipe 0.5–1.1 cm long. Flowers salverform 3.2–5.0 cm long, ca. 4 cm diam. at apex; hypanthium slightly funnel-shaped, 1.3–1.5 cm long, ca. 9 mm wide at apex, ca. 6 mm wide at base then inflated, with inflated portion 5 mm long, 1 cm wide; sepals oblong, 2.6–3.3 cm long, ca. 7 mm wide, with keel 2 3 mm wide on abaxial surface, subcoriaceous, red-purple; petals oblong, ca. 3.1 cm long, ca. 0.7 cm wide, rounded at apex, membranaceous, red-purple; corona in 2 series ca. 2 mm apart, filamentous, with inner series ca. 5 mm long, outer series ca. 2–3 mm long; operculum erect, nonplicate, ca. 4 mm long, lacerate at margin, transparent. Immature fruit ellipsoidal, 3.9–4.4 cm long, 2.0 2.9 cm wide (pressed).

Distribution. *Passiflora caatingae* is known only from two collections near Cândido Sales in the state of Bahia in eastern Brazil. It was collected along the highway in caatinga vegetation at 890 m elevation.

Additional collections examined. BRAZIL. BAHIA: along highway BR-116, caatinga, 890 m, 30 Mar. 1976, *G. Davidse, T. P. Ramamoorthy & D. M. Vital 11625* (MO).

Passiflora caatingae is placed in subg. *Tacsonioides*, where it most closely resembles *Passiflora mendoncae* Harms (Killip, 1938) but from which it differs by the linear-lanceolate stipules and smaller bracts. The bracts resemble those of *P. racemosa* Brot. of the monotypic subg. *Calopathanthus*, but this species possesses flowers with a folded operculum and strongly keeled sepals.

Passiflora pascoënsis L. Escobar, sp. nov. TYPE: Peru. Pasco: Oxapampa, Cordillera Yanachaga, 12 km E of main Oxapampa–Villa Rica road, remnant cloud forest, 2,100–2,200 m, 10°35′S, 75°15′W, 2 Mar. 1982, *A. Gentry & S. Smith 35939* (holotype, MO). Figure 3.

Subgeneris *Plectostemmatis* sect. *Decalobae* referenda, foliorum ambitu et coronae filamentorium exteriorum forma *P. alnifoliam* et arcte affines simulans, sed floribus et fructibus magnis necnon foliis inferne crasse reticulatis diversa.

Herbaceous vine. Plants pubescent, with irregular, curved to wavy, white to yellowish transparent trichomes 0.1–0.4 mm long. Stems 3-angular, striate. Leaf blades entire, ovate to elliptic, (5.3–)9.5–14.8 cm long, (3.8–)6.5–8.6 cm wide, 2–3-lobed at apex, shallowly cordate to rounded at base, entire at margins; leaf lobes subdeltate, lateral lobes 0.8–1.5 cm long, 0.7–1.3 cm wide, mid-lobes (lacking on some leaves) 0.2–0.4 cm long, 1.7–3.0 cm wide, mostly glabrous adaxially, pubescent on abaxial surface, with expanded fine veins forming an incrassate reticulum, slightly coriaceous; laminar nectaries variable in number, 5–ca. 40, mostly concentrated at base and between major lateral veins in upper ½ of abaxial surface; petioles 1.0–2.5 cm long, eglandular; stipules falcate, 0.5 1.0 cm long, ca. 0.5 mm wide. Peduncles paired, 2.0–2.5 cm long; bracts setaceous, scattered on upper ½ of peduncle, 0.4–0.6 cm long, 0.5 mm wide; flower stipe ca. 3 mm long. Flowers widely campanulate, 7–8 cm diam., pendent; hypanthium patelliform, ca. 0.4 cm long, 1.8–2.0 cm wide; sepals ovate, 2.7–3.0 cm long, 1.8–2.0 cm wide, obtuse at apex, coriaceous, greenish white; petals subequal to sepals, membranaceous, pinkish or white edged with pink; corona in 2 series, filamentous, cream-white banded with red-purple, the inner filaments 0.3–0.7 mm long, 0.5–0.8 mm wide and outer ones ca. 1.5 cm long, ca. 2 mm wide, dilated at apex; operculum closely plicate, erect, ca. 6 mm long, minutely crenulate at margin; ovary glabrous. Fruit ellipsoid, 2.5–3.0 cm long, 2.3–2.6 cm wide (pressed), yellow; seeds obovoid, ca. 3.5 mm long, ca. 2.0 mm wide, with ca. 7 rugulose transverse ridges, dark brown at maturity.

FIGURE 3. Holotype of *Passiflora pascoënsis* L. Escobar, deposited in the herbarium of the Missouri Botanical Garden (MO).

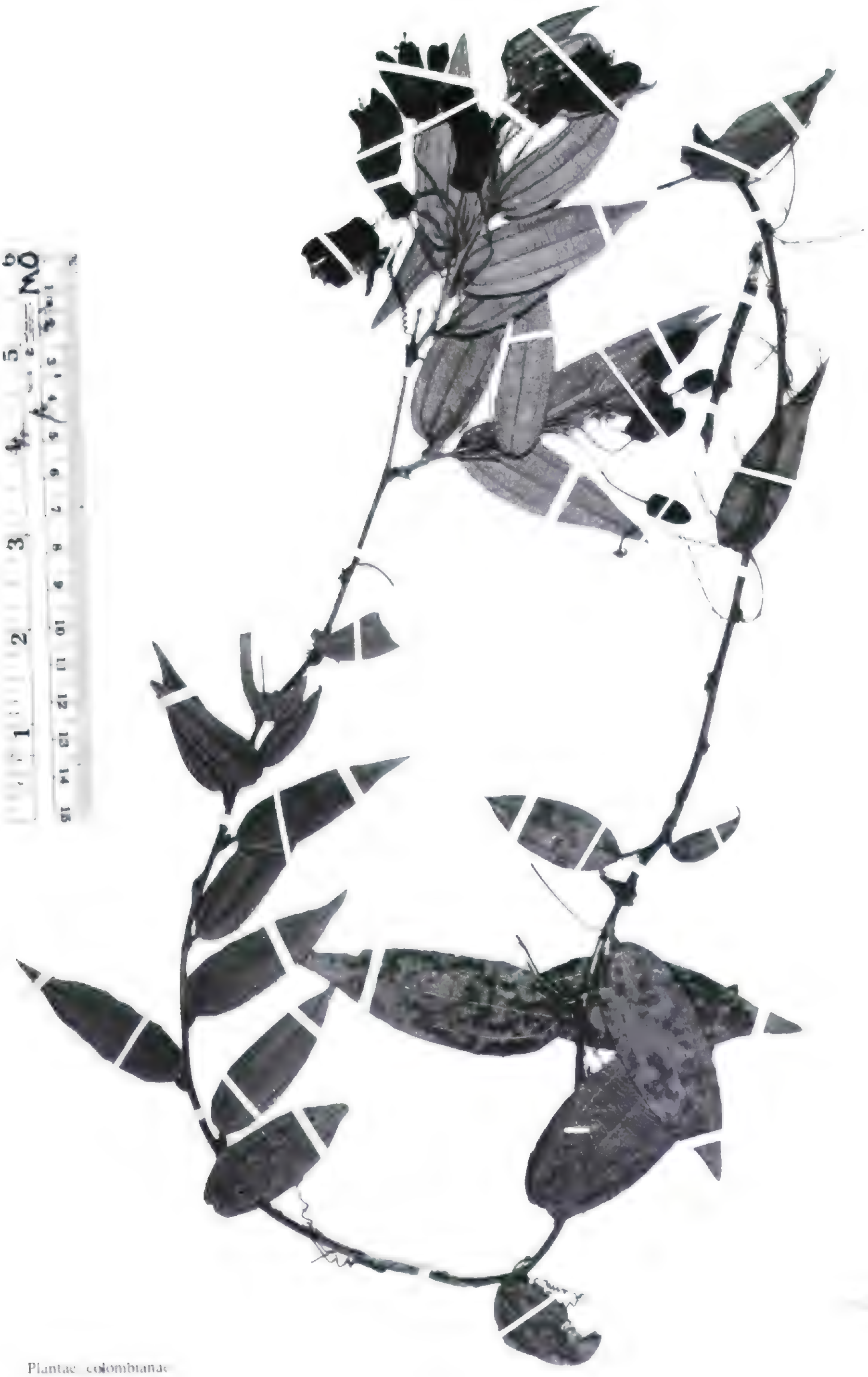

FIGURE 4. Holotype of *Passiflora sierrae* L. Escobar, deposited in the herbarium of the Smithsonian Institution (US).

FIGURE 5. Holotype of *Passiflora solomonii* L. Escobar, deposited in the herbarium of the Missouri Botanical Garden (MO).

Distribution. *Passiflora pascoënsis* is found on the borders of disturbed cloud forest at elevations of 1,850–2,500 m in the Department of Pasco, Peru.

Additional collections examined. PERU. PASCO: Oxapampa, Cordillera Yanachaga, new road in construction from Oxapampa to Villa-Rica, 7–9 km E of main road, 2,100–2,500 m, montane cloud forest, 10°45′S, 75°20′W, 1 Mar. 1982, *A. Gentry & D. Smith 35857* (MO); Valle de San Alberto, E of Oxapampa, above hydroelectric plant, at base of Cordillera Yanachaga; roadside forest remnants, 1,900 m, 1 Jan. 1984, *R. Foster, M. Chanco & J. Alban 7714* (HUA, MO); pastures in vicinity of Oxapampa, ca. 2 km E of the village, secondary growth, 1,850 m, 10°35′S, 75°35′W, 10 Mar. 1984, *S. Knapp, J. Mallet & W. Brack 6319* (MO, NY, US).

This beautiful, large-flowered species is placed in subg. *Plectostemma* sect. *Decaloba* (Killip, 1938), where it resembles members of the *Passiflora alnifolia* complex in leaf shape and form of the outer coronal filaments. It is easily distinguished from those species by the large flowers and fruits and by the incrassate reticulum formed by expansion of the fine veins of the lower leaf surface.

Passiflora subg. **Porphyropathanthus** L. Escobar, subgen. nov. TYPE. *Passiflora sierrae* L. Escobar.

Nectariis petiolaribus, operculo haud plicato necnon *Passiflora lancifoliae* subgen. *Chloropathantho* similis, sed cum eo petalis manifestis 1.3–1.8 cm longis, seminibus transverse rugulosis et nectariis in foliorum lamina sitis incongruum.

Passiflora sierrae L. Escobar, sp. nov. TYPE: Colombia. Magdalena: Sierra Nevada de Santa Marta, southeastern slopes, hoya del Río Donachuí, near Col, 3,100–3,070 m, 9 Oct. 1959, *J. Cuatrecasas & R. Romero-Castañeda 24675* (holotype, US; isotype, COL). Figure 4.

Iisdem notulis jam sub subg. *Porphyropathantho* indicatis unica.

Herbaceous vine. Plants pubescent, with straight to wavy, reddish trichomes ca. 0.5 mm long. Stems angulate, striate. Leaf lobes entire, ovate to lanceolate, (3.8–)4.3–9.0 cm long, (1.4–)2.4–4.5 cm wide, acuminate and mucronate at apex, rounded at base, entire at margins, stiff-coriaceous, lustrous on adaxial surface, yellow-green, pubescent on veins on both surfaces; laminar nectaries 0–3, scarcely visible between major veins of abaxial surface; petioles 3–6 mm long, with 1 pair of stipitate, cup-shaped nectaries ca. 1 mm diam. at apex; stipules linear-lanceolate, ca. 5 mm long, reddish. Peduncles paired, 1.5–2.0 cm long; bracts 3, scattered on upper ½ of peduncle, linear-lanceolate, 1.5 2.0 mm long, ca. 0.3 mm wide; flower stipe 1.6-2.2 cm long. Flowers campanulate, 1.7–2.0 cm long, 3.5–4.0 cm diam., pendent, red-purple; hypanthium patelliform, 3 4 mm long, 0.5–1.0 cm wide; sepals oblong, 1.7–2.0 cm long, 2–6 mm wide, obtuse at apex, subcoriaceous, pubescent on abaxial surface; petals oblong, 1.3–1.8 cm long, 1.3–3.5 mm wide, rounded at apex, delicately membranaceous, pink to light purple; corona in 1 series, filamentous, ca. 1.5 mm long, but irregular, each filament ca. 0.1 mm wide; operculum erect, ca. 2 mm long, nonplicate, crenate at margin; ovary ellipsoid, glabrous, light green. Fruits globose, ca. 1.5 cm long, 1.3 cm wide (pressed); seeds obovoid, ca. 6.0 mm long, ca. 3.1 mm wide, with ca. 13 rows of transverse rugulose ridges.

Distribution. This species is known only from subpáramo vegetation in the Sierra Nevada de Santa Marta in northeastern Colombia, where it is found in dense shrubby growth above 3,000 m elevation.

Additional collections examined. COLOMBIA. MAGDALENA: Sierra Nevada de Santa Marta, entre San Pedro y cabeceras del Río Sevilla, ca. 3,195 m, 31 Jan. 1959, *H. Barclay & P. Juajibioy 6783* (COL, MO); Transecto del Alto Buriticá, cuchilla y cerros a 3,300 m, lev. 33, 9 Aug. 1977, *R. Jaramillo M., T. van der Hammen, M. A. Cleef & O. Rangel 5472* (COL).

The presence of petiolar nectaries and purple flowers with a nonplicate operculum, suggests a relationship to *P. lancifolia* Desv., of subg. *Chloropathanthus* (Harms, 1925; Killip, 1938), which is known only from Jamaica. Unlike that species and others of subg. *Chloropathanthus*, *P. sierrae* has well-developed petals, poorly developed laminar foliar nectaries, and seeds with transverse rugulose ridges. This unique combination of characters requires the creation of a new subgenus. Data from pollen studies (Presting, 1965; Spirlet, 1965; Escobar, unpubl.) suggest that several purple- or red-flowered species (usually with a tubular hypanthium and therefore presumably hummingbird-pollinated) have arisen independently from the large and variable subg. *Plectostemma*. They do not suggest that all species with the hummingbird-pollinated syndrome are monophyletic.

Passiflora solomonii L. Escobar, sp. nov. TYPE: BOLIVIA. LA PAZ: Prov. Nor Yungas, 9.1 km NE (below) Chuspipata on road to Yolosa, 2,400 m, 16°16′S, 67°47′W, 29 Oct. 1984,

J. C. Solomon & M. Nee 12592 (holotype, MO; isotype, HUA). Figure 5.

Foliorum forma, nisi ambitu transverse lineari (nec ovato), *P.* (subg. *Plectostemma*) *exoperculatam* Mast. referens, sed haec a nostra pedunculis longioribus, foliorum lobis brevioribus, nectariis petiolaribus prominulis necnon coronae filamentis capitellatis differt.

Herbaceous vine. Plants sparsely pubescent with wavy, transparent trichomes ca. 0.1 mm long. Stems angulate, striate. Leaf blades transversely linear, coriaceous, sparsely pubescent on abaxial surface, dull yellowish green, 2-lobed, the lobes divergent by ca. 90° from mid-vein, each 1.1–1.5 cm long, 7.1–10.0 cm wide, acuminate and mucronate at apex, shallowly cordate at base, entire at margins; petioles 4–9 mm long, eglandular; stipules linear-lanceolate, ca. 2.5 mm long, ca. 0.2 mm wide. Peduncles paired, 6–12 mm long, very slender; bracts 3, setaceous, ca. 2 mm long, drying black, scattered along peduncle; flower stipe ca. 1 mm long. Flowers campanulate, 2 3 cm diam., pendent, greenish white; hypanthium patelliform, 2.5–3.0 mm long, ca. 3.5 mm wide; sepals triangular, 8–12 mm long, ca. 10 mm wide at base, acute at apex; petals lanceolate, 11 12 mm long, 3–6 mm wide, delicately membranaceous, greenish white; corona in 2 series, the outer series linear, 7–8 mm long, ca. 1 mm wide, the inner filaments ca. 3 mm long, 0.2 mm wide, operculum dependent then recurved, loosely plicate; ovary globose, pubescent. Fruits unknown.

Distribution. *Passiflora solomonii* is known only from the type locality in La Paz Department of Bolivia at 2,400 m elevation.

The unusual leaf shape of *Passiflora solomonii* is reminiscent of *P. exoperculata* of subg. *Plectostemma* but is transversely linear rather than transversely ovate; *P. exoperculata* also differs from *P. solomonii* in possessing prominent petiolar nectaries and capitellate inner coronal filaments as well as longer peduncles and shorter leaf lobes.

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A REVISION OF MESOAMERICAN *PSYCHOTRIA* SUBGENUS *PSYCHOTRIA* (RUBIACEAE), PART III: SPECIES 48–61 AND APPENDICES[1]

Clement W. Hamilton[2]

Group 7. The *tenuifolia* Group

Shrub or small tree; young stems glabrous or puberulent; stipules often sheathing, ovate to triangular with apex long-biacuminate in *P. tenuifolia* (Fig. 2e), uniform in color, glabrous or puberulent, caducous. *Leaf* blades elliptic (to sometimes slightly ovate in *P. limonensis*), drying green-brown or red-brown; secondary veins 8–21(–24) pairs, *diverging (60°–) 70°–90°(–95°), brochidodromous with collector vein near margin*, the axils lacking domatia or hairs; tertiary veins orthogonal reticulate (to sometimes percurrent in *P. limonensis*). *Inflorescences umbelliform panicles of cymes* (Fig. 7f), the peduncle lacking or no more than 2 cm long; *secondary axes in one pair per rank*; *bracts not conspicuously enlarged. Corolla tubes 1.5–2 mm long, the lobes without apical extensions. Fruit* when dry ellipsoid; *persistent calyx inconspicuous or a beak*; seed dorsal surface with 4–5 longitudinal furrows (often irregular in *P. limonensis*), the ventral surface with 2 longitudinal furrows (often incompletely divided in *P. limonensis*).

The two species in the group, *Psychotria limonensis* and *P. tenuifolia*, are both widespread throughout Mesoamerica (Figs. 32, 33) and often occur together in lowland forest.

Both species appear to be normally distylous with no between-morph asymmetry in floral part lengths.

48. Psychotria limonensis K. Krause, Bot. Jahrb. Syst. 54, Beibl. 119: 43. 1916. TYPE: Costa Rica. Limón: Puerto Limón, July 1898 (fr), *Pittier 12681* (holotype, B, destroyed, fragment, F, photo, F neg. no. 518; isotypes, K, US). Figures 7f, 32.

Psychotria limonensis K. Krause var. *laxinervia* Loesener, Repert. Spec. Nov. Regni Veg. 18: 361. 1922. TYPE: Mexico. Chiapas: Ruinas del Palenque, 10 Mar. 1911 (fr), *C. Seler & E. Seler 5463* (holotype, B, destroyed, fragment, F, photo, US; isotype, GH).

Shrub to small tree 0.5–3(5) m tall; young stems glabrous or sparsely puberulent, the bark smooth; stipules sheathing, rounded-ovate to triangular, 6–9 × 5–10 mm, glabrous, caducous, leaving a pale or red-brown ridge with red-brown fringe. *Leaves* petiolate; petioles 2.5–6 cm long, glabrous, flat or channeled above; blades membranous to chartaceous, elliptic to slightly ovate, the apex acuminate, the base narrowly cuneate to attenuate, (12–)17–29 × (6–)7.5–15 cm, glabrous above and below, drying red-brown to green-brown; secondary veins (10)15–21(–24) pairs, diverging (60°–)70°–90°(95°), brochidodromous with collector vein undulating near margin, straight or slightly arcuate, prominulous below, glabrous, the axils lacking domatia or hairs; tertiary veins inconspicuous to evident, orthogonal reticulate to percurrent. *Inflorescences* terminal or pseudoaxillary, umbelliform panicles of cymes (Fig. 7f); panicle branched to 4–5 degrees; main axis 1.5–5.5 cm long, the peduncle usually lacking or to 2 cm long; secondary axes in (4–)5–6 ranks, the first-rank axes 2, 1.5–5.5 cm long, the second-rank axes 2, 1–3 cm long, the third-rank axes 2, 0.6–2 cm long, the fourth-rank axes 2, 0.3–1 cm long, the fifth-rank axes 2, 0.3–0.5 cm long, the sixth-rank axes 2, 0.1–0.2 cm long; cymes branched to 1–2 degrees; bracts and bracteoles acute-triangular, 0.5–1.2 mm long, minutely ciliate. *Flowers* pedicellate, the pedicels 0.5–1 mm long; calyx cup-shaped, the tube 0.2 mm long, the lobes (4–)5, triangular, to 0.5 mm long, glabrous or puberulent; corolla white, the tube cylindrical, 1.5–2 × 1–1.5

[1] Part I: Introduction and Species 1–16, and Part II: Species 17–47 appeared in the preceding two issues of the *Annals of the Missouri Botanical Garden*, Volume 76: 67–111, 386–429.

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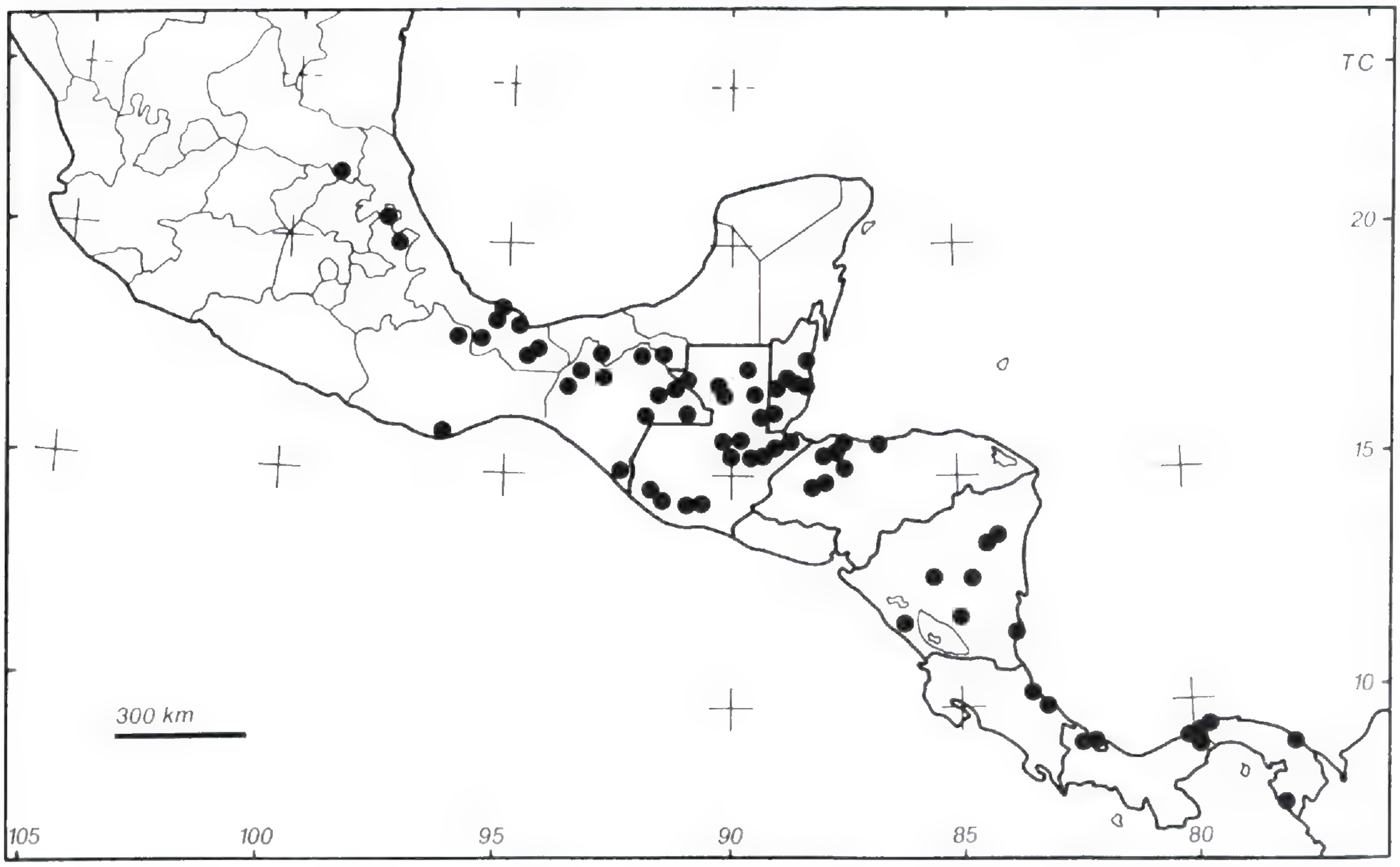

FIGURE 32. Distribution of *Psychotria limonensis* in Mesoamerica.

mm, white pubescent in throat, the lobes (4)5, lanceolate, 1.5–2 × 0.8 mm; stamens (4)5, the filaments 1.5–2 mm long in pins, 3–3.5 mm long in thrums, the anthers 0.7–0.8 mm long; style 3–3.5 mm long in pins, 2.2 mm long in thrums, the branches linear. *Fruit* when dry ellipsoid, (3.5–)4(–4.5) mm long, (3–)3.5(–4) mm diam., maturing red, drying dark red-brown; persistent calyx inconspicuous or a beak to 0.3 mm long; seed dorsal surface with 4–5 deep often irregular longitudinal furrows, the ventral surface with 2 often incompletely divided longitudinal furrows.

Distribution (Fig. 32). Common from Mexico through Panama, especially southern Mexico to western Honduras. The species occurs at elevations of 0–1,700 m, most frequently at 700 m and below, and in tropical moist to wet to sometimes premontane wet forest with equatorial to tropical (usually equatorial-tropical) climate. *Psychotria limonensis* has been collected in flower throughout the year—it appears to flower throughout the year in Panama but just primarily May–August in the rest of its range. Fruits form throughout the year, primarily August–April.

Selected specimens examined. MEXICO. CHIAPAS: Mpio. Rayón, Selva Negra 10 km above Rayón Mezcalapa along rd. to Jitotol, 1,700 m, 13 July 1972 (fl), *Breedlove 26139* (MEXU); Mpio. Palenque, 6–12 km S of Palenque on rd. to Ocosingo, 300 m, 27 July 1972 (fl), *Breedlove 26522* (MEXU, MO); Mpio. Huixtla, 6–8 km NE of Huixtla along rd. to Motozintla, 200 m, 6 Oct. 1972 (fr), *Breedlove 28501* (MEXU, MO); Mpio. La Independencia, valley of Sta. Elena along rd. to Ixcan, 30 km E of paved rd. at Montebello, 800 m, 29 Nov. 1976 (fr), *Breedlove 41971* (MEXU); Mpio. Ocosingo, adjacent to Laguna Ocotal Grande, 800 m, 27 Nov. 1972 (fr), *Breedlove & Dressler 29855* (MEXU, MO, NY); Mpio. Ocozocoautla de Espinosa, 18–20 km N of Ocozocoautla along rd. to Mal Paso, 800 m, 20 Oct. 1971 (fr), *Breedlove & Thorne 20976* (MEXU, MO); NE of Chapultenango, 410 m, 2 Aug. 1965 (early fr), *Chavelas 1947* (ENCB, MEXU); along gravel rd. between Palenque and Bonampak, 88–90 mi. SW of Palenque, 350–370 m, 5 July 1977 (fl), *Croat 40211* (MO); Río Lacantum 2 km por arriba de la unión con el Río Chajul, 16°05′N, 90°57′W, 19 Apr. 1976 (fr), *Shapiro & Elliott 437* (MEXU). OAXACA: Dto. Pochutla, Cafetal Concordia, 700 m, 14 Apr. 1917 (fl), *Conzatti et al. 3061* (GH, MEXU); Tuxtepec, camino al Naranjal, 12 Sep. 1947 (fr), *Miranda 4208* (MEXU—2 sheets). PUEBLA: Mpio. Hueytamalco, Rancho Las Margaritas, 17 Aug. 1975 (fr), *López-Forment 7* (MEXU); km 247 de la carret. México–Tuxpan, 27 Feb. 1962 (fr), *Sarukhán et al. s.n.* (MEXU). SAN LUIS POTOSÍ: Huichihuayán, km 402 de la carret. México–Nuevo Laredo, 250 m, 30 Oct. 1966 (fr), *R. Cruz C. 1448* (ENCB). TABASCO: Cerro las Campanas 3 km E of Teapa, 50–100 m, 12 Aug. 1974 (fr), *J. Conrad et al. 2890* (MO); Tenosique, Retiro, 19–25 June 1939 (fl), *Matuda 3437* (A, F, K, MO, NY). VERACRUZ: Mpio. San Andres Tuxtla, Laguna Tisatal 3 km al NE Tapalapan, 400 m, 19 June 1972 (fl), *Beaman 6205* (F, MEXU); Mpio. Playa Vicente, 30 Sep. 1971 (fr), *Chavelas et al. ES-1125* (MEXU); camino Montepio a Catemaco, 12 km

de Catemaco, 350 m, 6 July 1977 (fl), *Fay & C. Hernández 826* (F, NY, US); km 156–7 carret. Veracruz Coatzacoalcos, 27 Feb. 1960 (st), *González L. & Garza 604* (MEXU); Mpio. Hidalgotitlán, brecha Hermanos Cedillo–La Escuadra, 150 m, 26 Aug. 1977 (fl), *Márquez 346* (ENCB); Estación de Biología Los Tuxtlas, Sep. 1978 (fr), *Torquebiau 1012* (MEXU); Mpio. Minatitlán, 6.9 km al N de la terraceria La Laguna–Río Grande, 17°20′N, 94°22′W, 130 m, 13 July 1980 (fl), *Wendt & Villalobos 2560* (ENCB, MEXU). GUATEMALA. ALTA VERAPAZ: Semococh, 16 km from Sebol on Cobán rd., 14 May 1964 (fl), *Contreras 4679* (MEXU); 8 km W of Tucurú, 600 m, 18 July 1977 (fl), *Croat 41510* (MO); 6 km NE of Panzós, 500 m, 20 July 1977 (fl), *Croat 41594* (MO); Cubilgüitz, 350 m, July 1903 (fl), *Tuerkheim 8404* (US 2 sheets). ESCUINTLA: Torolá, 300 m, Mar. 1890 (fl), *Donnell-Smith 2042* (F, GH, US – 2 sheets); between Río Jute and Río Pantaleón, on rd. between Escuintla and Sta. Lucía Cotz, 540–720 m, 24 Jan. 1939 (fl), *Standley 63617* (A, NY); wooded barranco of Río Gavilan, NE of Escuintla, 720 m, 16 Mar. 1941 (fl), *Standley 89562* (F—2 sheets). IZABAL: El Estor, bordering Río Sarco, 24 May 1975 (fl), *Lundell & Contreras 19352a* (LL); between Escobas and Montaña Escobas, across bay from Puerto Barrios, 1–100 m, 13 Apr. 1940 (fl), *Steyermark 39302* (F); along Río Frío and tributaries, 75–150 m, 18 Dec. 1941 (fr), *Steyermark 41570* (NY, US). PETÉN: Uaxactún, 19 Mar. 1931 (fr), *Bartlett 12205* (F, NY); Lacandón, 3 km NW on Tenosique trail, 14 Feb. 1962 (fr), *Contreras 3385* (F, NY); La Libertad–Flores rd., 12 June 1933 (fl), *Lundell 4226* (F); Yaltutú entre Cristo Rey y Poptún, 433 m, 11 Nov. 1965 (fr), *A. Molina R. 15566* (F—2 sheets, NY); San Pedro, en orillando el camino para Cadenas a km 165, lado N saliente, 15 Dec. 1970 (fr), *Ortíz 1509* (ENCB, F, MO, NY); en orillando el camino para Santo Toribio, km 70, lado NE de Dolores, 17 Feb. 1971 (fr), *Ortíz 1595* (F, US); forest between Finca Yalpemech along Río San Diego and San Diego on Río Cancuen, 50–150 m, 25 Mar. 1942 (fr), *Steyermark 45393* (US). RETALHULEU: sin loc., May 1877 (fl), *Bernoulli & Cario 1717* (K). SUCHITEPÉQUEZ: vic. Tiquisate, 100 m, 17 June 1942 (fl), *Steyermark 47654* (A, F). BELIZE. BELIZE: between Belize River bridge and Belize sawmill on Northern Hwy., 20 June 1973 (fl), *Dwyer 11313* (F, MO—2 sheets). CAYO: Hummingbird Hwy., mi. 25 S of Belmopan, 22 Jan. 1974 (fr), *Dwyer & Liesner 12085* (F, GH, MO, NY); Valentin, limestone valley, June–July 1936 (fl), *Lundell 6250* (F, GH, NY, US). STANN CREEK: Mullins River Stann Creek rd., 14 Aug. 1940 (fr), *Gentle 3374* (A); Middlesex, 60 m, 14 July 1929 (fl), *Schipp 242* (A, F, GH, K, MO, NY, US). TOLEDO: San José, 11 km N of Columbia Forest Station, 13 June 1973 (fl), *Dwyer 11186* (DUKE, MO). HONDURAS. ATLANTIDA: Lancetilla, S of Tela, 20–50 m, 25 June 1970 (fl), *Davidse & Pohl 2183* (F, MO); base of hills S of San Alejo nr. Río San Alejo, 150–270 m, 22–27 Apr. 1947 (bud), *Standley 7674* (F); hills above Lancetilla, 450 m, 15 July 1934 (fl), *Yuncker 4591* (A, F, MO); vic. La Ceiba, lower slopes of Mt. Cangrejal, 16 July 1938 (early fr), *Yuncker et al. 8467* (F, GH, K, MO, NY, US). CORTÉS: matorrales de Río Lindo, 1 km de Canaverales, 600 m, 25–26 Aug. 1955 (early fr), *A. Molina R. 5519* (F); San Pedro Sula, 300 m, June 1887 (fl), *Thieme 5274* (F, US); NE shore of Lake Yojoa, 630 m, 30 Dec. 1952 (fr), *L. O. Williams & R. P. Williams 18750* (F, GH, US). SANTA BARBARA: alrededores de El Mochito, 22–25 July 1976 (fl), *Vargas 695* (TEFH). YORO: Subirana, 930 m, Oct. 1937 (early fr), *Hagen & Hagen 1103* (F, NY). NICARAGUA. CHONTALES: 4 km al NW de Sto. Domingo, 12°17′N, 85°06′W, 280 m, 12–13 May 1984 (fl), *Grijalva 3822* (MO). MANAGUA: Sierras de Managua, Hda. El Encanto, 920 m, 1981 (fl), *A. López 5* (HNMN). MATAGALPA: summit of Matagalpa Tuma rd., 9 km E of Hwy. 3 intersection, 12°57′N, 85°51′W, 1,000 m, 24 May 1981 (fl), *W. D. Stevens & Henrich 20335* (MO). ZELAYA: Guamil o breñas sobre areas pantanosas a lo largo del Río Grande, 0–15 m, 23 Apr. 1949 (fl), *A. Molina R. 2317* (F, GH); 1.5 km al N de Monkey Point, 11°36′N, 83°39′W, 5–10 m, 27 Oct. 1981 (fr), *P. P. Moreno & Sandino 12609* (MO); 10 km NE of Siuna gallery forest along Caño Madriguera, 250 m, 1 May 1978 (fl), *Neill 3726* (MO); nr. Río Okanwas, 12 km E of Rosita, 15 June 1978 (fl), *Neill 4465* (MO). COSTA RICA. LIMÓN: Port Limón, 0 m, 1 May 1903 (fl), *Cook & Doyle 440* (US); Isla Uvita, 13 Oct. 1941 (fl), *Echeverría 46* (F); 1 mi. toward Zent from Moin Junction, 30 m, 1 Sep. 1946 (fr), *Morley 819* (F); entre Barra Parismina y Río Chiquero, 9 Oct. 1951 (fr), *Shank & Molina 4354* (F, GH, US). PANAMA. BOCAS DEL TORO: Changuinola to 5 mi. S at junction of ríos Changuinola and Terebe, 30–60 m, 17–19 Dec. 1966 (fl, fr), *Lewis et al. 822* (GH, MO, US); Old Bank Island, 21 Feb. 1941 (fl), *Wedel 2137* (F, GH, MO). CANAL AREA: Coco Solo, Tropic Test Center study site, 27 Mar. 1972 (fl), *Gentry & Tyson 4848* (MO, NY); Barro Colorado Island, 17 June 1970 (fr), *Luteyn 760* (DUKE, NY); 20 Nov. 1931 (fl), *Shattuck 416* (F, MO); nr. old Fort San Lorenzo, 8 Mar. 1923 (fl, fr), *Piper 5986* (US). COLÓN: 3 mi. de Portobelo, 7 May 1971 (fl), *M. Correa A. et al. 1752* (DUKE, F, MO); rd. to Río Indios, 3 km S of Piña, 50 m, 7 July 1976 (early fr), *G. Sullivan 133* (MO, US). DARIÉN: ridge N of Enseñada El Guayabo, between Río Jaqué Valley and Pacific Ocean, 7°26′N, 78°05′W, 300–500 m, 26 Jan. 1982 (fl), *Knapp & Mallet 3174* (MO). SAN BLAS: 3–4 hours up Río Mulutupu, 17 Aug. 1967 (fr), *Kirkbride 226* (MO, NY).

Psychotria limonensis may be recognized by its broad-elliptic, thin-membranous leaves, brochidodromous secondary veins with collector vein near margin, broad umbelliform inflorescences, and small (usually 4 mm long) ellipsoid to subspherical fruit. Leaves on Mexican and Guatemalan specimens have fewer secondary veins than those from elsewhere; the secondaries diverge characteristically at acute (vs. right) angles in Nicaragua.

49. Psychotria tenuifolia Swartz, Prodr., 43. 1788. *Uragoga tenuifolia* (Sw.) Kuntze, Revis. Gen. Pl. 2: 963. 1891. TYPE: Hispaniola: *Swartz s.n.* (holotype, S, n.v.). Cf. also Swartz, Fl. Ind. Occid., 402. 1797. Figures 2e, 33.

Psychotria sessilifolia M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11: 228. 1844. *Uragoga sessilifolia* (M. Martens & Galeotti) Kuntze, Revis. Gen. Pl. 2: 962. 1891. TYPE: Mexico. Veracruz: Mirador and Zacuapan, 750–1,050 m, June 1840 (fl), *Galeotti 7078* (holotype, G, n.v., photo, F neg. 25826; isotype, K).

Psychotria granadensis Bentham in Oersted, Vidensk.

Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 34. 1853. *Uragoga granadensis* (Benth.) Kuntze, Revis. Gen. Pl. 2: 960. 1891. TYPE: Nicaragua: Granada, *Oersted s.n.* (holotype, C, n.v., photo, F neg. 22833).

Psychotria sulzneri Small, Fl. Miami, 176. 1913. No type cited.

Shrub 0.5–2(–3) m tall; young stems glabrous to puberulent, the bark smooth; stipules ovate, long-biacuminate (Fig. 2e), 8–13 × 3–6 mm, glabrous to puberulent, caducous, leaving pale ridge with red-brown fringe. *Leaves* petiolate; petioles (0.3–)0.5–4 cm long, glabrous to puberulent, grooved above; blades membranous, narrow- to medium-elliptic, the apex acuminate or sometimes acute, the base attenuate, (4–)7.5–23 × (1–)2.5–6(–7.7) cm, glabrous above, glabrous to puberulent below, the midvein puberulent below, drying green-brown to sometimes red-brown; secondary veins 8–18 pairs, diverging 70°–80°, brochidodromous with collector vein fairly near margin, slightly arcuate, prominulent and puberulent below, the axils lacking domatia or hairs; tertiary veins inconspicuous to evident, orthogonal reticulate, the tertiary loops between secondary loops and margin often evident. *Inflorescences* terminal or pseudoaxillary, panicles of cymes; panicle branched to 3–4(–5) degrees; main axis 1.4–4.5 cm long, the peduncle to 2 cm long or lacking; secondary axes in (2)3(4) ranks, the first-rank axes 2, (0.9–)1.8–3 cm long, the second-rank axes 2, (0.4–)0.8–1.2 cm long, the third-rank axes (1)2, 0.1–0.5 cm long, the fourth-rank axes 2, 0.1–0.3 cm long; cymes branched to 2–3 degrees; bracts and bracteoles lanceolate to linear, 0.5–1 mm long, puberulent. *Flowers* pedicellate, the pedicels 0.5–1.5 mm long; calyx cup-shaped, the tube 0.2–0.3 mm long, the lobes 5, triangular, 0.3–0.5 × 0.5 mm, minutely ciliate; corolla white, the tube cylindrical, 1.5–2 × 0.8–1 mm, white pubescent in throat, the lobes 5, triangular, 0.7–1 × 0.5–0.7 mm; stamens 5, the filaments 1–1.5 mm long in pins, 2.5–3 mm long in thrums, the anthers 0.5–0.7 mm long; style 2–3 mm long in pins, 1.5 mm long in thrums, the branches linear. *Fruit* ellipsoid when dry, 4–5 mm long, 3–4.5(–5) mm diam., maturing red, drying red-brown; persistent calyx inconspicuous or a tubular beak to 0.5 mm long; seed dorsal surface with 4–5 shallow longitudinal furrows, the ventral surface with 2 longitudinal furrows.

Distribution (Fig. 33). Widespread from Mexico through Panama at 0–2,000 m elevation, mostly below 1,000 m, in tropical dry to premontane moist forest with equatorial to tropical climate. *Psychotria tenuifolia* occurs also in Florida, Cuba, and Hispaniola. It has been collected in flower throughout the year, primarily May–July, and in fruit throughout the year, primarily August–February.

Selected specimens examined. MEXICO. CAMPECHE: Tuxpeña, 16 Feb. 1932 (fr), *Lundell 1339* (F); Champotón, 7–15 July 1932 (fl), *Steere 1786* (F, MEXU); km 17 de la carret. Escárcega–Champotón sobre la terraceria a Venustiano Carranza, 5 Feb. 1983 (fr), *Tellez et al. 6293* (MEXU). CHIAPAS: Mpio. Tenejapa, slopes nr. Habenal, paraje of Mahben Chauk, 1,050 m, 26 Nov. 1964 (fr), *Breedlove 7626* (ENCB, NY); Mpio. Ocozocoautla de Espinosa, Selva del Ocote 32 km NW of Ocozocoautla, 600 m, 27 Aug. 1972 (fr), *Breedlove 27437* (MEXU, MO); Mpio. Osumacinta, 11–15 km NW of Soyalo on rd. to La Bombana and Chicoasén, 1,000 m, 23 Feb. 1973 (fl), *Breedlove 33806* (MEXU, MO); Mpio. Cintalapa de Figueroa, nr. Francisco Madero, 20 km N of Cintalapa, 1,250 m, 25 Aug. 1974 (fr), *Breedlove 36637* (MEXU); Mpio. Catazajá, Playas de Catazajá, 30 m, 20 May 1978 (fl), *Sanchez 1029* (ENCB). GUERRERO: Montes de Oca, Vallecitos, oak woods, 17 July 1937 (fl), *Hinton et al. 10610* (K, NY, US); Galeana, Atoyac, 8 Sep. 1939 (fl), *Hinton et al. 14598* (F, MO); Acapulco, 13 Nov. 1956 (fr), *Paray 2316* (ENCB). HIDALGO: at San Luis Potosí border, km 343–344 on hwy. below Chapulhuacán, rocky slopes, 620 m, 30 June 1948 (fl), *Moore & Wood 3660* (A, MEXU). JALISCO: 10–12 mi. S of Talpa de Allende, headwaters of Río de Talpa, 3 mi. above Los Sauces, steep mountains, 26 Nov. 1960 (fr), *McVaugh 21463* (LL). MICHOACÁN: Mpio. Apatzingan, Tancitaro region, Hda. California, 1,200 m, 12 Aug. 1941 (fl), *Leavenworth & Hoogstraal 1460* (F). OAXACA: 18.4 mi. S of Valle Nacional, Hwy. 175 through Sierra de Juárez, 1,500 m, 19 Feb. 1979 (fl), *Croat 48077* (MO); Dto. Jamiltepec, predio particular Cafetal Natividad y Anexas, San José de las Flores, 810 m, 14 Nov. 1979 (fr), *Guízar 710* (ENCB, MEXU); Mpio. Tuxtepec, Chiltepec, 150 m, 9 Aug. 1965 (fl), *G. Martínez C. 186* (MEXU, NY); Temazcal, 20 May 1962 (st), *Sousa 1374* (MEXU). PUEBLA: km 247.3 de la carret. México–Tuxpan, 1 May 1962 (fl), *Sarukhán et al. 2132* (MEXU). QUINTANA ROO: W of Lake Coba, June–July 1938 (fl), *Lundell & Lundell 7677* (GH, US); 12 km S of Cacao, 11 Jan. 1980 (fr), *Tellez & Cabrera 1265* (MEXU). SAN LUIS POTOSÍ: Tamazunchale, 12 July 1937 (fr), *M. Edwards 533* (F, MO); 13 mi. S of Nuevo Morelos (Tamaulipas), 2 Sep. 1948 (fr), *Kenoyer & Crum 3954* (A); Mpio. de Ciudad del Maíz, 0.5 km NE de Las Abritas, 800 m, 30 June 1959 (fl), *Rzedowski 11126* (ENCB). TABASCO: a 12.5 km de Villahermosa, por la carret. a Escárcega, 1 Dec. 1965 (fr), *L. A. González L. & Pérez 4004* (ENCB, MEXU); Balancán, San Isidro, 7–11 June 1939 (fl), *Matuda 3390* (A, F, MEXU, NY). TAMAULIPAS: nr. Nuevo Morelos, 1 Sep. 1948 (fr), *Kenoyer & Crum 4062* (A); 4 km N of Ejido La Libertad, nacimiento del Río Sabinas, 200 m, (fl), *Valiente et al. 249* (MEXU). VERACRUZ: km 20 carret. Alemán–Cosamaloapan, 13 Nov. 1964 (fr), *Chavelas & Pérez 223* (ENCB); San Lorenzo Tenochtitlán, 30 Nov. 1967 (st), *Chavelas et al. ES-2469* (MEXU); Mpio. de Ozulauma, a 8 km de Ozulauma hacia Tampico, 7 Dec. 1970 (fr), *Chiang 250* (MEXU); 20 mi. W of Tuxpan on rd. from Alazán, 5 Jan. 1964 (fr), *Correll & Correll 28710* (LL); Mpio. de Coatzintla, Palmar de Zapata, 110 m, 11 Oct. 1982 (fr), *M. Cortés*

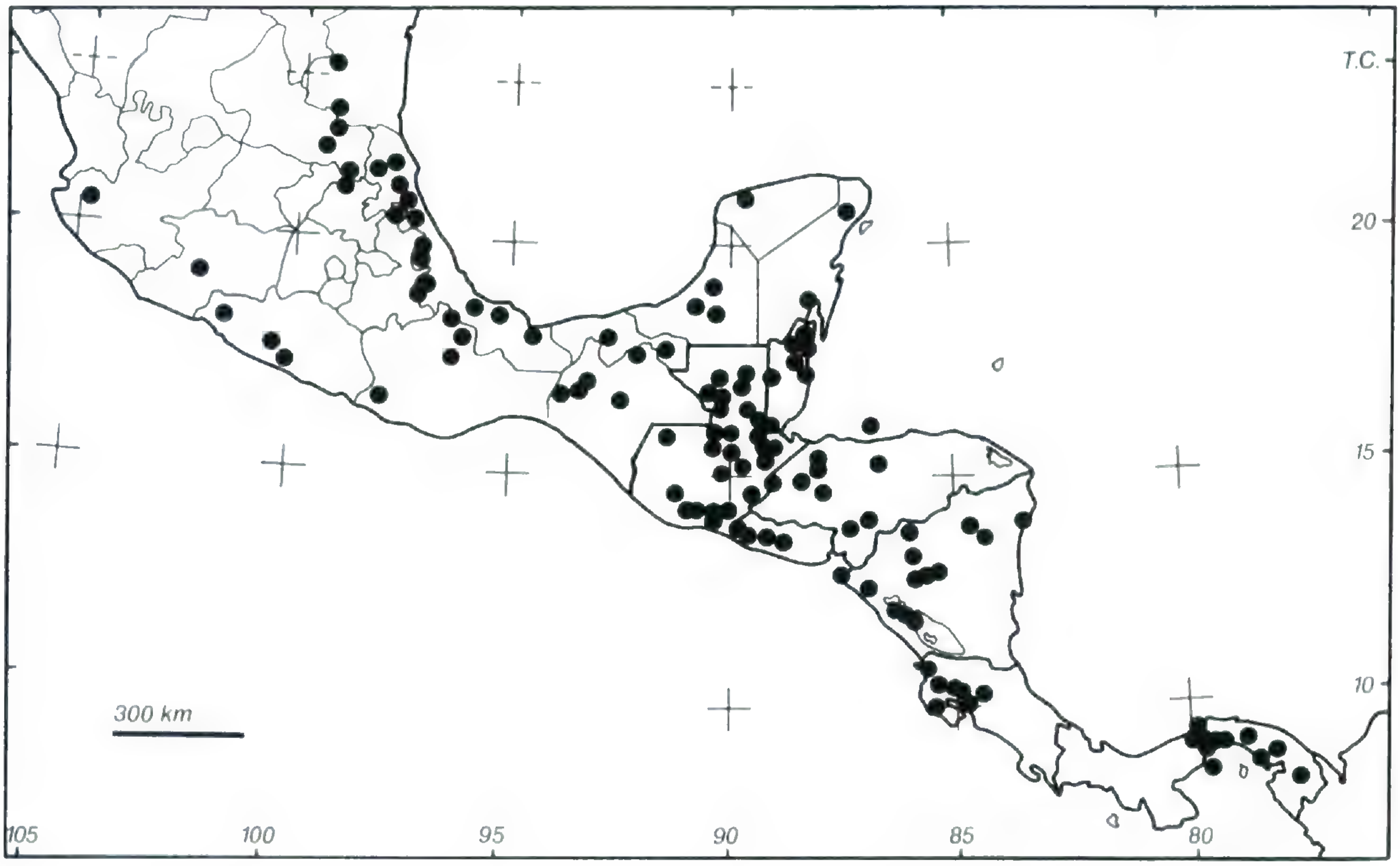

FIGURE 33. Distribution of *Psychotria tenuifolia* in Mesoamerica.

495 (MEXU); Mpio. Papantla, Cerro del Carbón, 240 m, 11 Dec. 1981 (fr), *M. Cortés 60* (MEXU, MO); Mpio. Espinal, brecha Entabladero–Espinal 1 km antes de Ojo de Agua, 140 m, 11 Nov. 1981 (fr), *Cortés-Vázquez 48* (MEXU); a 11.6 km de Plan de las Hayas, 700 m, 24 June 1972 (early fr), *Lot et al. 2022* (F, MEXU); Mpio. Totutla, 3 km SE of El Mirador, 19°12′N, 96°51′W, 900 m, 13 Nov. 1981 (fr), *Nee 22995* (MEXU, MO); Mpio. Tempoal, MEX 105 1.5 km NE of Tempoal, 50 m, 22 June 1980 (fl), *Nee & Hansen 18372* (F); Zacuapan, barranca de Tenampa, Oct. 1906 (fr), *Purpus 2268* (GH, MO, NY, US); Mpio. Minatitlán, orilla del Río Uxpanapa, un poco arriba del poblado de Uxpanapa, 120 m, 26 May 1981 (fl), *Wendt et al. 3322a* (MEXU). YUCATÁN: Mérida, Cancerillo, 6 July 1865 (fl), *Schott 524* (F, MO, NY). GUATEMALA. ALTA VERAPAZ: Sebol, 3 km S on old Petén rd., 18 Apr. 1964 (fl), *Contreras 4407* (MO); rd. from Tucurú to El Estor, 15 mi. W of Telemán, 550 650 m, 19 July 1977 (fl), *Croat 41556* (MO); SW of Lanquín, vic. caves, 600 1,000 m, 21 Feb. 1942 (fr), *Steyermark 44111* (F); vic. Laguna Sapalá (Chajvovuch), 2 km SW of Sibicté, 280 m, 11 Mar. 1942 (st), *Steyermark 44912* (F); Cubilgüitz, Aug. 1903 (fl), *Tuerckheim II-796* (F, US). BAJA VERAPAZ: Unión Barrios, 4 Mar. 1972 (fr), *Contreras 11101* (MO). CHIMALTENANGO: nr. Sibaja, 1,050 m, 6 Jan. 1939 (fr), *Standley 62278* (F). CHIQUIMULA: 4 km N of Esquipulas, Qda. Resimiento, 1,100 m, 27 Sep. 1971 (fr), *A. Molina R. & A. Molina 26778* (F). ESCUINTLA: 6 mi. N of Escuintla on rd. to Alotenango, 650 m, 27 July 1977 (early fr), *Croat 42052* (MO); below Las Lajas, 900–1,200 m, 9 Feb. 1939 (fr), *Standley 64775* (F). HUEHUETENANGO: along Río Azul, below Jacaltenango, Sierra de los Cuchumatanes, 1,400 m, 4 Sep. 1942 (fr), *Steyermark 51862* (F –2 sheets). IZABAL: Puerto Méndez/Cadenas, bordering Río Cadenas, 3 June 1970 (fl), *Contreras 9932* (MO); Modesto Méndez, 30 m, 13 Mar. 1970 (fl, fr), *Harmon & Fuentes 2090* (F, GH, MO); Finca Murcielago ca. 16 km E of El Estor, 8 July 1967 (fl), *Snedaker E-188* (A, F); vic. Quiriguá, 75–225 m, 15 31 May 1922 (fl), *Standley 24045* (US). JUTIAPA: nr. El Molino (Dept. Santa Rosa), 600 m, 26 Nov. 1940 (fr), *Standley 78446* (F). PETÉN: Tikal National Park, in secondary growth bordering airfield, 23 June 1960 (fl), *Contreras 1152* (LL); Dolores, on old Machaquila trail, 16 Sep. 1961 (fr), *Contreras 2914* (LL); Macanche, km 34–35 of Melchor de Mencos Rd., 24 May 1966 (fl), *Contreras 5855* (GH); Poptún Rd., km 82, 21 Nov. 1967 (fr), *Contreras 7242* (MO); Sayaxché, Ceibal, 17 Mar. 1970 (fl), *Contreras 9773* (MO); Paso Caballos, 80 m, 14 July 1956 (fl, early fr), *Cox & Guzman 2892* (ECON); La Cumbre, Pusila rd., 19 Aug. 1976 (fr), *Lundell & Contreras 20234* (MO); en el camino para La Libertad, a km 7 lado E del camino, 13 Sep. 1971 (fl, early fr), *Ortíz 1929* (F, US); en el camino a la aguada Paxcaman, a 3 km lado N de Uaxactún, 17 May 1973 (fl), *Ortíz 2572* (ENCB, F, MO, NY). SANTA ROSA: nr. Cuilapa, 900 m, 20 27 Nov. 1940 (fr), *Standley 77958* (F); S of Guazacapán, along the Avellana rd., 150 m, 6 Dec. 1940 (fl), *Standley 79472* (F). BELIZE. BELIZE: mi. 34.5 on Western Hwy., 5 July 1973 (fr), *Duyer 11470* (F, GH, MO, NY); Bomba, Northern River, Dec. 1933 (fl), *Gentle 1034* (A 2 sheets, F, GH, K, MO, NY); forest nr. Manatee Lagoon (Southern Lagoon), 15 Sep. 1905 (fl), *Peck 959* (GH, K, NY). CAYO: El Cayo, Mar. 1933 (fr), *Lundell 3984* (F); 4 km S of junction of Western and Humming Bird hwys., quarry hill, 75 m, 18 July 1970 (fl), *Spellman & Newey 1753* (MO). COROZAL: 1931–1932 (fl, fr), *Gentle 226* (F). ORANGE WALK: N of Orange Walk, vic. New River, 23 June 1973 (fl), *Gentry 8552* (MO); Freshwater Creek Reserve, co-

hune ridge, Feb. 1933 (fr), *Pelly 9* (F). TOLEDO: N side of Río Sarstun, opposite Modesto Méndez, 10 m, 29 June 1970 (early fr), *Harmon & Dwyer 2844* (MO). HONDURAS. COMAYAGUA: S shore of Lake Yojoa, 21 Aug. 1973 (fr), *Hazlett 684* (MO 2 sheets); Farallón El Pizote, Cerros El Cedral, 6 km NE de Taulabé, 1,940 m, 28–29 Feb. 1975 (fr), *C. Nelson & Vargas 2359* (MO, TEFH); Agua Caliente, vaguada de ríos Chamo y Humuya, 35 km E Lago Yojoa, 220 m, 22 Nov.–31 Dec. 1980 (fr), *C. Nelson et al. 6566* (TEFH). COPÁN: Copán River 2 km E of Copán Ruins, La Vegona, 500 m, 23 Nov. 1969 (fr), *A. Molina R. & A. Molina 24794* (F). CORTÉS: Montaña La Cumbre, Cordillera de Omoa al NE de San Pedro Sula, 200 m, 19 Apr. 1956 (fl), *A. Molina R. 6722* (F, US); orilla del Río Humuya, 40 km N Santa Cruz de Yojoa, 100 m, Nov. 1980 (fr), *C. Nelson et al. 5938* (TEFH). FRANCISCO MORAZÁN: El Zamorano, 800 m, 13 June 1945 (fl), *J. V. Rodríguez 3054* (F); Sabana Grande, 1,100 m, 26 Aug. 1945 (st), *J. V. Rodríguez 3270* (F). ISLAS DE LA BAHIA: E end of Utila Island, 5 m, 15 Aug. 1954 (fr), *Johannessen 499* (TEFH). SANTA BARBARA: nr. Santa Barbara, thickets along Sesecapa River, 500 m, 22 Aug. 1968 (fl), *A. Molina R. 22021* (NY 2 sheets). YORO: Aguan River valley, vic. Coyoles, nr. Medina, 200 m, 26 July 1938 (fl), *Yuncker et al. 8628* (F, GH). EL SALVADOR. AHUACHAPÁN: vic. Ahuachapán, 800–1,000 m, 9 27 Jan. 1922 (fr), *Standley 20007* (GH, NY, US). SAN SALVADOR: vic. San Salvador, 650 850 m, 30 Mar. 24 Apr. 1922 (fl), *Standley 22739* (GH, NY, US). SAN VICENTE: vic. San Vicente, 400 500 m, 7 14 Feb. 1947 (bud), *Standley & Padilla 3776* (F). SONSONATE: vic. Izalco, 19–24 Mar. 1922 (fl), *Standley 21849* (US). NICARAGUA. CHINANDEGA: cauce pluvial al SO del Volcán Cosigüina, 29 Sep. 1981 (fr), *Fonseca 131* (MO). GRANADA: Volcán Mombacho, 2 km al SE de la hda. Cutirre, "El Chipote," 11°48′N, 85°54′W, 190 m, 11 June 1982 (fl, fr), *P. P. Moreno 16450a, 16450b* (MO). LEÓN: Volcán Santa Clara, 18 Aug. 1981 (fr), *Quezada 52* (MO). MANAGUA: 7 km W of airport on Hwy. 1 to Tipitapa, nr. Lake Managua, 150 m, 17 Mar. 1977 (early fr), *Croat 39011* (MO). MASAYA: Sierra de Managua, region of Las Nubes, 650–950 m, 14 May 1947 (fl), *Standley & Garnier 8403* (F). MATAGALPA: Paiwita, 15 km al E de Matiguas, carret. a Río Blanco, 12°52′N, 85°18′W, 500 m, 5 May 1984 (fl), *P. P. Moreno 24119* (MO); 20 km E of Matagalpa, Río Yasica, nr. rd. to El Tuma, 25 May 1977 (fl), *Veill 1980* (MO); along rd. between Muy Muy and Esquipulas, ca. 9.5 km W of bridge at Muy Muy, at Qda. Yare, 12°45′N, 85°42′W, 310 m, 30 July 1978 (fl), *W. D. Stevens 9545* (MO); Qda. Sta. Cruz, between Puertas Viejas and Esquipulas, 12°35′N, 85°50′W, ca. 420 m, 27 July 1983 (fl), *W. D. Stevens 22338* (MO). NUEVA SEGOVIA: El Jícaro, "Fila de Monterrico," 13°44′N, 86°04′W, ca. 800 m, 26 Dec. 1981 (fr), *P. P. Moreno 13759* (MO). ZELAYA: region of Braggman's Bluff (Puerto Cabezas), 1928 (fl), *Englesing 228* (F); descent of Cerro Saslaya, down Cerro El Inocente E to El Hormiguero, 300–600 m, 6 May 1977 (fl), *Veill 1905* (MO); Cerro Waylawás, 13°38′N, 84°48′W, ca. 150 m, 9 Mar. 1979 (bud), *Pipoly 4171* (MO). COSTA RICA. ALAJUELA: San Miguel de San Ramón, May 1934 (fl), *Brenes 19218* (CR, F, NY); Guanacaste: 28 km N of Cañas, OTS area, 100 m, 2 Oct. 1969 (fr), *Frankie 296a* (MO); Comelco area N of Bagaces, nr. Potrero Falls, 6 June 1971 (fl), *Gentry 820* (F, MO, US); Comelco G, W of Bagaces, 23 May 1971 (fl), *Heithaus 113* (CR, MO); Santa Rosa National Park, 10°50′N, 85°37′W, 0–320 m, 20 Aug. 1981 (fr), *Janzen 12122* (MO); 7 km SW of Curime, 10°04′N, 85°31′W, 100 300 m, 5 Feb. 1978 (fr), *Liesner 4994* (MO). PUNTARENAS: Los Barrancas, along Pan-Am. Hwy. nr. Miramar turnoff, 2 June 1971 (fl), *Gentry 778* (MO); Monteverde, La Pacifica, 5 km N of Cañas, 17 June 1979 (fl), *Haber 380* (MO). PANAMA. CANAL AREA: Barro Colorado Island, 8 Jan. 1969 (fr), *Croat 7316* (MO); 8 June 1938 (fl), *P. White 123* (GH, MO); Cerro Galera, just W of Thatcher Bridge, 8°55′N, 79°35′W, 100 m, 15 Feb. 1983 (fr), *Hamilton & Palmer 2951* (MO); Balboa, Nov. 1923 Jan. 1924 (fr), *Standley 25566* (US); Las Cascadas Plantation, nr. Summit, 2 Dec. 1923 (fr), *Standley 25687* (US); between France Field and Cativá, 9 Jan. 1924 (fr), *Standley 30312* (US). DARIÉN: Río Chico, 1 hr. by outboard from Yaviza, 19 Dec. 1966 (fr), *Burch et al. 1118* (MO). PANAMÁ: dam site nr. Río Bayano beyond Cañita, 1 Sep. 1971 (early fr), *Gentry & Tyson 1669* (MO); Piriatí, S of Panam. Hwy., 9°00′N, 78°30′W, 200 400 m, 8 Aug. 1982 (early fr), *Hamilton 551* (CR, MO); Río Ipetí, S of Panam. Hwy., 9°03′N, 78°25′W, ca. 100 m, 17 Sep. 1982 (fr), *Hamilton & D'Arcy 1328* (MO); Chimán, 12 Dec. 1967 (fr), *Lewis et al. 3310* (MO); Taboga Island, Dec. 1923 (fr), *Standley 27049* (US); between Las Sabanas and Matías Hernández, 21 Jan. 1924 (fl), *Standley 31831* (US).

This variable species includes *P. sessilifolia* (Mexico; narrow leaves), *P. granadensis* (Nicaragua; broad leaves), and *P. sulzneri* (Florida; small, narrow leaves).

Psychotria tenuifolia may be recognized by its narrow-elliptic, thin-membranous leaves; brochidodromous secondary veins with collector vein near the margin; small umbelliform panicles of cymes; and small (4–5 mm long) ellipsoid fruits. Specimens from Honduras and further north are more puberulent, especially on the leaf underside, than from Nicaragua and south. Honduran inflorescences have especially conspicuous linear bracts.

GROUP 8. THE *CHLOPHYLLA* GROUP

Shrub or subshrub or herb (sometimes *P. hammelii* and *P. rosulatifolia*) or small tree (*P. calophylla*); *young stems* glabrous or *red-brown pubescent*; *stipules usually sheathing*, ovate or truncate *with apex usually biaristate or bifurcate* (Fig. 2g), uniform in color, glabrous or ferrugineous-pubescent (or fringed in *P. insueta*), caducous or often persistent at terminal 3–5 nodes in *P. hammelii* and *P. psychotriifolia*. *Leaf* blades elliptic or obovate or oblanceolate (or lanceolate in *P. rosulatifolia*), drying red-brown to green-brown, sometimes paler below; secondary veins (7)10–25(–42) pairs, diverging (45°–)50° 85°(110°), usually brochidodromous with collector vein (Fig. 3c) or sometimes without collector vein or eucamptodromous, the axils lacking domatia; tertiary veins orthogonal reticulate (or sometimes percur-

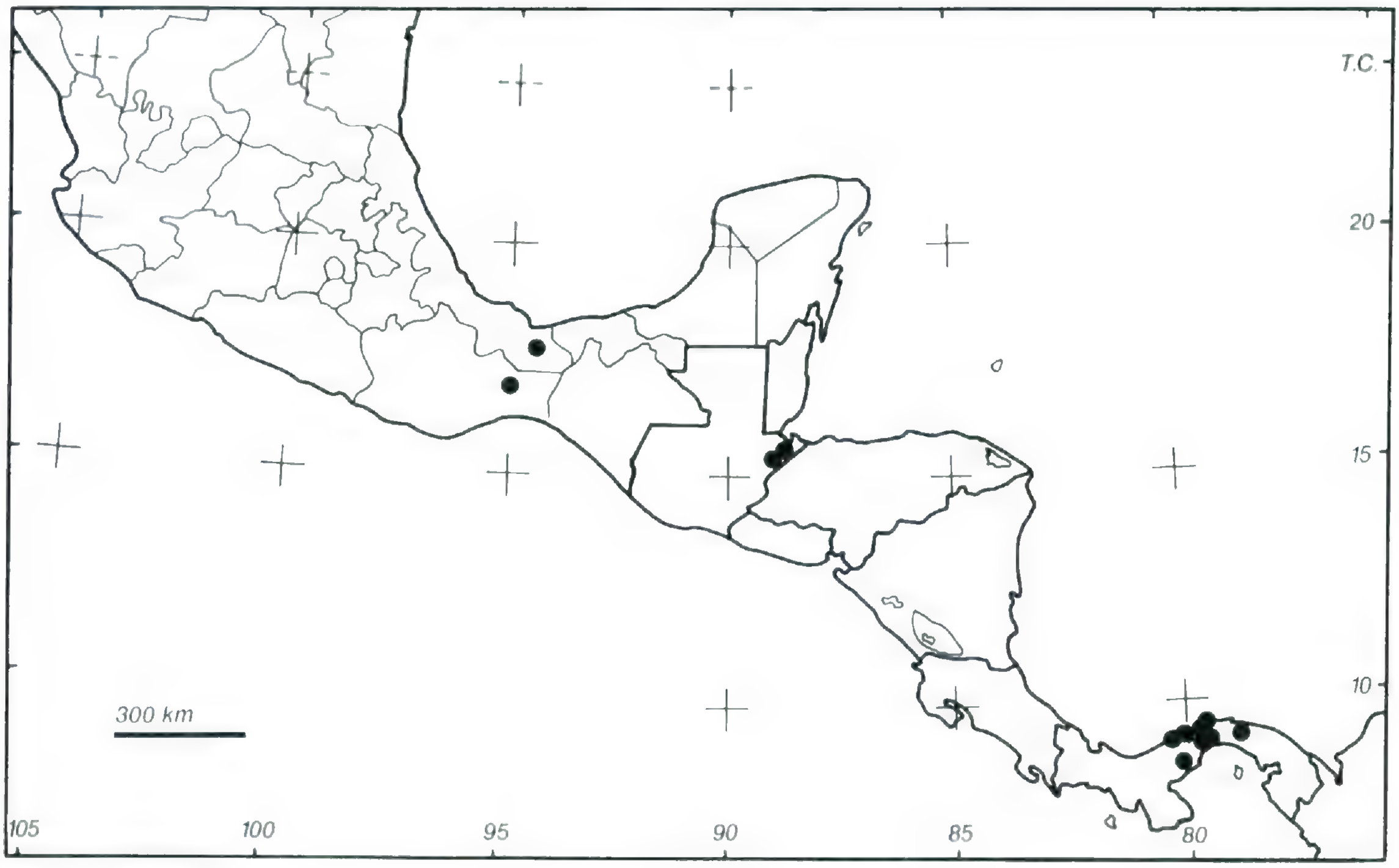

FIGURE 34. Distribution of *Psychotria calophylla*.

rent in *P. calophylla*, *P. insignis*, and *P. rosulatifolia*). *Inflorescences* panicles of cymes or of glomerules, pedunculate except for *P. insignis*, *P. psychotriifolia*, and often *P. calophylla*; secondary axes in 1–2(–3) sometimes size-differentiated pairs per rank and/or in clusters (*P. alfaroana*, *P. chitariana*, *P. dressleri*; Fig. 7d), delicate only in *P. rosulatifolia*; *bracts often conspicuous*. *Corolla* tubes (1.5–)2–5 mm long (10–12 mm in *P. dressleri*), *the lobes usually with apical extensions, protuberances, or thickenings*. *Fruit when dry ellipsoid*; *persistent calyx* inconspicuous or *a beak or a tube* to 3.5 mm long; seed dorsal surface with (3–)4–5 usually deep longitudinal furrows, the ventral surface with 2 shallow, often incompletely divided longitudinal furrows.

Only *Psychotria calophylla* (Fig. 34) and *P. psychotriifolia* (Fig. 35) are not narrow endemics; only the former has been collected north of Nicaragua. *Psychotria rosulatifolia* and *P. dressleri* occur in eastern Panama (Figs. 35, 36) and share inflorescence secondary axes often in size-differentiated pairs, and therefore may be closely related; but phylogenetic relationships among these mostly narrowly endemic species are difficult to hypothesize.

Of the twelve species in the group, four are normally distylous; only one of those—*Psychotria alfaroana*—shows any between-morph asymmetry in floral part length. *Psychotria rosulatifolia* appears pin-monomorphic, based on five flowering collections examined. *Psychotria monteverdensis* appears long-homostylous. The remaining six species are represented by few or no flowering collections and cannot be assessed.

50. Psychotria alfaroana Standley, J. Wash. Acad. Sci. 18: 273. 1928. TYPE: Costa Rica. Guanacaste: El Arenal, 500 m, 18 Jan. 1926 (fr), *Standley & Valerio 45179* (holotype, US). Figure 36.

Subshrub 0.3–0.6 m tall; young stems glabrous, the bark irregularly furrowed longitudinally; stipules sheathing with the sheath 5–7 mm long, biaristate with the extensions 7–12 mm long, glabrous, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 7–25(30) mm long, glabrous, grooved above; blades membranous, obovate, the apex acuminate to cuspidate, the base attenuate, 11–29 × 4.5–10 cm, glabrous above, glabrous below with minute organic detritus adhering to midvein, drying dull green; secondary veins (7–)11–14(–16) pairs, diverging (60°–)70°–80°(-90°), eucamptodromous, arcuate at midvein—then straight—then arcuate near margin, or constantly arcuate, elevated below, glabrous,

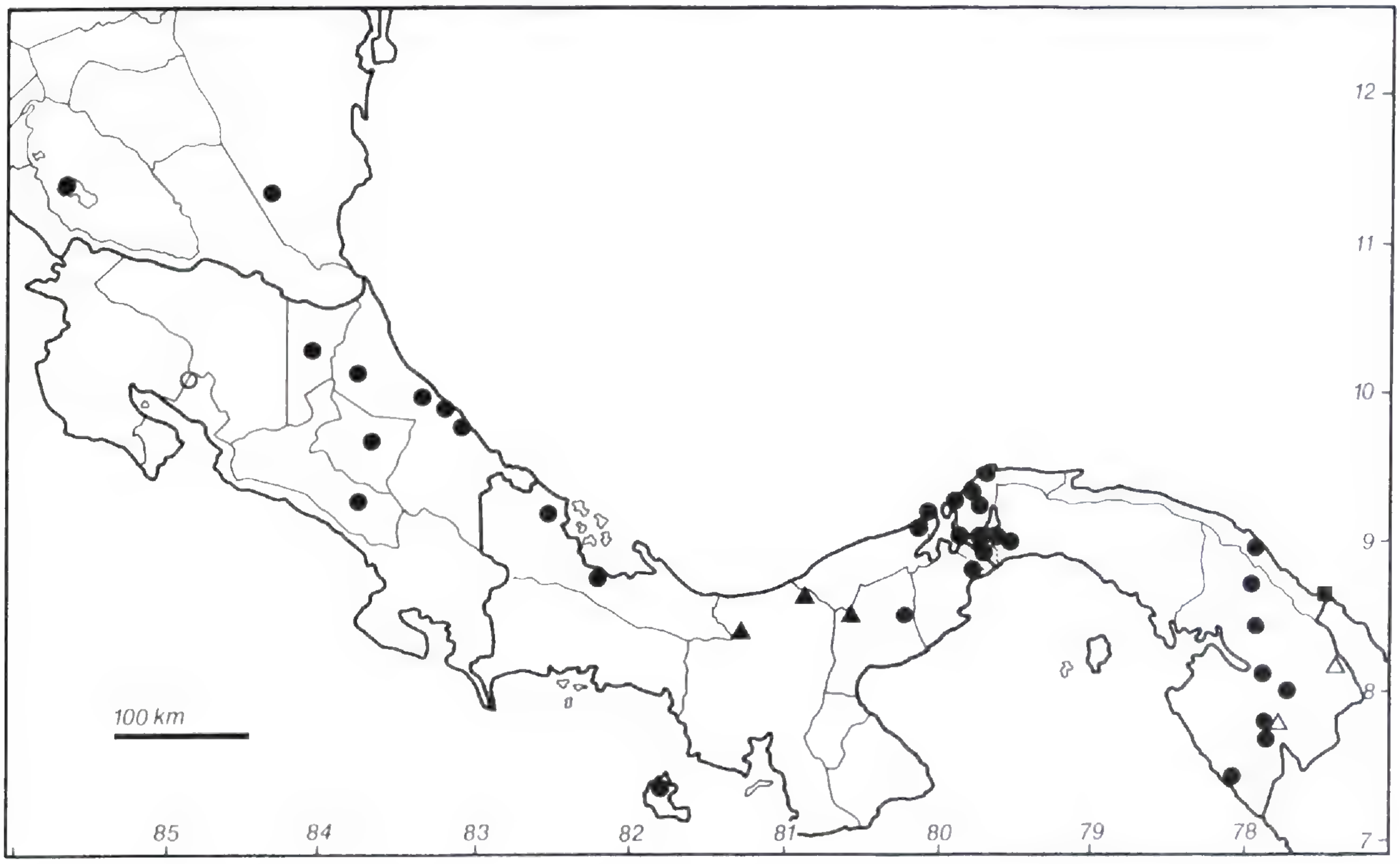

FIGURE 35. Distributions of *Psychotria insignis* (solid square), *P. insueta* (solid triangles), *P. monteverdensis* (open circle), *P. psychotrifolia* (solid circles), and *P. rosulatifolia* (open triangles) in Mesoamerica.

the axils lacking domatia or hairs; tertiary veins evident, orthogonal reticulate. *Inflorescences* terminal, compact-globose panicles of cymes; panicle branched to 2–3 degrees; main axis (1–)2–4 cm long, the peduncle 1–3 cm long; secondary axes in 1 cluster, several, 5–7 mm long; cymes branched to 1–2 degrees; bracts not evident. *Flowers* pedicellate, the pedicels 1–2 mm long; calyx drying pale brown, cup-shaped, the tube 1 mm long, the lobes 5, linear, 1–2 × 1 mm, glabrous to sparsely ciliate; corolla white, the tube cylindrical, 2.5–4 × 2 mm, white pubescent in throat, the lobes 5, linear, thickened at apex, 2–3 × 1 mm; stamens 5, the filaments 2.5 mm long in pins, 6 mm long in thrums, the anthers 0.8–1.2 mm long; style 4–5 mm long in pins, 3.5 mm long in thrums, the branches linear. *Fruit* when dry ellipsoid, 8–10 mm long, 4 mm diam., maturing red, drying black; persistent calyx 1–3 mm long, drying pale brown; seed dorsal surface with 4–5 deep irregular longitudinal furrows, the ventral surface with 2 irregular, incompletely divided longitudinal furrows.

Distribution (Fig. 36). Fairly widespread in Costa Rica, from upland Guanacaste to southeastern Limón, collected in tropical moist forest with equatorial to tropical-equatorial climate at elevations of 100 to 900 m. *Psychotria alfaroana* has been collected in flower January, March, June, and July, and in fruit July (immature), August, January, and February.

Selected specimens examined. COSTA RICA. ALAJUELA: 2 km N of Bijagua on trail to San Miguel, 7 km N of Río Naranjo, 400–500 m, 8 July 1976 (early fr), *J. Utley & K. Utley 5316* (DUKE). CARTAGO: vic. Pejibaye, 900 m, 7–8 Feb. 1926 (fr), *Standley & Valerio 46985* (US). GUANACASTE: El Silencio, nr. Tilarán, 750 m, 13 Jan. 1926 (fr), *Standley & Valerio 44603* (US); El Arenal, 600 m, 6 Mar. 1923 (fl), *J. Valerio 62* (US). HEREDIA: Finca La Selva, OTS field station, Río Puerto Viejo, 100 m, 25 Aug. 1979 (fr), *Beach & Grayum 1504* (DUKE); 29 May 1980 (early fr), *Grayum 2871* (DUKE); 17 Mar. 1980 (fl), *Hammel 8107* (DUKE); 4 Aug. 1980 (fr), *Hammel 9443* (DUKE); 8 Aug. 1980 (fr), *Hammel 9489* (DUKE); Río Sarapiquí ca. 10 km from Cariblanco upstream from bridge on way to La Virgen del Socorro, 10 June 1982 (fl), *Hammel et al. 12808* (DUKE). LIMÓN: Los Diamantes, Río Sta. Clara, 1.6 km E of Guapiles, ca. 200 m, 9 July 1949 (fl), *Holm & Iltis 354* (MO); 2 km N of Bribrí, along Río Sand Box, 100 m, 18 July 1976 (early fr), *J. Utley & K. Utley 5511* (DUKE). PANAMA. BOCAS DEL TORO: Río Teribe nr. Qda. Lukulon, ca. 100 m, 12 Apr. 1968 (fl), *Kirkbride & Duke 511* (MO).

Psychotria alfaroana may be recognized by its suffruticose habit; leaves drying green; compact globose, pedunculate inflorescences with clustered secondary axes only 5–7 mm long; and large (8–10 × 4 mm) ellipsoid fruits usually drying black.

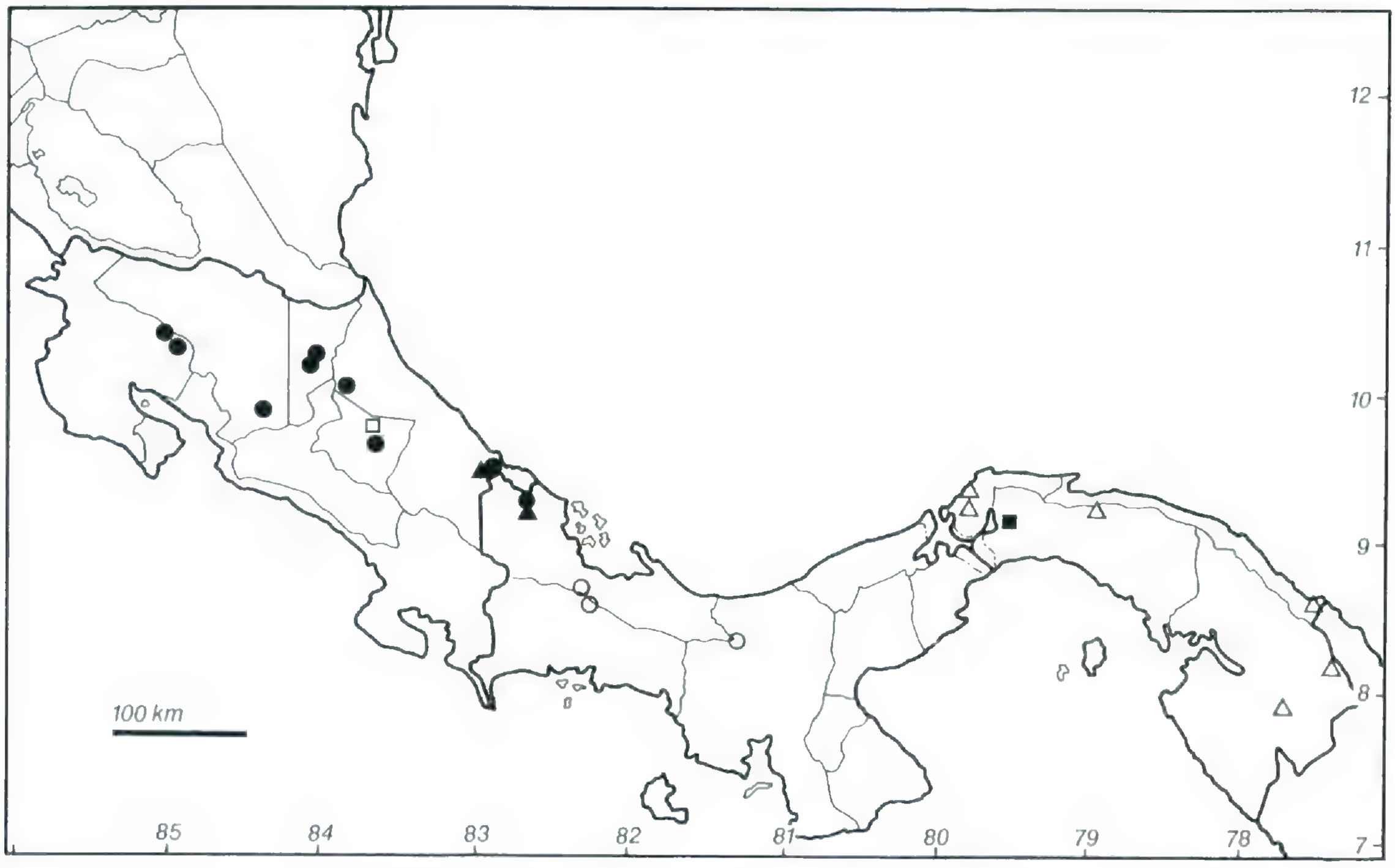

FIGURE 36. Distributions of *Psychotria alfaroana* (solid circles), *P. chitariana* (open square), *P. dressleri* (open triangles), *P. hammelii* (open circles), *P. pacorensis* (solid square), and *P. sixaolensis* (solid triangles).

The corolla tube of the pin morph appears conspicuously shorter (2.5 3 mm) than that of the thrum (3–4 mm).

51. Psychotria calophylla Standley, Contr. U.S. Natl. Herb. 18: 129. 1916. TYPE: Panama. Panamá: Chagres, Isthmus of Panama, 15 Mar. 1850 (early fr), *Fendler 60* (holotype, US; isotypes, GH, MO). Figures 3c, 34.

Psychotria cerroazulensis Dwyer, Ann. Missouri Bot. Gard. 53: 107. 1966. TYPE: Panama. Panamá: Cerro Azul, Goofy Lake area, 1 Sep. 1963 (fl), *Dwyer 2875* (holotype, MO).

Psychotria gatunensis Dwyer & Hayden, Ann. Missouri Bot. Gard. 54: 142. 1967. TYPE: Panama. Canal Area: area W of Limón Bay, Gatun Locks and Gatun Lake, 5 Aug. 1955 (early fr), *Johnston 1554* (holotype, MO; isotypes, A—2 sheets).

Psychotria grandicarpa Dwyer & Hayden, Ann. Missouri Bot. Gard. 55: 42. 1968. TYPE: Panama. Panamá: Cerro Jefe, 12 Mar. 1967 (fr), *Dwyer et al. 7244* (lectotype, MO 2002447, here designated; isolectotypes, MO—2 sheets).

Tree 3–8(–15) m tall; young stems brown-puberulent, the bark smooth; stipules ovate with irregular lobes and 2 aristate to narrow-triangular extensions 3–6 mm long, 8–15 × 5–15 mm, fringed, densely red-brown pubescent, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 1–3 cm long, red-brown pubescent, grooved above; blades membranous to subcoriaceous, elliptic to obovate, the apex acuminate, the base attenuate, (10–)13–26(–31) × 5–12 cm, glabrous above, red-brown tomentose to sometimes glabrous below, drying green-brown above and red-brown below; secondary veins (8–)10–15(–18) pairs, diverging 50°–75°, brochidodromous with collector vein undulate (Fig. 3c), constantly arcuate, elevated below, red-brown tomentose, the axils lacking domatia or hairs; tertiary veins inconspicuous to evident, orthogonal reticulate to percurrent. *Inflorescences* terminal, panicles of glomerules; panicle branched to 3(4) degrees; main axis 2.5–15 cm long, the peduncle lacking or 1.5–4.5 cm long; secondary axes in (2)3(4) ranks, the first-rank axes 2, 1.2–8 cm long, the second-rank axes 2, 0.6–4 cm long, the third-rank axes 2, 0.2 2.5 cm long, the fourth-rank axes 2, 0.7 1 cm long; bracts inconspicuous, triangular, 1 mm long, brown pubescent. *Flowers* sessile; calyx cup-shaped, the tube 1–2 mm long, the lobes 5, broad, barely evident, to 0.5 mm long, red-brown pubescent; corolla green-white, the tube cylindrical, 3.5–4 × 2–3 mm, very densely white pubescent in throat, puberulent without, the lobes 5(6), ovate to lanceolate, thickened apically, 2–2.5 × 0.7 mm; stamens 5(6), the filaments 2.5–3.5 mm long in pins,

4.5 mm long in thrums, the anthers 1–1.5 mm long; style 4–6 mm long in pins, 3 mm long in thrums, the branches linear or club-shaped. *Fruit* when dry ellipsoid, 10–14 mm long, 6–9 mm diam., maturing red, drying red-brown, sometimes red-brown puberulent; persistent calyx 2–3.5 mm long; seed dorsal surface with 4–5 longitudinal furrows, the ventral surface with 2 longitudinal furrows.

Distribution (Fig. 34). Known from southern Mexico and Izabal, Guatemala, and disjunct to Colón and Coclé to Panamá Province, Panama. This species is found at elevations of 30 to 1,000 m, mostly below 400 m, in tropical moist to premontane wet forest with equatorial to tropical climate. It has been collected in flower in March and May in Mexico and July–September and in December in Panama. Fruiting collections date from December in Guatemala and August and November–March in Panama.

Selected specimens examined. MEXICO. OAXACA: Mpio. Matías Romero, 3.2 km al SSO del Aserradero La Floresta, 16 km al S de Esmeralda, 17°03′N, 94°47′W, 300 m, 28 May 1981 (fl), *Hendt et al. 3332* (MEXU). VERACRUZ: Mpio. Hidalgotitlán, Río Solosuchil 5–6 km al ESE de Hermanos Cedillo, 150 m, 25 Mar. 1982 (fl), *Lorence et al. 3935* (MEXU). GUATEMALA. IZABAL: along Río Bonita, 30–150 m, 21 Dec. 1941 (fr), *Steyermark 41740* (A, F); along Río Tameja, 50 m, 24 Dec. 1941 (fr), *Steyermark 41785* (A, F); Cerro San Gil, 300–900 m, 25 Dec. 1941 (st), *Steyermark 41924* (F). PANAMA. CANAL AREA: Pipeline Road 5–10 mi. N of Gamboa, 21 Nov. 1971 (fr), *Gentry 2659* (GH, MO, NY); 11 Feb. 1974 (fr), *Nee 9600* (F, MO); nr. Piña, 0–100 m, 6 Dec. 1973 (fr), *Gentry & Nee 8721* (MO); Pipeline Road, 9°15′N, 79°45′W, 50 m, 10 Mar. 1983 (st), *Hamilton et al. 3255* (MO). COCLÉ: hills above El Valle, ca. 1,000 m, 24 Dec. 1972 (fr), *Gentry 6898* (F, GH, MO, NY). COLÓN: Miguel de la Borda, hill nr. beach, 24 Apr. 1970 (early fr), *Croat 10036* (F, MO—2 sheets); Río Guanche, 1–4 km upstream from Portobelo Road, 0–100 m, 10 Dec. 1973 (fr), *Gentry 8791* (MO—2 sheets); headwaters of Río Boqueron nr. fork with Río Nombre de Diosito, 150 m, 21 July 1978 (fl), *Hammel 3959* (MO); Salud, 50 m, 4 Aug. 1971 (fr), *Lao & Holdridge 207* (MO—2 sheets); Santa Rita Ridge rd., 10.2 km from Boyd–Roosevelt Hwy., 350 m, 15 Mar. 1975 (fr), *Mori & Kallunki 3065* (GH, MO); Río Guanche, 2.5 km upstream from bridge on Portobelo Road, 20 m, 27 Aug. 1975 (fl), *Mori & Witherspoon 7973* (MO, US). PANAMÁ: Cerro Azul, 23 Jan. 1967 (fr), *Duke 9363* (DUKE, MO); Cerro Jefe, to 850 m, 1 Jan. 1972 (early fr), *Gentry et al. 3513* (ENCB, MO, NY); El Llano Cartí rd., 9.6–11 km from Inter-American Hwy., 330–360 m, 4 Dec. 1974 (fr), *Mori & Kallunki 3528* (GH, MO).

The three species named from central Panama—*Psychotria cerroazulensis*, *P. gatunensis*, and *P. grandicarpa*—have morphologies well within the range of *P. calophylla* and are therefore included. One of the three specimens at MO of *Dwyer et al. 7244*, cited as the type of *P. grandicarpa*, is hereby chosen as the lectotype.

Psychotria calophylla may be recognized by its arborescent habit, large (usually 13–26 × 5–12 cm), elliptic to obovate leaves (these usually red-brown tomentose below), undulate collector vein, large panicles of glomerules with secondary axes usually in 3 ranks, and large (10–14 × 6–9 mm) ellipsoid fruits. Collections from Guatemala are noteworthy in that the leaf blades are obovate, as opposed to the more comon elliptic shape, and have fewer secondary veins than elsewhere in the range of the species.

52. Psychotria chitariana Dwyer & C. Hamilton in C. Hamilton, Phytologia 64: 221. 1988. TYPE: Costa Rica. Cartago: 13 km E of Turrialba, hwy. to Limón, canyon of Río Chitaría, 9°55′N, 83°36′W, 750–800 m, 10 May 1983 (fl), *Liesner et al. 15400* (holotype, MO; isotype, CR). Figure 36.

Shrub 1 m tall; young stems glabrous, the bark irregularly furrowed, with organic material accumulated in leaf axils; stipules not seen. *Leaves* petiolate; petioles ca. 1.5 cm long, glabrous, winged, flattened above; blades membranous to chartaceous, obovate, the apex rounded to obtuse, the base attenuate, 28–33 × 13–15 cm, glabrous above and below, drying pale brown to greenish red-brown; secondary veins 16–19 pairs, diverging (50°–)60°–65°(–70°), brochidodromous, straight to arcuate near margin, elevated below, glabrous, the axils lacking domatia or hairs; tertiary veins evident, orthogonal reticulate, the intersecondaries conspicuous. *Inflorescences* terminal, dense globose panicles of cymes; panicle branched to 3 degrees; main axis 7.5 cm long, the peduncle 4.5 cm long; secondary axes in 1 rank plus terminal cluster, the first-rank axes 2, 1 cm long, the clustered axes ca. 8, equal, 0.7–1 cm long; cymes branched to 1–2 degrees; bracts linear to triangular, 5 × 2.5 mm, glabrous. *Flowers* pedicellate, the pedicels 3–5 mm long; calyx cup-shaped, the tube 1 mm long, the lobes 5, barely evident, glabrous; corolla greenish white, the tube cylindrical, 4.5–5 × 1.5 mm, white pubescent in throat, the lobes 5, triangular, 2.3 × 1.5 mm; stamens 5, the filaments 4.5 mm long in pins, not seen in thrums, the anthers 1.5 mm long; style 7 mm long in pins, not seen in thrums, the branches minute. *Fruit* not seen.

Distribution (Fig. 36). Known only from the type collection from Cartago, Costa Rica, at 750–800 m in an area of premontane to lower montane

rainforest with equatorial-mountainous climate. *Psychotria chitariana* was collected in flower on May 10.

Psychotria chitariana may be recognized by its large (28–33 × 13–15 cm), obovate leaves with rounded to obtuse apex, and inflorescence secondary axes in one rank plus a terminal cluster.

The only flowering collection seen was a pin.

53. Psychotria dressleri (Dwyer) C. Hamilton, Phytologia 64: 223. 1988. *Cephaëlis dressleri* Dwyer, Ann. Missouri Bot. Gard. 67: 68, fig. 15. 1980. TYPE: Panama. San Blas: SE of Puerto Obaldía, 18 Aug. 1971 (fl), *Croat 16801* (holotype, MO). Figures 7d, 36.

Cephaëlis panchocoënsis Dwyer, Ann. Missouri Bot. Gard. 67: 78. 1980. TYPE: Panama. Darién: S slope of Cerro Tacarcuna above Río Pucro base camp, 700 1,000 m, 25 Jan. 1974, *Gentry & Mori 13895* (holotype, MO, n.v.).

Shrub or subshrub 0.2 1.5 m tall; young stems glabrous, the bark irregularly fissured and fluted, with organic material accumulated in leaf axils; stipules sheathing, slightly cleft at apex, 17–26 × 8 10 mm, glabrous, caducous, leaving a pale ridge with interrupted red-brown fringe. *Leaves* sessile to subsessile; petioles to 1 cm long; blades membranous, obovate, the apex acuminate to cuspidate, the base attenuate, (13–)20–47 × (8–)10–24 cm, glabrous above and below, drying red-brown to green-brown, paler below; secondary veins 17–25 pairs, diverging 50°–70°, eucamptodromous to brochidodromous, straight to slightly arcuate toward margin, elevated below, red-brown puberulent below, the axils lacking domatia or hairs; tertiary veins very conspicuous, orthogonal reticulate, the percurrent tertiaries especially prominent, the looping tertiaries between the secondary loops and the margin also prominent. *Inflorescences* terminal, panicles of glomerules; panicle branched to 2–3 degrees; main axis 2–9 cm long, the peduncle (0.5–)1.5–5 cm long; secondary axes in 1 2 ranks or clustered (Fig. 7d), the first-rank axes 2 or 4, the longer pair 0.5 1.5 cm long, the shorter pair when present 0.5–0.7 cm long, the second-rank axes 2 or 4, the longer pair 0.5 cm long, the shorter pair when present 0.2 cm long; bracts and bracteoles spathulate, 10 15 × 6–8 mm, glabrous. *Flowers* sessile; calyx cup-shaped, the tube 2 mm long, the lobes 5, linear, 1.5–2 × 0.8 mm, fringed; corolla white, the tube cylindrical, 10–12 × 1–2 mm, white pubescent in tube in zone ca. 8 mm from base, the lobes 5, linear with apical appendage 1 mm long, 2 3 × 1 mm; stamens 5, the filaments 10 mm long in pins, 13–14 mm long in thrums, the anthers 2.5 mm long; style 14 mm long in pins, 8–10 mm long in thrums, the branches linear, puberulent. *Fruit* when dry ellipsoid, 8–9 mm long, 3.5–4.5 mm diam., maturing color unknown, when dry deep red-brown; calyx persistent, 1–3 mm long; seed dorsal surface with 3–4 deep longitudinal furrows, the ventral surface with 2 incompletely divided longitudinal furrows.

Distribution (Fig. 36). Known only from eastern Panama near the ridge running along the Caribbean coast south to Cerro Pirre at elevations of 20–1,000 m and across the border into Colombia in tropical wet to premontane wet forest with equatorial-mountainous to equatorial-tropical climate. *Psychotria dressleri* has been collected in flower January–August, and in fruit August–December and March.

Additional specimens examined. PANAMA. COLÓN: Santa Rita lumber road, nr. Aqua Clara rain gauge, 26 July 1974 (fl), *Dressler 4677* (MO—2 sheets); Santa Rita Ridge, ca. 12 km from Transisthmian Hwy., 28 June 1978 (early fr), *Hammel 3665* (MO); Río Guanche, 2.5 km upstream from bridge on rd. to Portobelo, 20 m, 27 Aug. 1975 (fr), *Mori & Witherspoon 7954* (MO); along banks of Río Guanche, above bridge, 50 m, 8 July 1976 (fl), *G. Sullivan 183* (MO). DARIÉN: La Boca de Pirre, 13 Oct. 1967 (early fr), *Bristan 1277* (MO); trail from Tacarcuna Village on Río Tacarcuna to Cerro Malí, 800 1,300 m, 16 Jan. 1974 (fl), *Gentry 13598* (MO); Serranía del Darién, trail from Cerro Malí to Río Pucro camp, 20 July 1976 (fl), *Gentry et al. 16826* (MO). PANAMÁ: El Llano–Cartí Rd., 4 mi. beyond hwy., 500 m, 5 Dec. 1979 (fr), *Croat 49145* (MO).

Material annotated *Cephaëlis panchocoënsis* by Dr. Dwyer does not differ substantially from *P. dressleri* and is therefore included.

Psychotria dressleri may be recognized by its large (usually 20–47 × 10 24 cm), obovate leaves with organic material accumulated in the leaf axils and by its contracted (2–9 cm long) panicles of glomerules with clustered secondary axes and enlarged (10–15 × 6–8 mm) spathulate bracts.

54. Psychotria hammelii Dwyer, Ann. Missouri Bot. Gard. 67: 383, fig. 72. 1980. TYPE: Panama. Veraguas: mountains W of Alto de Piedras W of Santa Fe, 960–1,680 m, 8 Sep. 1978 (early fr), *Hammel 4634* (holotype, MO—2680614; isotype, MO—2806155). Figure 36.

Herb or subshrub 0.1 0.3 m tall, stoloniferous; young stems glabrous, angled, the bark smooth; stipules sheathing, bifurcate, often split down center, 15 22 × 5–10 mm, glabrous, caducous, per-

sistent at top 3–5 nodes, leaving a red-brown ridge. *Leaves* petiolate; petioles 7–18 mm long, glabrous, grooved above; blades membranous, bullate, elliptic, the apex cuspidate, the base narrowly cuneate, (5–)8–12 × (2–)3–4.5 cm, glabrous above, puberulent on veins below, drying deep red-brown; secondary veins 11–15 pairs, diverging (45°–)60°–70°, eucamptodromous, constantly arcuate, elevated below, red-brown puberulent below, the axils lacking domatia or hairs; tertiary veins conspicuous, orthogonal reticulate. *Inflorescences* terminal, panicles of cymes; panicle branched to 3 degrees; main axis 4–4.5 cm long, the peduncle 1.5–3 cm long; secondary axes in 2 ranks, the first-rank axes 2, 1.2–1.3 cm long, the second-rank axes 2, 0.4–0.5 cm long; cymes branched to 1 degree; bracts linear, 8–9 × 3 mm, glabrous. *Flowers* pedicellate, the pedicels ca. 1 mm long; calyx cylindrical, the tube 1–2 mm long, the lobes 5, linear, 1–2 × 0.7 mm, glabrous, fringed; corolla white, the tube cylindrical, 4 × 1.5 mm, white pubescent in throat, the lobes 5, ovate with apical extension 0.5 mm long, 1 × 0.7 mm; stamens 5, the filaments 3 mm long in pins, not seen in thrums, the anthers 1 mm long; style 5 mm long in pins, not seen in thrums, the branches linear. *Fruit* when dry ellipsoid, 5–7 mm long, 3.5–4 mm diam., maturing red, drying deep red-brown; persistent calyx 1–2 mm long; seed dorsal surface with 4 deep longitudinal furrows, the ventral surface with 2 shallow longitudinal furrows.

Distribution (Fig. 36). Known only from the western cordillera in Panama at ca. 1,000 m elevation in low montane wet forest to rainforest with equatorial-mountainous climate. This species has been collected in flower in March and June–July, in fruit in April, and with immature fruit in June and September.

Additional specimens examined. PANAMA. BOCAS DEL TORO: E slope of La Zorra, 19 Apr. 1968 (fr), *Kirkbride & Duke 812* (MO—2 sheets). CHIRIQUÍ: vic. Gualaca ca. 8.5 mi. from Planes de Hornito, La Fortuna, 1,300 m, 10 July 1980 (fl), *Antonio 5060* (MO); behind Vivero Forestal de Boquete, 12 km N of Los Planes de Hornito, IRHE Fortuna Hydroelectric Project, 8°43′N, 82°14′W, 1,100–1,200 m, 17 June 1982 (fl, early fr), *Knapp & Vodicka 5538* (MO); Qda. de Arena, N of Carretera de Oleoducto, IRHE Fortuna Hydroelectric Project, 8°46′N, 82°12′W, 1,100 m, 12 Mar. 1982 (fl), *Knapp et al. 4083* (MO).

Psychotria hammelii may be recognized immediately by its bullate leaves, small (4–4.5 cm long) panicles of cymes with enlarged bracts, and ellipsoid fruits with conspicuous persistent calyx.

The only two flowering collections seen are of the pin morph.

55. Psychotria insignis Standley, Contr. U.S. Natl. Herb. 18: 130. 1916. Not *Ixora insignis* (Muell. Arg.) Kuntze (based on *Rudgea insignis* Muell. Arg. in Martius). TYPE of *P. insignis*: Panama. San Blas: hills of Sperdi, nr. Puerto Obaldía, 20–200 m, Sep. 1911 (fl), *Pittier 4410* (holotype, US; isotype, F). Figure 35.

Shrub; young stems densely ferrugineous-pubescent; stipules ovate, 12 × 4 mm, ferrugineous-pubescent, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 2.5–5.5 cm long, ferrugineous-pubescent, perfectly terete or often grooved above; blades membranous, ovate, the apex acuminate to cuspidate, the base cordate, 14–22 × 7–10 cm, glabrous above except for the adaxially puberulent midvein, ferrugineous-pubescent below, drying deep red-brown; secondary veins 17–20 pairs, diverging 100°–105°, brochidodromous with collector vein undulating near margin, constantly arcuate, elevated and densely pubescent below, the axils lacking domatia or hairs; tertiary veins evident, orthogonal reticulate to percurrent. *Inflorescences* terminal, panicles of glomerules; panicle branched to 3–4 degrees; main axis 2.5 cm long, the peduncle lacking; secondary axes in 1 rank, the first-rank axes 1–2, 1.5 cm long; bracts triangular, 2–2.5 mm long, 5 mm across, ferrugineous-pubescent and fringed. *Flowers* sessile; calyx cylindrical, the tube 1 mm long, the lobes 5, linear, 1–1.2 × 0.8 mm, red-brown puberulent; mature corolla, stamens, and style not seen. *Fruit* not seen.

Distribution (Fig. 35). Known only from the type collection from near Puerto Obaldía, San Blas, Panama, at ca. 100 m elevation in tropical moist forest with tropical-subtropical climate. It was collected in flower in September.

Psychotria insignis may be recognized immediately by its large (14–22 × 7–10 cm) ovate leaves with bases cordate and drying deep red-brown, numerous (17–20) secondary veins diverging 100°–105°, and by small (2.5 cm long) ferrugineous-pubescent panicles of glomerules.

56. Psychotria insueta (Dwyer) C. Hamilton, Phytologia 64: 226. 1988. *Cephaëlis insueta* Dwyer, Ann. Missouri Bot. Gard. 67: 73. 1980. TYPE: Panama. Veraguas: 11 km from

Escuela Agricola Alto de Piedra, along Río Dos Bocas, Atlantic slope, 15 Nov. 1974 (early fr), *Mori & Kallunki 3108* (holotype, MO). Figure 35.

Shrub 0.4–1.7 m tall; young stems glabrous to minutely puberulent, the bark furrowed longitudinally, with organic material accumulated in leaf axils; stipules with a sheath 9 mm long and with 2 linear extensions 2 mm long, minutely fringed, caducous, leaving a red-brown ridge without fringe. *Leaves* sessile; blades membranous, obovate to oblanceolate, the apex cuspidate, the base decurrent, 30 42 × 8–19 cm, glabrous above and below, drying dull green or brown-green above, paler dull green below; secondary veins 34–42 pairs, diverging 75°–110° with higher angles toward base, brochidodromous, the collector vein straight along margin, constantly arcuate, elevated below, glabrous, axils lacking domatia or hairs; tertiary veins evident, orthogonal reticulate to percurrent. *Inflorescences* terminal, rounded-umbellate panicles of cymes; panicle branched to 4 degrees; main axis 17–18 cm long, the peduncle 3.5–7 cm long; secondary axes in 4 ranks, the first-rank axes 2, 9 cm long, the second-rank axes 2(3), 3–4.5 cm long, the third-rank axes 2, 2–2.5 cm long, the fourth-rank axes 2, 0.7–1 cm long; cymes branched to 3 degrees; bracts subtending branches, broad irregular, 1 mm long, irregularly fringed. *Flowers* pedicellate, the pedicels 0.5–1.5 mm long; calyx cup-shaped, the tube 1–1.5 mm, the lobes 5, barely evident to none, with pubescent fringe; corolla white, the tube cylindrical, 2 × 1.5 mm, white pubescent in throat, the lobes 5, linear, 2 × 1 mm; stamens 4, the filaments 2 mm long in pins, not seen in thrums, the anthers 1 mm long; style 3.5 4 mm long in pins, not seen in thrums, the branches spathulate. *Fruit* ellipsoid when dry, 7–10 mm long, 4–5 mm diam., maturing blackish (?), drying black; persistent calyx a beak to 0.5 mm long; seed dorsal surface with 5 longitudinal furrows, the ventral surface with 2 incompletely divided longitudinal furrows appearing as 1 furrow.

Distribution (Fig. 35). Known only from the continental divide north of El Copé, Coclé, Panama, at ca. 750 m and north down to ca. 200 m elevation, and from the Atlantic slope in Veraguas; it is found in tropical wet to premontane rainforest with equatorial-mountainous climate. This species has been collected in flower on June 21 and in fruit October–November.

Additional specimens examined. PANAMA. COCLÉ: El Copé, on Pacific side, half-hour walk from sawmill, 780 m, 16 Oct. 1979 (fr), *Antonio 2090* (MO); nr. Aserradero El Copé, N of El Copé, second stream E of sawmill, 700–750 m, 2 Nov. 1980 (fr), *Dressler 5964* (MO); E of El Copé sawmill, along stream, ca. 660 m, 21 June 1978 (fl), *Hammel 3595* (MO). VERAGUAS: trail from Coquyito mine to Río Barrera junction with Río Concepción, 150–300 m, 17 Oct. 1978 (early fr), *Hammel 5227* (MO).

Psychotria insueta may be recognized by its large (30–42 × 8–19 cm), glabrous, obovate to oblanceolate leaves with many (34–42) secondary veins diverging 75°–110° and joining in a collector vein; large (17–18 cm long) panicles of cymes; and ellipsoid fruits drying black.

The only flowering collection seen is a pin morph.

57. Psychotria monteverdensis Dwyer & C. Hamilton in C. Hamilton, Phytologia 64: 230. 1988. TYPE: Costa Rica. Guanacaste-Puntarenas: al oeste de Reserva de Monteverde, 1,520–1,590 m, 24 June 1977 (fl), *Dryer 1531* (holotype, MO; isotype, CR). Figure 35.

Shrub 2.5 m tall; young stems glabrous, the bark irregularly furrowed longitudinally; stipules sheathing, truncate with 2 aristate appendages 2 mm long from apical corners, 7–8 × 4 mm, glabrous, caducous, leaving a pale ridge with long red-brown fringe. *Leaves* sessile to petiolate; petioles to 0.5 cm long, glabrous, grooved above; blades subcoriaceous, elliptic, the apex acuminate, the base cuneate, (9–)13–15 × (2–)3–4.5 cm, glabrous above and below, drying pale green-brown; secondary veins 9–11 pairs, diverging 45°–60°, brochidodromous with collector vein undulating near margin, constantly arcuate, prominent below, glabrous, the axils lacking domatia or hairs; tertiary veins inconspicuous, orthogonal reticulate. *Inflorescences* terminal, few-branched panicles of glomerules; panicle branched to 2 degrees; main axis 3.6 cm long, peduncle 2.4 cm long; secondary axes in 2 ranks, the first-rank axes 2, 0.6–0.7 cm long, the second-rank axes 2, reduced; bracts linear, 8 mm long, ciliate; bracteoles ovate, 3–4 mm long, ciliate. *Flowers* sessile or with pedicels to 1.5 mm long; calyx cup-shaped, the tube ca. 1 mm long, the lobes 5, triangular to lanceolate, to 1 mm long, ciliate; corolla green-yellow, leathery, the tube cylindrical, 3 × 2 mm, pubescent in throat, the lobes 5, triangular with robust keel-like appendages, 2 × 1 mm; stamens 5, the filaments 2.5 mm long, the anthers 1.2 mm long; style 4 mm long, the branches clublike. *Fruit* not seen.

Distribution (Fig. 35). Known only from the type collection from near the Monteverde Reserve

near the Guanacaste Puntarenas border, Costa Rica, at ca. 1,550 m elevation in low montane wet forest with equatorial-mountainous climate. *Psychotria monteverdensis* was collected in flower on June 24.

Psychotria monteverdensis may be recognized by its subcoriaceous medium-sized (usually 13–15 × 3 4.5 cm) leaves with collector vein, small (3.6 cm long) inflorescences with secondary axes 2 per rank in 2 ranks, those of the second rank sessile, and leathery greenish corollas with keel-like abaxial appendages on the lobes.

Only one flower was dissected, but the minute separation (0.3 mm) between stigma and anthers suggests that the species is long-homostylous.

58. Psychotria pacorensis C. Hamilton, Phytologia 64: 232. 1988. TYPE: Panama. Panamá: vic. Cerro Jefe, Altos de Pacora, 720 m, 18 Dec. 1980 (early fr), *Antonio 3241* (holotype, MO; isotype, ENCB). Figure 36.

Shrub 2–3 m tall; young stems minutely red-brown puberulent, the bark longitudinally grooved and fluted; stipules ovate, 10 × 4 mm, glabrous, caducous, leaving a red-brown ridge with or without fringe. *Leaves* petiolate; petioles 5–13 mm long, glabrous, grooved above; blades membranous, elliptic to obovate, the apex acute to caudate, the base cuneate, (13–)16 25 × (4)5–10 cm, glabrous above, glabrous below except on veins, drying red-brown, paler below; secondary veins 12 14 pairs, diverging 70° 80°, eucamptodromous to brochidodromous, constantly arcuate, elevated and minutely puberulent below, the axils lacking domatia or hairs; tertiary veins conspicuous, orthogonal reticulate, the percurrent tertiaries especially conspicuous, the tertiary arches near margin numerous. *Inflorescences* terminal, panicles of cymes; panicle branched to 3 degrees; main axis 4.5 cm long, the peduncle 3.5 cm long; secondary axes in 3 ranks, the first-rank axes 4, the longer pair 0.5 0.6 cm long, the shorter pair 0.3 cm long, the second-rank axes 4, the longer pair 0.2 0.3 cm long, the shorter pair reduced, the third-rank axes 2, 0.2 cm long; cymes branched to 1–2 degrees; bracts and bracteoles broad, to 1 mm long, fringed. *Flowers* sessile to pedicellate, the pedicels to 2 mm long; mature flowers not seen. *Fruit* when dry ellipsoid, 5.5–7 mm long, 3.5 5 mm diam., maturing purple, drying red-brown; persistent calyx cup ca. 0.5 mm long; seed dorsal surface with 4-5 deep longitudinal furrows, the ventral surface with 2 shallow longitudinal furrows.

Distribution (Fig. 36). Known only from the Altos de Pacora region near Cerro Azul and Cerro Jefe, eastern Panamá Province, Panama, at ca. 750 m elevation in premontane wet forest with tropical-equatorial climate. *Psychotria pacorensis* has been collected with immature fruit in December and in fruit in February.

Additional specimens examined. PANAMA. PANAMÁ: Cerro Jefe, 6 mi. past Cerro Azul on rd. to Altos de Pacora, 780 m, 19 Feb. 1981 (fr), *Sytsma & D'Arcy 3689* (MO -2 sheets).

Psychotria pacorensis may be recognized by its large (usually 16–25 × 5–10 cm) leaves drying red-brown and with brochidodromous veins with secondary loops (not marginal collector vein) and conspicuous tertiary veins including numerous arches between the secondaries and the margin.

59. Psychotria psychotriifolia (Seemann) Standley, Contr. U.S. Natl. Herb. 18: 133. 1916. *Cephaëlis psychotriifolia* Seem., Bot. Voy. Herald: 138. 1854. *Uragoga psychotriifolia* (Seem.) Kuntze, Revis. Gen. Pl. 2: 962. 1891. *Psychotria psychotriaefolia* auctt. TYPE: Panama: *Seemann 182* (holotype, BM, n.v., photo, MO). Figures 2g, 35.

Psychotria sinuensis Standley, Publ. Field Columbian Mus., Bot. Ser. 7: 114. 1930. TYPE: Colombia. Bolívar: Boca Verde, on Río Sinu, 4 Mar. 1918 (fl), *Pennell 4572* (holotype, NY).

Shrub 0.5–2 m tall; young stems ferrugineous-pubescent, the bark smooth; stipules with a sheath 8–13 × 4–5 mm, truncate, biaristate with the extensions 1.5–4 mm long from apical corners (Fig. 2g), glabrous to ferrugineous-pubescent, caducous, often persistent at terminal 3 5 nodes, leaving a ridge. *Leaves* petiolate; petioles 2–15 mm long, ferrugineous-pubescent, grooved above; blades membranous, oblanceolate to elliptic, the apex acute, the base attenuate or subcordate, (5.5–)7.5 17(–20) × (1.5)3 6.5(8) cm, glabrous above, glabrous to red-brown puberulent below, the midvein puberulent, drying green-brown to red-brown, paler below; secondary veins (10)14 20(23) pairs, diverging 70° 85°, brochidodromous, with collector vein almost parallel near margin, constantly arcuate, prominulous below, puberulent below, the axils lacking domatia or hairs; tertiary veins inconspicuous, orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of glomerules; panicle branched to 2(3) degrees; main axis 8–17 mm long, the peduncle absent; secondary axes in 1–2(–3) ranks, the first-rank axes 2

or 4(6), equal, 0.8–2 cm long, the second-rank axes 2 or 4, equal, 0.5–1 cm long; bracts sheathing, biaristate, 3–5 mm long, glabrous to puberulent; bracteoles subtending glomerules enlarged, cuplike, 3–4 mm long, glabrous to puberulent. *Flowers* sessile; calyx cup-shaped, the tube 0.5 mm long, the lobes 5, lanceolate, 1 × 0.7 mm, puberulent, ciliate; corolla green-white, the tube cylindrical, 1.5 × 1–1.5 mm, white pubescent in throat, the lobes 5, lanceolate with minute apical appendage, 1 × 0.6 mm; stamens 5, the filaments 1.5 mm long in pins, 2–2.5 mm long in thrums, the anthers 0.5–0.7 mm long; style 2.5–3 mm long in pins, 1.3 2 mm long in thrums, the branches short. *Fruit* narrow-ellipsoid when dry, 5 6 mm long, 3–4 mm diam., maturing red, drying red-brown; persistent calyx conspicuous, tubular, 0.5 2 mm long; seed dorsal surface with (4)5 longitudinal furrows, the ventral surface with 2 longitudinal furrows.

Distribution (Fig. 35). Known from southern Nicaragua through Panama, with very discontinuous distribution, at 0–800 m elevation in tropical moist to premontane wet forest with equatorial to tropical climate. This species occurs also in Colombia, Venezuela, and Ecuador. It has been collected in flower and in fruit throughout the year.

Selected specimens examined. NICARAGUA. RIVAS: N de Volcán Concepción, Isla de Ometepe, 11°32′N, 85°38′W, 800–1,000 m, 7 Aug. 1982 (fr), *Sandino 3469* (MO). ZELAYA: along Río El Zapote W of Nueva Guinea, 11°42′N, 84°26′W, 130 m, 21 Aug. 1983 (fr), *J. Miller & Sandino 1254* (MO); Mpio. de Siuna, Santa Rosa, 6 Sep. 1982 (fr), *Ortíz 115* (MO). COSTA RICA. CARTAGO: 12 km S of Turrialba by air, 4 km SE of Pejibaye along Río Gato, 9°48′N, 83°42′W, 700 m, 16–17 Apr. 1983 (fr), *Liesner 14383* (CR, MO). HEREDIA: Finca La Selva, OTS field station on the Río Puerto Viejo, 100 m, 24 May 1980 (fl), *Hammel 8790* (DUKE); 1 Aug. 1980 (fr), *Wilbur 30166* (DUKE). LIMÓN: camino a La Estrella, 0 5 m, 28 Feb. 1958 (fl), *Córdoba 470* (MO); Golden Grove, 30 m, 28 July 1936 (fl, fr), *Dodge & Goerger 9468* (CR, F, GH, MO, US); Las Colonias-Guapiles, 300 m, 17 Apr. 1941 (fr), *León 653* (F); 1 mi. toward Zent from Moin Junction, 30 m, 1 Sep. 1946 (fr), *Morley 808* (F, US); drenajes de los ríos Parismina y Reventazón, 0 m, 3 Oct. 1951 (fr), *Shank & Molina 4195* (F, GH, US). SAN JOSÉ: vic. El General, 610 m, Jan. 1939 (fl, fr), *Skutch 3883* (GH, K, MO, NY, US). PANAMA. BOCAS DEL TORO: Changuinola to 5 mi. S at junction of ríos Changuinola & Terebe, 30–60 m, 17–19 Dec. 1966 (fr), *Lewis et al. 963* (GH, MO, NY, US); Chiriquicito to 5 mi. S along Río Guarumo, 5–7 June 1967 (fl, fr), *Lewis et al. 2103* (GH, MO, US). CANAL AREA: Frijoles, 17 June 1960 (fr), *Ebinger 90* (F, MO, US); Fort Sherman and nearby, 9°20′N, 80°00′W, 0 100 m, 16 June 1983 (fl), *Hamilton & Stockwell 3692* (MO); Pipeline Rd., 1 May 1973 (early fr), *Kennedy & Wilder 3103* (F, MO); Río Pedro Miguel, nr. East Paraiso, 7 Jan. 1924 (fr), *Standley 29941* (US). COCLÉ: Cerro Gaital Caracoral, 800–1,000 m, 25 July 1968 (fl), *Dwyer & Lallathin 8950* (MO). COLÓN: along river ca. 4 mi. SW of Portobelo, 7 Apr. 1971 (fl), *Croat 14114* (MO); Río Guanche, 3–5 km above bridge on Portobelo Rd., 50–200 m, 8 July 1976 (early fr), *Croat 36982* (MO, NY); trail from headwaters of Río Boquerón back to fork with Río Escandaloso, route of abandoned railroad, 75–150 m, 21 July 1981 (fr), *Hammel 3995* (MO); between France Field and Cativa1, 9 Jan. 1924 (fl), *Standley 30370* (US); Palmas Bellas, 30 May 1971 (fl), *Thoms 31* (ENCB, F). DARIÉN: from Punta Guayabo to Río Jaqué, 50–200 m, 24 Apr. 1980 (fl), *Antonio 447* (ENCB, MO); Río Aruza, 24 Oct. 1967 (fr), *Bristan 1368* (GH, MO); Cativo Swamp ca. 6 mi. NW of El Real, 15 June 1962 (fl), *Duke 4824* (F, GH, MO); Río Mortí, 250 m, 18 Sep. 1967 (fr), *Duke 14185* (F, MO, NY); base of Cerro Pirre, 3 hours from Piji Vasal, 10 20 July 1977 (fl, fr), *Folsom et al. 4185* (MO); 0.5 1.5 mi. E of Manené, 21 Dec. 1980 (st), *Hartman 12099* (ENCB, MO); Río Tuquesa, Qda. Venado, 100 m, 4 July 1975 (fl), *Mori 6933* (MO). PANAMÁ: Río Chagres, 1 mi. above Madden Lake, 7 Oct. 1961 (fr), *Duke 4474* (GH 2 sheets, MO); 25 km NE of Cerro Azul on Río Piedras, Gorgas Memorial Labs, 550 m, 25 Nov. 1974 (fr), *Mori & Kallunki 3465* (MO—2 sheets); Río Tapia, 7 Dec. 11 Jan. 1924 (fr), *Standley 26133* (US); Arraiján, 15 m, 22 June 1938 (fl), *Woodson et al. 776* (F, MO). SAN BLAS: Río Kwadi, ca. 6 air mi. SW of Mulatupu, ca. 100 m, 20 Sep. 1967 (early fr), *Duke 14210* (F, MO, NY). VERAGUAS: Coiba Island, 31 Aug. 1924 (fl), *Collenette 466* (US).

The original spelling "*psychotriaefolia*" has been corrected to "*psychotriifolia*" in accordance with the International Code of Botanical Nomenclature (Article 73.8).

Psychotria psychotriifolia may be recognized by its oblanceolate to elliptic leaves drying green-brown to red-brown with collector vein near margin, epedunculate inflorescences with enlarged cup-like bracts subtending the ultimate glomerules, and narrowly ellipsoid (5–6 × 3 4 mm) fruits with conspicuous persistent calyx tube.

60. Psychotria rosulatifolia Dwyer, Ann. Missouri Bot. Gard. 67: 423, fig. 77. TYPE: Panama. Darién: trail from Río Pucro base camp up W ridge of Cerro Malí, 640 1,000 m, 6 Feb. 1975 (fr), *Gentry & Mori 14174* (holotype, MO). Figure 35.

Subshrub or herb 0.5 m tall; young stems glabrous or puberulent, the bark irregularly furrowed; stipules sheathing, ovate, often split down center, 15–20 × 6–7 mm, glabrous, caducous, leaving a red-brown ridge. *Leaves* sessile; blades membranous, lanceolate, the apex caudate, the base sagittate, 16–28 × 4.5–8.5 cm, glabrous above and below, drying deep red-brown or sometimes green-brown; secondary veins 27–32 pairs, diverging

80°–95°, brochidodromous with collector vein near margin, constantly arcuate, elevated below, glabrous or red-brown puberulent below, the axils lacking domatia or hairs; tertiary veins evident, orthogonal reticulate to percurrent. *Inflorescences* terminal, spreading panicles of cymes; panicle branched to 4 degrees, the axes delicate; main axis 8–13 cm long, the peduncle 2.5 6.5 cm long; secondary axes in 3 ranks, the first-rank axes 2, 2.5–4 cm long, the second-rank axes 2 or 4, the longer pair 1–2 cm long, the shorter pair when present 1 -1.2 cm long, the third-rank axes 2, 0.5 0.9 cm long; cymes branched to 1–2(–3) degrees; bracts linear, 4 mm long, glabrous; bracteoles triangular, to 1.2 mm long, glabrous. *Flowers* pedicellate, the pedicels 1–2 mm long; calyx cup-shaped, the tube 0.5–0.7 mm long, the lobes 5, often barely evident, triangular, to 0.2 mm long, glabrous; corolla white, the tube narrow-cylindrical, 2.5–4 × 1.2 mm, white pubescent in throat, the lobes 5, linear with 1-mm-long extension from apex, not spreading, 2.5–4 × 1 mm; stamens 5, the filaments 2 mm long in pins, not seen in thrums, the anthers narrow, 2 mm long; style 6 mm long in pins, not seen in thrums, the branches clublike. *Fruit* ellipsoid when dry, 5–6 mm long, 4–4.5 mm diam., maturing red, drying red-brown; persistent calyx a beak ca. 0.5 mm long; seed dorsal surface with 5 deep longitudinal furrows, the ventral surface with 2 barely evident longitudinal furrows.

Distribution (Fig. 35). Known only from the regions of Cerro Pirre and Cerro Malí, eastern Darién, Panama, at ca. 700 1,300 m elevation in premontane to low montane rainforest with equatorial-mountainous climate. *Psychotria rosulatifolia* has been collected in flower in April, July, and August, and in fruit in August, November, and February.

Additional specimens examined. PANAMA. DARIÉN: Cerro Pirre, 11 Apr. 1967 (fl), *Bristan 515* (MO); ascent of Cerro Pirre, Río Pirre, S of El Real, 750 1,030 m, 11 Aug. 1962 (fl, early fr), *Duke 5339* (MO); Cerro Pirre, 750 1,350 m, 9 10 Aug. 1969 (fl, fr), *Duke & Elias 13788* (MO); Cerro Pirre, ridgetop nr. Rancho Plastico, 1,200 m, 10–20 July 1977 (fl), *Folsom 4295* (MO); Cerro Pirre, valley between Pirre and next most southerly peak, 10 20 July 1977 (fl), *Folsom 4428* (MO); top of ridge leading to Cerro Pirre, nr. Rancho Plastico, 1,200–1,400 m, 13 Nov. 1977 (fr), *Folsom et al. 6285* (MO).

Psychotria rosulatifolia may be recognized by its large (16–28 × 4.5–8.5 cm), sessile, oblanceolate leaves with 27–32 secondary veins plus a collector vein; delicate panicles of cymes; flower buds appearing narrow and acuminate due to narrow 1-mm-long apical extensions from corolla lobes; and medium-sized (5–6 × 4–4.5 mm), ellipsoid fruits.

Five pin and no thrum collections suggest strongly that *Psychotria rosulatifolia* is pin-monomorphic.

61. Psychotria sixaolensis C. Hamilton, Phytologia 64: 234. 1988. TYPE: Costa Rica. Limón: rd. between Limón and Shiroles, Río Sixaola, 0.9 mi. SW of Bambu, 6.5 mi. SW of Bribrí, 0 50 m, 12 Aug. 1977 (fr), *Croat 43303* (holotype, MO). Figure 36.

Shrub or subshrub to 1.5 m tall; young stems ferrugineous-pubescent; stipules sheathing, ovate, 10 × 6 mm, ferrugineous-pubescent, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 1–3.5 cm long, red-brown puberulent, grooved above; blades membranous, elliptic to obovate, the apex acuminate, the base attenuate, (14)16–30 × (5.5–)8–13 cm, glabrous above, sparsely red-brown tomentose below, the midvein more densely tomentose, drying red-brown; secondary veins (20–)25–35 pairs, diverging 75°–80°, brochidodromous with collector vein near margin, constantly arcuate, elevated below, red-brown tomentose below, the axils lacking domatia or hairs; tertiary veins inconspicuous, orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of glomerules; panicle branched to 2–3 degrees; main axis in fruit 9.5–15 cm long, the peduncle in fruit 7.5 13.5 cm long; secondary axes in 2 ranks, the first-rank axes 2, 1.5–2 cm long, the second-rank axes 2, 0.5 cm long; bracts and bracteoles ovate, 7 × 6 mm, ferrugineous-pubescent. *Flowers* sessile; calyx cup-shaped, the tube 1–2 mm long, the lobes 5, linear, 2–3 × 0.8 mm, ferrugineous-pubescent; corolla white, the tube cylindrical, 4 × 2.5 mm, white pubescent in throat, the lobes 5, ovate with blunt robust protuberance from near apex, 3 × 1.5 mm; stamens 5, the filaments 3 mm long in pins, not seen in thrums, the anthers 1.3 mm long; style ca. 6 mm long in pins, not seen in thrums, the branches linear. *Fruit* ellipsoid when dry, 7 9 mm long, 5 mm diam., drying red-brown; persistent calyx 2 3 mm long; seed dorsal surface with 4 deep longitudinal furrows, the ventral surface with 2 shallow longitudinal furrows.

Distribution (Fig. 36). Known from southeastern Limón, Costa Rica, and Bocas del Toro, Panama, at 0–50 m elevation in tropical moist forest with equatorial-tropical climate. This species

has been collected in flower in April, in mature fruit in August.

Additional specimens examined. COSTA RICA. LIMÓN: nr. Río Sixaola, ca. 0.5 mi. SW of Bambu, ca. 3 mi. NE of Bratsi, 15 m, 12 Aug. 1977 (early fr), *Croat 43250* (CR, MO). PANAMA. BOCAS DEL TORO: Río Teribe between Qda. Treglo and Puerto Palenque, 2 Apr. 1968 (fl, early fr), *Kirkbride & Duke 536* (MO—2 sheets).

Psychotria sixaolensis may be recognized by its ferrugineous aspect, large (usually 16–30 × 8–13 cm) leaves with usually 25–35 secondary veins and a collector vein, and long-pedunculate panicles of glomerules with large (7 × 6 mm) ovate bracts.

The lone flowering collection seen is a pin morph.

EXCLUDED TAXA

Psychotria microdon (A. P. de Candolle) Urban, Symb. Antill. 9: 539. 1928. *Rondeletia microdon* DC., Prodr. 4: 408. 1830. *Mapouria microdon* (DC.) Bremek., Recueil Trav. Bot. Néerl. 31: 286. 1934.

Psychotria pinularis Sessé & Mociño, Fl. Mexic. ed. 2, 57. 1894.

Steyermark (Mem. New York Bot. Gard. 23: 446–447. 1972) included this species in subgenus *Psychotria*, from which it differs, however, in having leaves drying pale green, a seed cross-section with only a central keel on the dorsal surface (vs. several longitudinal furrows), marcescent stipule remnants persisting at the nodes, and lateral branches in opposite pairs (vs. diverging singly from a main axis). This species does not appear closely related to any neotropical members of *P.* subg. *Heteropsychotria* Steyerm., either. Instead, the above character states plus the leaf secondary veins arching broadly toward the margin suggest affinity with African *P.* subg. *Tetramerae* (Hiern) E. Petit, many species of which have bacterial "nodules" on the leaf undersides (Petit, Bull. Jard. Bot. État 34: 1–229, 1964; 36: 65–190, 1966). *Psychotria microdon* and *P. nutans* Sw. may be the sole neotropical species—aside from *P. punctata* Vatke, introduced in Florida—of that subgenus.

APPENDIX I. Numerical list of taxa.

Group 1

1. *Psychotria carthagenensis* Jacq.
2. *P. clivorum* Standl. & Steyerm.
3. *P. lamarinensis* C. Hamilton
4. *P. micrantha* Kunth
5. *P. neillii* C. Hamilton & Dwyer
6. *P. quinqueradiata* Polak.
7. *P. viridis* Ruiz & Pavón

Group 2

8. *P. balancanensis* C. Hamilton
9. *P. costivenia* Griseb.
   a. var. *altorum* (Standl. & Steyerm.) C. Hamilton
   b. var. *costivenia*
10. *P. fendleri* Standl.
11. *P. flava* Oerst. ex Standl.
12. *P. grandis* Sw.
13. *P. horizontalis* Sw.
14. *P. papantlensis* (Oerst.) Hemsl.
15. *P. pleuropoda* Donnell-Smith
16. *P. sylvivaga* Standl.

Group 3

17. *P. bakeri* Dwyer
18. *P. graciliflora* Benth. in Oerst.
19. *P. jimenezii* Standl.
20. *P. laselvensis* C. Hamilton
21. *P. liesneri* Dwyer
22. *P. marginata* Sw.
23. *P. orosiana* Standl.
24. *P. parvifolia* Benth. in Oerst.
25. *P. philacra* Dwyer

Group 4

26. *P. remota* Benth.

Group 5

27. *P. aguilarii* Standl. & Steyerm.
28. *P. boquetensis* Dwyer
29. *P. chagrensis* Standl.
30. *P. erythrocarpa* Schldl.
31. *P. fosteri* C. Hamilton
32. *P. fruticetorum* Standl.
33. *P. jinotegensis* Nelson, Molina & Standl.
   a. var. *jinotegensis*
   b. var. *morazanensis* C. Hamilton
34. *P. mirandae* C. Hamilton
35. *P. nervosa* Sw.

Group 6

36. *P. cascajalensis* C. Hamilton
37. *P. chiriquina* Standl.
38. *P. cocosensis* C. Hamilton
39. *P. dueri* C. Hamilton
40. *P. hornitensis* Dwyer & C. Hamilton
41. *P. lundellii* Standl.
42. *P. mexiae* Standl.
43. *P. olgae* Dwyer & Hayden
44. *P. panamensis* Standl.
   a. var. *compressicaulis* (K. Krause) C. Hamilton
   b. var. *ixtlanensis* C. Hamilton
   c. var. *magna* (Standl.) C. Hamilton
   d. var. *panamensis*
45. *P. sarapiquensis* Standl.
46. *P. stockwellii* C. Hamilton
47. *P. trichotoma* M. Martens & Galeotti

Group 7

48. *P. limonensis* K. Krause
49. *P. tenuifolia* Sw.

Group 8

50. *P. alfaroana* Standl.
51. *P. calophylla* Standl.
52. *P. chitariana* Dwyer & C. Hamilton
53. *P. dressleri* (Dwyer) C. Hamilton
54. *P. hammelii* Dwyer
55. *P. insignis* Standl.
56. *P. insueta* (Dwyer) C. Hamilton
57. *P. monteverdensis* Dwyer & C. Hamilton
58. *P. pacorensis* C. Hamilton
59. *P. psychotriifolia* (Seem.) Standl.
60. *P. rosulatifolia* Dwyer
61. *P. sixaolensis* C. Hamilton

Appendix II. List of exsiccatae.

Acosta, M. A., 29, 31 (19)
Aguilar, I., 21 (13); 126, 215 (27)
Aguilar, J. I., 750, 1140, 1143, 1371, 1729 (30)
Aguilar H., M., 260 (13); 292 (35); 499 (18); 509 (22)
Aguilera R., V., 2 (12)
Allen, P., 11 (22); 25, 27 (18); 308 (44d); 936 (1); 951 (12); 1187 (22); 1387 (44d); 2035 (12); 2186 (29); 2563 (13); 3507 (44d); 4060 (1); 4144 (22); 6498 (32)
Alonso, P., 26 (30)
Alston, A., 1853, 8716 (6); 8881 (35)
Andersson, N., *s.n.* (13)
Antonio, T., 1586 (37); 1771 (29); 1804 (44d); 2090 (56); 2305 (22); 2339 (13); 3241 (58); 3338 (22); 3461 (44d); 4447 (59); 4545 (13); 4796 (22); 4908 (6); 5060 (54)
Antonio, T. & W. Hahn, 4317 (29); 4340 (22); 4407 (26)
Araquistain, M., 3168 (44a); 3247 (22); 3248, 3403 (29); 3645 (37); 3818 (1)
Araquistain, M. & P. P. Moreno, 833 (6); 876 (1); 901a (6); 1213 (44d); 2490 (18)
Arnason, T., *s.n.* (49)
Arnason, T. & J. Lambert, 17081 (13); 17293, 17320 (35); 17615 (49)
Atencio, G., 11 (12)
Atwood, J., 57, 212b (44d); 224, 275, 306 (18); 4235 (22); 4678 (29); 4819 (22); 5258 (29)
Atwood, J. & A. D. Moore, 364 (29)
Atwood, J. & F. Seymour, 2990 (35)
Avendaño, S. & J. Calzada, 516 (47)
Avendaño D., M., 39 (2); 174 (18)
Aviles, S., 9 (13); 932 (22); 973 (48)
Bailey, L. H. & E. Z. Bailey, 63 (4); 161 (22); 393 (13)
Baker, C. F., 609 (6)
Bakes, R., 17 (13); 20 (35)
Bangham, W., 235 (22)
Barkley, F. & M. L. Smith, 40856 (6)
Barlow, F. D., 3 5A (6); 10 5, 10 5B (14); 14 4 (6); 30 14B, 30 14D (47)
Barrera, A. et al., 228 (9b); 298 (47)
Bartlett, H., 11435 (35); 11499 (6); 11622, 11869 (32); 12038 (7); 12043 (22); 12043a (13); 12205 (48); 12244 (35); 12397 (32); 12533 (41); 12534 (42); 12633 (9b); 12686 (35); 12722 (6); 12809 (9b); 12819, 12824 (32); 12834 (9b); 12835 (32); 12884 (35); 12907 (9b); 13002 (6); 13122 (32); 13143 (6)
Bartlett, H. & T. Lasser, 16343 (22); 16444, 16957 (35)
Basurto-Rafael P., F., 185 (9b); 246 (11)
Bawa, K. S., 139 (1)
Beach, J., 1339 (29); 1361 (22); 1365, 1366 (29); 1418, 1422 (44a); 1494, 1495 (22); 1511 (18); 1515 (44a)
Beach, J. & M. Grayum, 1504 (50)
Beaman, J., 5162 (11); 5190 (14); 5307 (45); 5310 (18); 5410 (42); 5564 (44d); 5573, 5594 (42); 6007 (44d); 6081 (11); 6094 (34); 6183 (6); 6187 (42); 6205 (48); 6391 (44d); 6448 (48)
Beaman, J. & C. Alvárez, 5364, 5772, 5976 (42)
Bequaert, J., 101 (35)
Bernal, W., 11 (13)
Bernoulli, C. & R. Cario, 1714 (13); 1717 (48)
Biolley, P., 4065 (1); 7391 (59); 17321 (49)
Blackmore, S. & G. Heath, 1956 (1)
Blake, S. F., 7619 (9b); 7755 (4); 7756 (9b)
Blum, K., 1213, 1221 (35); 1361 (22); 1385 (4); 1402 (35); 1414 (12); 1494 (13)
Blum, K. & J. Dwyer, 395 (59); 398 (12); 2107 (22); 2108 (48); 2148, 2152 (22); 2459 (35); 2494 (1); 2652, 2657 (44d)
Blum, K. et al., 1699 (18); 1708 (22)
Boege, W., 1239 (47)
Boster, J., *s.n.* (15)
Botteri, M., 542 (49); 920, 1056 (44d)
Bourgeau, E., *s.n.* (49); 2321 (9b), 2454 (49)
Bourgeau, M., *s.n.* (35)
Bravo H., H., 116, 208 (49)
Breedlove, D., 6319 (49); 6334 (6); 6485 (9b); 6489 (32); 7544 (9a); 7626 (49); 9537, 9744, 9792 (9a); 9993 (9b); 10593, 11392 (30); 12034 (9b); 13969 (9a); 14126 (30); 15397 (9b); 20102, 20672 (30); 21140 (44d); 23196 (9b); 23269 (42); 23396 (9a); 23901 (32); 23974, 24698 (30); 24913 (18); 24948 (9b); 25337 (9a); 25348 (9b); 25671 (9a); 25966 (6); 25975 (13); 26006 (30); 26139 (48); 26311 (44d); 26314 (9b); 26461 (47); 26522 (48); 26989 (13); 27173 (30); 27286 (13); 27360 (30); 27427 (32); 27437 (49); 27455 (48); 27577 (9a); 27821, 27877 (9b), 28107 (48); 28265, 28360, 28450 (30); 28501 (48); 28958 (30); 28971 (42); 31270 (30); 32880 (9a); 32945 (48); 33059 (18); 33093 (47); 33806 (49); 34380 (18); 34530 (9b); 34538 (42); 34559 (9b); 35102 (9a); 35141 (44d); 35316 (34); 36637 (49); 37190 (30); 38394 (13); 38672 (11); 38753 (9b); 39816 (13); 39944 (30); 40061 (13); 41341 (9a); 41971 (48); 42043 (30); 42076 (9a); 42189 (30); 42841 (13); 44372 (30); 53213 (9a)
Breedlove, D. & R. Dressler, 29565 (44d); 29846 (32); 29855 (48)
Breedlove, D. & E. McClintock, 34065 (22)
Breedlove, D. & P. Raven, 8205 (9a); 8336, 8347, 13161, 13205, 13331 (30); 13568 (9b)
Breedlove, D. & A. R. Smith, 21542 (30); 21713, 22174 (9b); 31291 (18); 31292 (9b); 32414 (44d)
Breedlove, D. & R. Thorne, 20640 (47); 20960 (42); 20976 (48); 21079 (9a); 21140 (9b); 21140a (44d); 21156 (9a); 21203 (42); 21313 (30); 30180 (18); 30660 (47); 30802 (44d); 30828 (9b)
Brenan, J. et al., 14484 (30)
Brenes, A. M., *s.n.* (6); 1902 (18); 3902, 3908, 4233, 4547, 5377 (6); 5534 (23); 5681 (24); 6249 (6); 12603 (13); 12624 (1); 13634, 13683 (18); 14281, 14310, 14531, 15528 (6); 19204 (13); 19218 (49); 21427, 21905 (6); 22006 (19); 22484 (1)
Bristan, N., 83 (18); 515 (60); 1018 (18); 1037 (59); 1051 (44d); 1170 (12); 1277 (53); 1368 (59); 1386 (22); 1457 (12); 1494 (18)
Broome, C., 704 (42)

Brown, B. & M. Artavia, 7252 (22)
Brown, M., 143, 161, 163 (22)
Buitrago, G., 1 (35)
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oerstedtiana Kuntze 91
oligotricha (DC.) Kuntze 410
papantlensis (Oerst.) Kuntze 108
parvifolia (Muell. Arg.) Kuntze 396
psychotriifolia (Seem.) Kuntze 899
quinqueradiata (Polak.) Kuntze 91
remota (Benth.) Kuntze 398
rufescens (Kunth) Kuntze 410
sessilifolia (M. Martens & Galeotti) Kuntze 888
tenuifolia (Sw.) Kuntze 888
trichotoma (M. Martens & Galeotti) Kuntze 427
trispicata (Griseb.) Kuntze 94
undata (Jacq.) Baill. 410
undata (Jacq.) Kuntze 410
viridis (Ruiz & Pavón) Kuntze 94

NOTES

NOTES ON ARACEAE

Anthurium iramirezae Bunting, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Río Negro, Serranía de Tapirapeco: afloramiento de roca granítica, 1°20′N, 64°55′W, 1,350 m, 25 Mar. 1988, *I. Ramírez & L. Laskowsky 310* (holotype, VEN). Figure 1A, B.

Herba perennis ca. 75 cm alta. Caulis horizontalis brevis crassusque. Petioli subteretes sed adaxialiter canaliculati, 19–40 cm longi. Foliorum laminae cartilagineae, ovatae, 30–37 cm longae (petiolos subaequantes vel eis usque ad duplo longiores), 19–24 cm latae, basi non profunde cordatae sinu plus minusve arcuato 1.0–1.7 cm profundo, apice breviter acuminatae, abaxialiter sparsim obscureque fusco-punctatae, nervis lateralibus primariis utrinque ca. 7 sub angulo 45–55° ex costa oreuntibus. Pedunculi 45–71 cm longi. Spathae anguste oblongo-ovatae, usque ad 11 cm longae, in sicco 1.8 cm latae, basi decurrentes per 0.8 cm, recurvatae vel reflexae, virides, persistentes. Spadices atropurpurei, 13.3–15.3 cm longi, sessiles sed axe antice nudo.

Perennial herb ca. 75 cm tall. Stem horizontal, thick, with very short internodes, some dry cataphyll remains, and few leaves. Petioles subterete but adaxially canaliculate, the canal narrower than petiole width and with rounded margins, 19–40 cm long; geniculum 1.7–2.3 cm long, 1.0–1.2 cm thick. Leaf blades nearly erect on petiole, cartilaginous (drying stiff), ovate, 30–37 cm long (subequaling or to twice as long as petioles), 19–24 cm wide (1.5–1.7 times longer than wide), basally shallowly cordate with sinus 1.0–1.7 cm deep, apically obtuse and briefly acuminate ending in a cusp to 1.3 cm long, adaxially glossy, abaxially sparsely and obscurely brown-punctate; midrib and all veins prominently elevated; primary lateral veins 7(–8) arising from each side of midrib at angles of 45–55° and running to margins; lesser veins forming a rather fine reticulum prominent on both faces; lowermost primaries not naked in sinuses. Peduncles solitary, 45–71 cm long. Spathes narrowly oblong-ovate, to 11 cm long (including 8-mm-long slender tip), drying 1.8 cm wide, basally decurrent for 0.8 cm, recurved or reflexed, green, persistent. Spadices cylindric, 13.3–15.3 cm long, 0.75 cm thick, dark purple becoming green in age, exceeding 1.5 cm thick in fruit, sessile but axis naked on front for 0.8 cm, with 6–8 flowers visible in the principal spiral. Fruits unknown.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: same locality as type collection, *Ramírez & Laskowsky 318* (VEN).

This species is closely related to *Anthurium guanchezii* Bunting but differs by having a cartilaginous leaf blade not basally stipitate, the lowermost primary lateral veins not naked in the basal sinus, a proportionally narrower spathe, and a nonstipitate spadix. In *A. guanchezii* Bunting, the blade is pergameneous or semicoriaceous, and the spathe is 3.6 times longer than broad. Additionally, *A. iramirezae* grows at an altitude of 1,350 m on granitic outcrops with thin soil and woody vegetation to 10 m tall, whereas *A. guanchezii* occurs in moist forests at 120 m altitude some 500 km to the north.

From *A. wurdackii* Bunting, the new species differs by having leaf blades that tend to be ovate and proportionally broader with an arcuate basal sinus, while the peduncle is shorter and the base of the spathe is more shortly decurrent. In *A. wurdackii*, the leaf blade is often elliptic-ovate, about 1.9 times longer than wide with an angular basal sinus, and the spathe is decurrent for 3.5–7.5 cm. Further, the leaf blade of *A. wurdackii* apparently lacks abaxial, dark punctations such as occur in *A. iramirezae*.

The species is named in honor of a collector of the type material, Ivón Ramírez, a young Venezuelan botanist who also successfully introduced it into cultivation. I observed the plant in Maracay, Venezuela, among a collection of unusual Venezuelan aroids and other plants growing at the family home of her husband, Germán Carnevali.

Philodendron triplum Bunting, sp. nov. TYPE: Venezuela. Edo. Bolívar: carretera El Dorado–Santa Elena de Uairén, en aprox. km 120 al sur de El Dorado, en bosque al lado de la vía, 1,200 m, 22 Feb. 1968, *G. S. Bunting 3102* (holotype, NY; isotype, MY). Figure 1C.

Herba perennis subrosulata. Caulis brevis validusque cataphyllorum reliquiis fibrosis ferrugineis tectus. Petioli abaxialiter rotundati superficie adaxiali late sed leviter concava, usque ad 19 cm longi. Foliorum laminae subcoriaceae, oblongae, usque ad 58 cm longae, 16.5 cm latae, basi rotundatae sinu acuto 1 cm profundo, apice acutae vel obtusae et breviter acuminatae, nervis later-

A

B

C

alibus primariis utrinque 9–11 sub angulo 55–65° ex costa abeuntibus. Inflorescentia ignota.

Subrosulate, perennial herb. Stem short, stout, with accumulated, rust-colored, fibrous cataphyll remains. Petioles abaxially rounded, with adaxial face broadly but shallowly concave, to 19 cm long. Leaf blades subcoriaceous, oblong, to 58 cm long (3 times longer than petioles), 16.5 cm wide (ca. 3.5 times longer than wide), at base rounded and notched (1 cm deep), at apex acute or obtuse and briefly acuminate; primary lateral veins 9–11 arising from each side of midrib at angles of 55–65°, with some secondary lateral veins manifest. Inflorescence unknown.

The type collection was taken from a plant growing as an epiphyte 2 m above the ground; it is not certain that it represents the fully mature adult phase of this species. A similar though somewhat less adult plant, collected in the same area as the type, has recently been seen in cultivation at the family home of Lic. Germán Carnevali in Maracay, Venezuela. A juvenile specimen, *Bunting 2916* (MY), collected in the same sector at km 126 south of El Dorado, Bolívar, Venezuela, apparently pertains to this taxon. It has leaves of similar form, texture, and color, but, as is typical of juvenile shoots, has a more slender stem with elongate internodes and has wide-winged petioles basally encircling the stem and sheathed up to the base of the blade.

This species differs from *Philodendron melinonii* Brongn. ex Regel by the proportionally shorter petioles and narrower leaf blades. In *P. melinonii*, the blade length is 1.4 times longer than the petiole and 1.5–2.4 times longer than wide.

The specific epithet reflects the fact that the leaf blade is three times longer than the petiole and more than three times longer than wide.

I am grateful to Lic. Germán Carnevali and his wife, Sra. Ivón Ramírez de Carnevali, for making available dried and living specimens of the aroids collected by them during recent botanical explorations. My appreciation is expressed to the Director and personnel of the Herbario Nacional (VEN), Jardín Botánico, Caracas, for the loan of herbarium material.

—George S. Bunting, *101 Linden Ave., Pocomoke City, Maryland 21851, U.S.A.*

←

FIGURE 1. A, B. *Anthurium iramirezae*.—A. Holotype.—B. Paratype.—C. *Philodendron triplum*, habit. Type specimen prepared from this plant.

HOSTA JONESII (LILIACEAE/FUNKIACEAE), A NEW SPECIES FROM KOREA

Hosta Tratt. is an economically important genus of approximately 22–25 species restricted to eastern Asia. *Hosta* has been placed in the Liliaceae (Cronquist, 1981; Hutchinson, 1964) or Funkiaceae (Dahlgren et al., 1985). Bailey (1930), Stearn (1931), and Hylander (1954) all pointed out that the major difficulty with the classification of the *Hosta* lies in the uncertainty regarding criteria for delimiting the species. The taxonomic difficulties have been attributed to relatively few diagnostic characters (Fujita, 1976), the extreme difference in appearance between living plants and dried herbarium specimens (Hylander, 1954), and possible widespread hybridization (Maekawa, 1940). Thus the treatment of species within *Hosta* has varied depending on authors. For example, Maekawa (1969) described several new species but combined others recognized in his 1940 treatment. Fujita (1976) noted that Maekawa (1940, 1969) did not consider the variability of natural populations when developing his classification. Fujita recognized only 15 species as native to Japan, while Maekawa (1969) had recognized 25 species there. Although Fujita carefully described morphological characters and ecological and geographical distribution, his studies were confined to Japan.

In 1985, 1987, and 1988, I conducted field trips to collect hostas from natural populations in Korea and on Tsushima Island of Japan in order to understand better the variation patterns. While visiting several islands off the coast of southern Korea, I encountered a morphologically distinct group of *Hosta* populations not referable to any described species of *Hosta*. The herbaria at Seoul National University (SNU), Tokyo University (TI), and Kyoto University (KYO) were visited and there were several undetermined specimens of this group collected by Young Chung (SNU) and one specimen collected by T. Nakai (TI). Loans were examined from BH, BM, E, K, L, and PE, but no herbarium specimens of the group were encountered. This series of populations is a new species as described below.

Hosta jonesii M. Chung, sp. nov. [subgen. *Bryocles* (Salisb.) F. Maekawa sect. *Tarthanthae* (F. Maekawa) F. Maekawa]. TYPE: KOREA: Kyeongsang Nam Do, Namhae Gun, Sangju Myeon, Namhae Island, Mt. Kumsan, N 13 mi. ascent from Yangha Ri. Among rocky and humus soil on south-facing slope, shade, ca. 250 m, common, 28 Aug. 1988, *M. G. Chung & M. S. Chung 1613* (holotype, GA). Figure 1.

Rhizoma breve repens. Folia erecto-patentia; laminae elliptico-lanceolatae vel anguste ovatae, 6–13 cm longae 3–5 cm latae, obtusae vel breviter acuminatae in apice, leviter angustatae in base, distincte petiolatae, supra atro-virentes vel viridulae, utrinque 5–7 nervatae, nervis infra paullo laevibus; petioli 4.5 13 cm longi 4–7 mm lati. Scapi oblique ascendentes, 35–60 cm longi 2–4 mm lati, in infera parte purpureo-punctati, teretes; inflorescentia ca. 15 cm longa (1–)3–20 florifera, bracteis acutis, navicularibus, viridibus, clausis. Infra inflorescentiam bracteae ascendentes, lanceolatae, 15–40 mm longae 4–20 mm latae. Pedicelli ascendentes, 4 8 mm longi, albo-virentes, minute purpureo-punctati. Alabastra viridescentia. Perianthia 40–50 mm longa, ca. 25 mm in diametro; pars inferior tuborum angustiorum saepe albescens; pars superior tuborum dilatatorum paullo campanulata, dilute purpurea; nervi interiores leviter colorati; lobi oblongi, acuti, 13 15 mm longi 7 8 mm lati. Stamina 39 48 mm longa, fere aequilonga corollae; antherae ca. 3 mm longae subflavescenti-purpureae. Pistillum 45–52 mm longum.

Herbaceous perennials from short, creeping rhizomes. Leaves erect-patent, spirally arranged at the base of stem; petioles 4.5–13 cm long, 4–7 mm wide, dotted with purple, slightly winged; blades elliptic-lanceolate or narrowly ovate, 6–13 cm long, 3–5 cm wide, dark dull green, slightly rigid, obtuse or acuminate at the apex, gradually narrowed at the base into the petioles, the nerves of upper leaf surface inconspicuous when fresh, nearly glabrous on the 5–7 pairs of somewhat smooth, not-elevated nerves of lower leaf surface, margins thinly white-lined. Scapes obliquely ascending, terete, 35–60 cm long, 2–4 mm wide, dotted with purple dots basally, usually with 2 lanceolate bracts below inflorescence, these 15–40 mm long, 4–20 mm wide; bracts within inflorescence acute, navicular, green, 8–13 mm long, 3–4 mm wide, not open at flowering, relatively persistent after flowering; pedicels obliquely ascending, 4–8 mm long, whitish green, minutely purple-dotted, usually shorter than the subtending bracts. Perianths 40–50 mm long, ca.

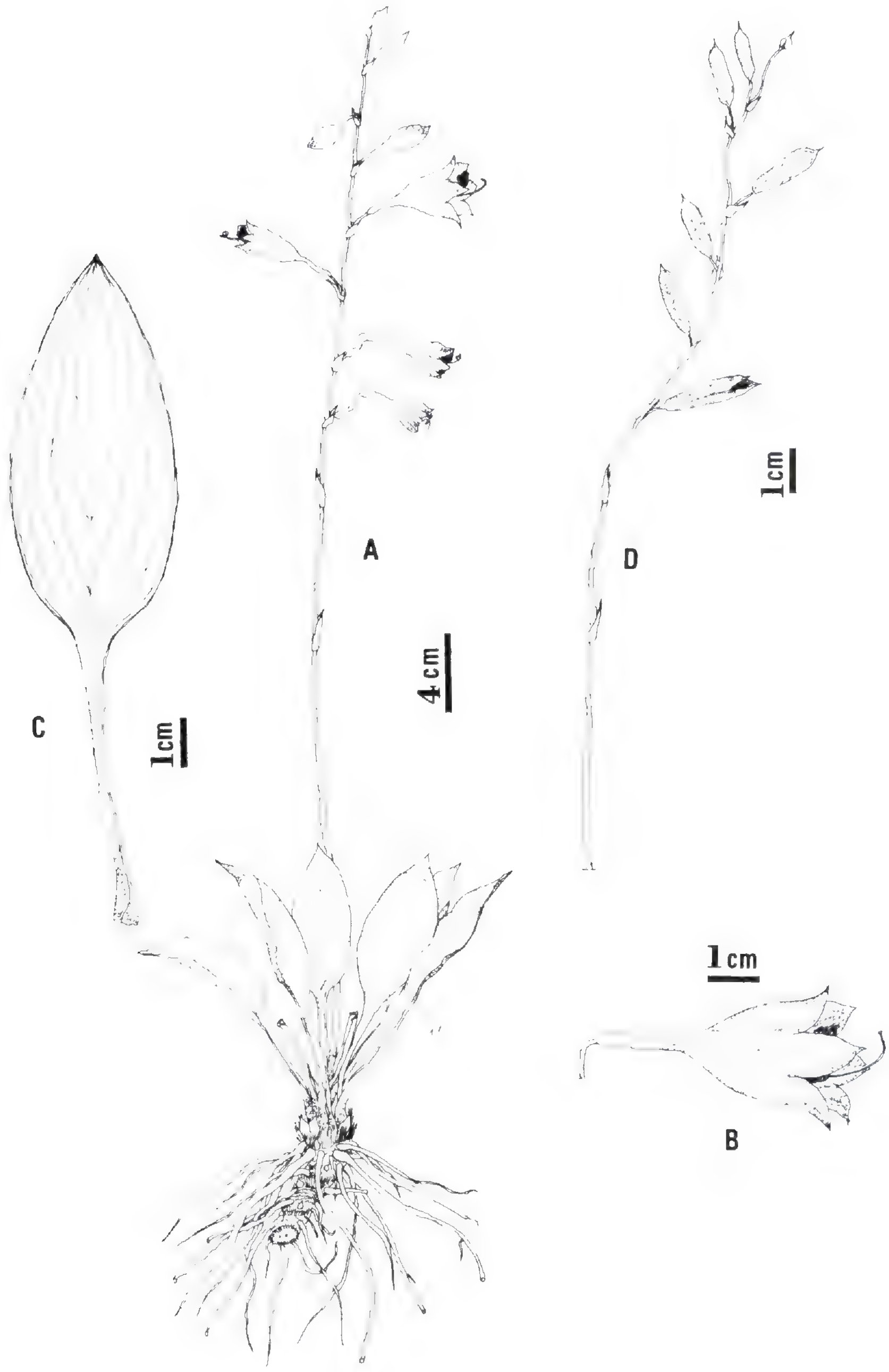

FIGURE 1. *Hosta jonesii* (A–C, holotype).—A. Habit. -B. Flower viewed from the side.—C. Leaf, adaxial surface. -D. Fruits on the obliquely ascending scape.

25 mm diam., about (1–)3 20 flowers on each raceme, whitish purple, greenish in bud; the basal narrower portion of perianth tubes whitish; the upper dilated portion of perianth tube somewhat bell-shaped; the inner nerves not intensely colored; lobes oblong, acute, 13–15 mm long, 7–8 mm wide; 6 translucent lines originating from the dividing parts of the lobes extend to the middle of lower narrower perianth tube; stamens 39–48 mm long, nearly equal to or longer than perianth; anther ca. 3 mm long, yellowish purple. Pistil 45–52 mm long. Capsule cylindric, 22–33 mm long, 4–6 mm wide. Flowering in mid August to early September.

Korean name. Tadohae-bibich'u.

Paratypes. KOREA: Kyeongsang Nam Do, Namhae Gun, Namhae Island; Mt. Kumsan, *Y. Chung s.n.* (NA);

Cholla Nam Do, Yoch'on Gun, Dolsan Island, *M. Chung 957* (GA); *S. Lee 101* (GA), *103* (KYO), *106* (MO), *107* (SNU), *112* (TI). Each collection from shade of pine–oak forest on rocky and rich humus soil near ocean.

Hosta jonesii is distinguished from other species of *Hosta* by the navicular, green, persistent bracts; thick, adaxially dark dull green leaves; and white-lined leaf margins. This species appears to be related to *H. minor* (Baker) Nakai by the shape of bracts and perianths and by the creeping rhizomes. It differs by the terete scapes, elliptic-lanceolate leaf blades, and flowering period from middle August to early September. *Hosta minor* flowers in mid July to early August and is endemic to southeastern Korea, including Wando and Kojae islands. The new taxon also is very close to *H. tsushimensis* N. Fujita (Fujita, pers. comm., 1988) but differs by having short creeping rhizomes; longer perianth lobes; upper dilated portions of perianth tubes bell-shaped; whitish purple inner perianth nerves; scapes dotted basally with purple; thinly white-lined leaf margins; somewhat smooth, not-elevated nerves of lower leaf surfaces; and thick, dark dull green leaves. *Hosta yingeri* S. B. Jones is distinct from *H. jonesii* by having ovate, adaxially lustrous leaves; delicate raceme of flowers spread around the central axis of the inflorescence; decurrent, flat bracts; relatively longer pedicels; and distinct, exserted 3+3 stamens.

The new species is named in honor of Dr. Samuel B. Jones, who has provided encouragement with my studies of *Hosta*. I thank Dr. Richard A. LaFleur for correcting the Latin description and Nancy C. Coile for comments on this manuscript. I also thank Dr. N. Fujita, Dr. H. Obha, and Mr. Haynes Currie for discussions on the classification of *Hosta*. Special thanks go to my parents, Mun Su and Jeom Ryo Chung, my wife, Min Suk Chung, Mr. Jong Sae Son, Seok Myeon Lee, and Chin Seop Hwang for their company on field trips. Gratitude is due the directors and curators of BH, BM, E, GA, K, KYO, L, PE, SNU, TI, and US.

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A NEW SPECIES OF *ALLOMARKGRAFIA* (APOCYNACEAE) AND NOTES ON THE GENUS

Allomarkgrafia laxiflora A. Gentry, sp. nov. TYPE: Colombia. Nariño: Tumaco Tuquerres road, W of Junín, 900 m, tropical pluvial forest, 25 Nov. 1981, *A. Gentry, C. Barbosa, E. Barrera, C. Bonifaz, H. Cuadros, L. Quiñones, E. Renteria & D. Sanchez 34939* (holotype, COL; isotypes, COL, MO).

Frutex scandens, glaber. Folia anguste oblonga, acuminata, coriacea, prope basin supra glandulifera. Inflorescentia laxa. Flores calyce 5-lobato, corolla infundibuliformi, parte superiore anguste campanulata, parte basali tubulosa, intra pilosa infra insertionem antherarum sagittatarum. Fructus linearis, 31–35 cm longus, ca. 2 mm latus.

Vine, stems terete, glabrous, drying dark with pale lenticels. Leaves very narrowly oblong, acuminate, cuneate at base, 7–13 × 1.5–2.8 cm, coriaceous, completely glabrous, the secondary and tertiary venation not evident, glandular adaxially at base of midvein, the petiole 0.5–0.8 cm long. Inflorescence axillary, open, dichotomously branched, the dichotomies subtended by minute triangular bracts. Calyx lobes round-tipped, 1–2 mm long; corolla pale yellow, narrowly campanulate above a narrowly tubular base, constricted at intersection of upper and lower tubes at level of stamen insertion, glabrous outside, inside densely pilose in upper half of lower part of tube, the base plus upper tube ca. 2.5 cm long, the lobes round, ca. 5 mm long, glabrous outside; filaments pilose, 1 mm long, the anthers sagittate, connivent, 5 mm long, the obtuse basal auricles ca. 1 mm long, the thin apical connective ca. 1 mm long; gynoecium 2 mm long, glabrous, apocarpous. Follicles paired, long and narrow, glabrous, 31 35 cm long, terete and ca. 2 mm wide before dehiscing, flat and to 5 mm wide when dehisced, the seeds narrow, acute, 5–6 mm long, with a dense apical tuft of tan trichomes to 3 cm long.

Although this distinctive new species resembles species of *Mandevilla*, it belongs to *Allomarkgrafia*, which differs from *Mandevilla* primarily in the paniculately branched inflorescence. However, this species is not at all close to *A. plumeriiflora* Woods., with which it was first identified. Among the obvious features differentiating *A. laxiflora* from *A. plumeriiflora* are the very openly branched inflorescences with small bracts, very differently shaped, narrower flowers, and narrower leaves.

Allomarkgrafia laxiflora is probably more closely related to *A. foreroi* A. Gentry and *A. ovalis* (Mgf.) Woodson, both of which occur in Chocó, Colombia, and both of which have similar laxly branching inflorescences. The new species differs vegetatively from both of these species in having very obscure leaf venation like that of *A. plumeriiflora*. The distinctive corolla shape of *A. laxiflora* likewise helps separate it from its two probable closest relatives. In *A. ovalis* the corolla is broadly (vs. narrowly) infundibuliform-campanulate above

FIGURE 1. *Allomarkgrafia laxiflora* (*Gentry et al. 34939*).

the basal tube, and in *A. foreroi* it is more narrowly campanulate above the basal tube, which is longer and narrower than that of the new species. *Allomarkgrafia foreroi* differs further from *A. laxiflora* in having slender, more tenuous inflorescence branches; longer, thinner calyx lobes; and differently colored flowers (white with upper tube greenish and lower tube reddish).

There are only two other *Allomarkgrafia* species in addition to those discussed above: Peruvian *A. tubiflora* Woodson ex Dwyer has leaves like *A. ovalis* and a longer campanulate upper corolla tube much like that of many Bignoniaceae, while Costa Rican *A. brenesiana* Woods. has white flowers with a gradually and narrowly infundibuliform upper part of the corolla tube. Another Costa Rican species described by Woodson is conspecific with *A. plumeriiflora*.

Thus from a bitypic genus (Woodson, 1933) *Allomarkgrafia* has now grown to six species. As currently known, it is strongly Chocó-centered, with four out of the six species occurring in trans-Andean Colombia: *Allomarkgrafia laxiflora* and *A. foreroi* are endemic to Chocó; *A. ovalis* is wide-ranging from Amazonian Peru to Panama; and *A. plumeriiflora* ranges from trans-Andean Colombia to Nicaragua. The two localized outliers are *A. brenesiana* at middle elevations in Costa Rica and *A. tubiflora* in upper Amazonian Peru (900–950 m).

The species of *Allomarkgrafia* may be separated by the following key:

1a. Inflorescence closely branching with strongly ascending, crowded, conspicuously bracteate branches; corolla tube base with conspicuous medial or submedial swelling; flowers shorter than 3 cm, the upper tube broadly infundibuliform ..... *A. plumeriiflora*

1b. Inflorescence laxly branching with small, inconspicuous bracts (reduced to 2–3 few-flowered branches in *A. tubiflora*); corolla tube base lacking prominent swelling; flowers longer than 3 cm, the upper tube campanulate or narrowly infundibuliform.

2a. Corolla tube very gradually narrowly infundibuliform above the narrow basal part; Costa Rica above 1,000 m ..... *A. brenesiana*

2b. Corolla tube abruptly campanulate above the narrow basal part; South America to Panama, below 1,000 m.

3a. Leaves broadly elliptic to oblong, the finely parallel tertiary venation conspicuous; base of corolla tube much shorter than campanulate to obconical upper part.

4a. Upper part of corolla tube broadly infundibuliform-campanulate, the mouth 2–3 cm across ..... *A. ovalis*

4b. Upper part of corolla tube campanulate, the mouth less than 1.5 cm across ..... *A. tubiflora*

3b. Leaves narrowly to very narrowly oblong or elliptic, the tertiary venation inconspicuous or not evident; base of corolla tube longer than narrowly campanulate upper part.

5a. Leaves abruptly acuminate, coriaceous, the secondary and tertiary venation not visible or very obscure below; young branchlets drying dark with light lenticels; inflorescences ca. twice branched, the branches drying black or dark brown; basal part of corolla tube pilose inside in upper half ..... *A. laxiflora*

5b. Leaves tapering gradually to long acumen, chartaceous, the secondary and tertiary veins not pronounced but clearly visible below; young branchlets drying light with dark lenticels; inflorescences 3–4 times dichotomous, the branches drying light brownish; basal part of corolla tube pilose inside only near apex ..... *A. foreroi*

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—Alwyn H. Gentry, *Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.*

CHROMOSOME NUMBER IN *WALLERIA* (TECOPHILAEACEAE)

The small African genus *Walleria*, comprising three species (Carter, 1962), is generally considered to be allied to the Lilialean family Tecophilaeaceae. The five core genera of Tecophilaeaceae, *Tecophilaea*, *Zephyra*, and *Conanthera* (all Chilean), *Odontostomum* (Californian), and *Cyanella* (southern African), are small seasonal perennials united by their tunicate cormous rootstock, basally clustered leaves, racemose inflorescences, and flowers with poricidal anthers, partly inferior ovary, and subulate style with a punctiform stigma. In addition, the pollen grains have an operculate sulcus and tectate-columellate ektexine (Simpson, 1985), and the smooth seeds have a multilayered testa with a black, phytomelan-encrusted outer layer. As treated by Hutchinson (1934), the first modern phylogenist to recognize the family, Tecophilaeaceae also included the African *Cyanastrum*, now generally treated as the sole genus of Cyanastraceae (Dahlgren et al., 1985; Simpson, 1985). In 1959 Hutchinson transferred *Walleria* to Tecophilaeaceae from Liliaceae–Dianelleae (Hutchinson, 1934). Dahlgren et al. (1985: 165) accepted *Walleria* in Tecophilaeaceae with reservations; Dahlgren & van Wyk (1988) concluded that it did belong in the family, although they placed it in its own subfamily, Wallerioideae.

Walleria is discordant in Tecophilaeaceae for several reasons. The rootstock is a fleshy naked tuber, the leaves are cauline (not basal), the inflorescence is foliose, and the ovary is completely superior. Also, the seeds are warty and dark brown, not smooth and black, and it is uncertain whether they contain phytomelan (Dahlgren & van Wyk, 1988), although this is said to be absent by Huber (1969). Simpson (1985) demonstrated that the pollen grains of *Walleria* resemble those of other Tecophilaeaceae in having a medial apertural operculate sulcus and an endexinous basal layer of the operculum and aperture border. Although the operculum of *Walleria* differs from other Tecophilaeaceae in being very scanty and in having a granular (vs. tectate-columellate) ektexine, its basic structural similarity with that of the core genera of the family supports inclusion of *Walleria* there (Simpson, 1985). Embryologically, *Walleria* differs in having mostly campylotropous ovules (anatropous in other Tecophilaeaceae) and a large embryo (Dahlgren & van Wyk, 1988). With this background in mind, we undertook this investigation of the chromosome number in the two tropical African members of the genus, previously unknown cytologically.

Materials and Methods

Root tips were harvested at mid-morning from greenhouse-grown wild-collected material, tubers of *W. mackenzii* and seeds of *W. nutans*. The tips were placed in saturated aqueous mono-bromonaphthalene, and left at room temperature for four hours before fixation in 3 : 1 absolute ethanol glacial acetic acid for two minutes. After hydrolysis in 10% HCl for six minutes at 60°C, the apical portions of the tips were squashed in FLP orcein (Jackson, 1972).

Voucher data are as follows:

Walleria nutans Kirk—Namibia. Gobabis: Steinhausen road, *Goldblatt & Manning 8802* (MO).

W. mackenzii Kirk—Malawi, Zomba district, near Thondwe village, *Goldbatt 7519* (MO).

Observations and Discussion

The diploid chromosome number in both species of *Walleria* examined is $2n = 24$. The chromosomes are of moderate size, 2–4 μm in the method used. The chromosomes are mostly acrocentric but four of the smaller pairs are sub-metacentric.

Basic chromosome number in Tecophilaeaceae is probably $x = 12$ (Ornduff, 1979; Goldblatt, 1980). *Cyanella* has predominantly $n = 12$ or 24, although a population of *C. hyacinthoides* has $n = 14$, and one population of *C. lutea* has $n = 8$ (Ornduff, 1979). Of the New World genera examined cytologically, *Tecophilaea* has $n = 12$ (La Cour, 1955) and *Odontostomum* $n = 10$ (Cave, 1949, 1970). The chromosome cytology of *Walleria* thus accords well with Tecophilaeaceae and, viewed in conjunction with data reviewed above, supports its placement here.

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NEW COMBINATIONS AND TAXONOMIES IN CLUSIACEAE

On preparing treatments of Clusiaceae for various floras in Central America, I have found the need to make several new combinations.

Dystovomita paniculata (J. D. Smith) Hammel, comb. nov. *Rheedia paniculata* J. D. Smith, Bot. Gaz. 55: 431. 1913. TYPE: Costa Rica. San José: between Río Union and Río Convento, 800 m, Feb. 1898, *Pittier 11957* (holotype, US).

Tovomita pittieri Engler, Bot. Jahrb. Syst. 58, Beibl. 130: 8. 1923. *Dystovomita pittieri* (Engler) D'Arcy, Ann. Missouri Bot. Gard. 65: 695. 1978. TYPE: Costa Rica. Cartago: Tuis Mountains, 1,000 m, May 1899, *Pittier 16094* (holotype, B, not seen; isotype, US).

Chrysochlamys clusiifolia subsp. *panamaensis* Maguire, Phytologia 36: 395. 1977. TYPE: Panama. Darién: Cerro Mali, 1,400 m, Jan. 1975, *Gentry & Mori 13769* (holotype, MO).

The following specimens probably represent most of the collections of this species.

Additional specimens examined. COLOMBIA. CHOCÓ: Río Truando, 40 200 m, *Duke 13320* (MO); Hoya del Río San Juan, 5 m, *Forero 4464* (MO); area of Baudó, 8 m, *Fuchs 21764* (MO); Serranía del Darién, 1,400 m, *Gentry 16775* (MO); Quibdó to Tutunendo, 90 m, *Gentry 24258a* (MO); 80 m, *Gentry 30286* (MO); Río Tagachi, 100 m, *Gentry 37059* (MO). VALLE: Bahía de Malaga, 0 20 m, *Gentry 40433* (MO). COSTA RICA. HEREDIA: Finca La Selva, 100 m, *Folsom 9612* (DUKE), *9689* (DUKE, MO); *Hammel 10966, 11545* (DUKE); *Hartshorn 1520* (MO); *D. Smith 173* (DUKE, MO). PUNTARENAS: near San Vito de Java, 1,700 m, *Raven 21791* (MO). PANAMA. CHIRIQUÍ: Fortuna area, 1,150 m, *McPherson 7310, 12505* (MO). COCLÉ: El Valle, 1,100 m, *de Nevers 4398* (MO); 1,000 m, *Duke 15102* (MO); 900 m, *McPherson 11246* (MO); 1,000 m, *McPherson 11959* (MO); 900 m, *Stein 995* (MO). DARIÉN: Cerro Mali, 1,300 m, *Cuadros 3984* (MO); 1,400 m, *Gentry 13769* (MO); slopes of Cerro Tacarcuna, 1,400 m, *Hammel 16570* (MO). VERAGUAS: N of Santa Fe, Cerro Tute area, 750 m, *McPherson 12093* (MO), *Mori 2612* (MO).

This is the only species of *Dystovomita* in Central America. Its large, ovate to nearly round leaves with very distant parallel lateral veins and large ligulate swellings at the bases of the petioles make even sterile material unmistakable. The holotype at US consists of two sheets: US—1382472, a twig with the remains of an inflorescence, and US—1382473, leaves.

At MO we still have very little material of this genus from Venezuela, where a second species, *D. clusiifolia* (Maguire) D'Arcy, is endemic (one collection, *Schultes 14755*, is from Vaupés in southeastern Colombia). Although I can see no way to distinguish sterile material of *D. clusiifolia* from *D. paniculata*, seemingly minor differences in the staminate flowers, along the lines indicated by Maguire (1977) and D'Arcy (1978), do hold up for the many new collections of the latter species, which is restricted to Colombia, Panama, and Costa Rica. However, contrary to somewhat inaccurate and contradictory interpretations of prior authors, the flowers of both species have two bracteoles; the internode between the bracteoles and sepals is shorter in *D. clusiifolia* than in *D. paniculata*.

In addition to differences in the staminate flowers, the fruits of *D. clusiifolia* appear to have somewhat longer stigmas (or at least they persist longer) and are slightly larger at maturity than those of *D. paniculata*.

Garcinia intermedia (Pittier) Hammel, comb. nov. *Rheedia intermedia* Pittier, Contr. U.S. Natl. Herb. 13: 454. 1912. TYPE: Guatemala. Alta Verapaz: Río Lanquín, 300 m, Mar. 1902, *von Türckheim 8180* (holotype, US, photo MO; isotypes, F, MO).

Calophyllum edule Seemann, Bot. Voy. Herald 89. 1853. *Rheedia edulis* (Seemann) Planchon & Triana, Ann. Sci. Nat. Bot. Ser. 4. 14: 310. 1860. Not *Garcinia edulis* Exell, in Journ. Bot. 1927. TYPE (of *C. edule* Seemann): Panama. Veraguas: San Lorenzo, *Seemann s.n.* (BM, not seen, photo MO).

Rheedia tonduziana Engler, Bot. Jahrb. 58 Beibl. 130: 10. 1923. TYPE: Costa Rica. San José: along Río Virilla near San Juan, 1,100 m, May 1897, *Tonduz 11249* (holotype, B, not seen, photo MO; isotype, US, photo MO).

Robson (1958) discussed the logical error in maintaining *Rheedia* separate from *Garcinia*, essentially saying that no basis for separating them exists. Previously, *Garcinia* was not considered to occur naturally in the New World, only *Rheedia*. Features thought to distinguish *Rheedia* from *Garcinia* (number of perianth parts and degree of fusion of the stamens) are not constant in *Rheedia* and occur in both genera. Adams (1972) and Four-

net (1978) treated *Rheedia* as a synonym of *Garcinia* for floras within the West Indies. D'Arcy (1980) nevertheless kept the two genera separate on grounds that transferring the species of subg. *Rheediopsis* from *Garcinia* to *Rheedia* would be "more correct" than uniting *Rheedia* with *Garcinia*. Recent comparative work within the family supports Robson's position (P. Stevens, pers. comm.).

Seemann's epithet (*edule*) cannot be transferred to *Garcinia* as it would create a later homonym. *Rheedia intermedia* clearly belongs in *Garcinia* and provides the oldest available epithet for the species.

Garcinia intermedia is the only Central American member of the genus with a soft, edible, exocarp. All others have a thick, tough, inedible exocarp and delicious, white, acidic, sweet endocarp (as in the mangosteen, *Garcinia mangostana* L.). Leaf sizes and shapes are variable in the species and encompass the narrow-leaved material named as *Rheedia tonduziana*.

Garcinia macrophylla C. Martius, Flora 24. 2. Beibl. 35. 1841. *Rheedia macrophylla* (C. Martius) Planchon & Triana, Ann. Sci. Nat. Bot. Ser. 4. 14: 309. 1860. *Garcinia megaphylla* Verdc., Kew Bull. 31: 262. 1977, nom. illeg. (superfluous new name based on *Rheedia macrophylla* (C. Martius) Planchon & Triana). Not *Garcinia macrophyla* Miq. (1864). Not "*G. macrophylla* Anderson ex Hooker" (manuscript name listed in *Index Kewensis* (1895), this species published as *G. andersonii* Hooker, 1872). TYPE: Brazil. *Martius s.n.* (not seen).

Rheedia macrantha Standley & Steyermark, Field Mus. Nat. Hist. Bot. 23: 65. 1944. TYPE: Guatemala. Alta Verapaz: along Río Frío near Tactic, 1,400 m, Apr. 1941, *Standley 90524* (holotype, F).

In a footnote to a description of a new African species of *Garcinia*, Verdcourt (1977) transferred *Rheedia macrophylla* to *Garcinia* giving it the new but superfluous name, *G. megaphylla*. His citation states that *Rheedia macrophylla* Planchon & Triana is "non *Garcinia macrophylla* T. Anders., nec Mart., nec Miq." However, Planchon & Triana gave a complete citation of *G. macrophylla* C. Martius in synonymy of their *R. macrophylla*. Clearly, the basionym of *Rheedia macrophylla* (C. Martius) Planchon & Triana and oldest usage of the epithet "macrophylla" in *Garcinia* is *G. macrophylla* C. Martius. *Garcinia macrophylla* Miq., from Sumatra, published more than 20 years after Martius's Brazilian species, may need a new name. It is not certain that *G. macrophylla* C. Martius occurs in southern Central America (see discussion under *Garcinia magnifolia* Pittier).

Garcinia madruno (Kunth) Hammel, comb. nov. *Calophyllum madruno* Kunth, Nov. Gen. & Sp. 5: 202. 1822. *Rheedia madruno* (Kunth) Planchon & Triana, Ann. Sci. Nat. Bot. Ser. 4. 14: 315. 1860. TYPE: Colombia. Antioquia: Magdalena and Cauca valleys, 300–1,000 m, *Bonpland 1723* (P, not seen, photo MO).

Verticillaria acuminata Ruíz Lopez & Pavón, Syst. Fl. Peruv. 140. 1798. *Rheedia acuminata* (Ruíz Lopez & Pavón) Planchon & Triana, Ann. Sci. Nat. Bot. Ser. 4. 14: 314. 1860. Not *Garcinia acuminata* Planchon & Triana (1860). TYPE: Peru: *Ruíz & Pavón s.n.* (G, not seen, photo, MO).

Ruíz and Pavón's older epithet, *acuminata*, cannot be transferred to *Garcinia* as it would create a later homonym. *Calophyllum madruno* appears to provide the next-oldest available epithet for this distinctive species with tuberculate fruits.

Garcinia magnifolia (Pittier) Hammel, comb. nov. *Rheedia magnifolia* Pittier, Contr. U.S. Natl. Herb. 13: 454. 1912. TYPE: Costa Rica. Cartago: above Río Hondo near Matina, 400 m, Aug. 1901, *Pittier 16165* (holotype, US, photo MO).

Rheedia chocoensis Cuatrec., Ann. Inst. Biol. 20: 106. 1949. TYPE: Colombia. Valle: Río Calima, La Trojita, 5–50 m, Feb. 1944, *Cuatrecasas 16387* (holotype, F).

I consider Panamanian material previously identified as *Rheedia lateriflora* L. and *R. macrophylla* to be conspecific with *Garcinia magnifolia*. Stigmas of *G. humilis* (Vahl) C. Adams (= *R. lateriflora*) and *G. macrophylla* are lobed, and the mature fruits are apiculate, whereas *G. magnifolia* has globose mature fruits with a disc-shaped stigma. Recent Colombian collections demonstrate that *R. chocoensis* falls within the variability of *Garcinia magnifolia*.

Under the taxonomy adopted here, with fruiting material most important for identifying specimens, four native species of *Garcinia* occur in Central America. They can be distinguished by the following key:

KEY TO NATIVE SPECIES OF *GARCINIA* IN CENTRAL AMERICA

1a. Fruits with a soft, edible exocarp and 1 or 2 seeds; leaves usually drying dull on both surfaces ..... *G. intermedia*

1b. Fruits with a hard, inedible exocarp and often more than 2 seeds; leaves usually drying shiny above.
2a. Exocarp tuberculate; mature fruit mostly less than 4 cm in diam.; leaves drying metallic silver-green below, resin lines obvious on leaves ..... *G. madruno*
2b. Exocarp smooth; mature fruit often 6 cm or more in diam.; leaves drying green or brown below, resin lines inconspicuous.
3a. Leaves very coriaceous, drying greenish below; fruits globose, not apiculate ..... *G. magnifolia*
3b. Leaves ± membranaceous, drying brownish below; fruits ovoid, apiculate ..... *G. macrophylla*

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A NEW SPECIES OF *CALYCOLPUS* (MYRTACEAE) FROM THE VENEZUELAN GUAYANA

In preparation of a treatment of the subtribe Myrtinae (Myrtaceae) for the *Flora of the Venezuelan Guayana* a new species of *Calycolpus* has come to my attention. It is known to me through two collections, both from Estado Bolívar, Venezuela. It clearly belongs to *Calycolpus* as shown by the following combination of characters: flowers pentamerous and erect; stamens exserted, the anthers elongate, with several glands in the connective; seed coat lustrous with no pulpy covering, the outer seed coat ca. 1 cell thick at narrowest point, the superficial cells of the seed coat nearly isodiametric.

Calycolpus bolivarensis Landrum, sp. nov. TYPE: Venezuela. Bolívar: entre kms 146 y 145 de carretera a San Juan de Manapiare, 150 m, 5 Mar. 1977 (fl), *A. Fernández 3068* (holotype, MY). Figure 1.

C. cochleato McVaugh primo adspectu simillima, sed folio sessili vel subsessili, oblongo-lanceolato; petioli 0–1 mm longi; nervi laterali prominenti subtus; pedunculis in brachyblastos bracheatos aggregatos in extremitatibus ramunculorum.

Frutex circa 1-metralis; pili albi, simplices; ramuli juventute dense puberulentes; folia 4.5–10 cm longa, 1.8–3.3 cm lata, 2–3-plo longiora quam latiora; apex acuminatus; basis subcordata; laminae coriaceae, in sicco pallido-brunneae vel atrorufo-brunneae; hypanthium campanulatum, circa 4 mm longum, dense puberulum; stamina circa 185, circa 8 mm longa, antheris circa 0.8 mm longa, connectivum circa 10-glandulis; ovarium 3-loculare, loculis 15–19-ovulatis; stylus 7–10 mm longus, glaber.

Shrub ca. 1 m high, the twigs, leaves, and flowers sparsely to densely puberulent on most surfaces; hairs whitish, simple, mainly appressed, <0.1–ca. 0.8 mm long; young twigs grayish to reddish brown, densely puberulent. Leaves sessile or subsessile; blades stiffly coriaceous, drying light brown to dark reddish brown, oblong-lanceolate, 4.5–10 cm long, 1.8–3.3 cm wide, 2–3 times as long as wide, moderately to sparsely puberulent or densely puberulent along the midvein, the margin revolute, the apex acuminate, the base subcordate; midvein impressed to nearly flat above, prominent below; lateral veins ca. 20–22 pairs, nearly straight, leaving the midvein at nearly a 90° angle, visible or not visible above, prominent below; marginal veins about equaling laterals in prominence, running about parallel to and ca. 2–3 mm from the margin; petiole 0–1 mm long, 1–3 mm wide. Peduncles ca. 1–2 cm long, ca. 1.5 mm wide at apex, velvety puberulent, borne in the axils of bracts, clustered in bracteate shoots at the tips of branches; bracteoles clasping the hypanthium, triangular, ca. 0.6–1.5 mm wide, 1–2 mm long. Calyx lobes before anthesis about triangular, ca. 2–3 mm long, 2–2.5 mm wide, densely to sparsely appressed puberulent within, sparsely puberulent without, the hypanthium tearing 1–3 mm between the lobes at anthesis, the calyx lobes thus longer than before; petals sparsely to moderately puberulent; hypanthium campanulate, ca. 4 mm long, densely velvety puberulent; disk ca. 5 mm across, densely puberulent on staminal ring; stamens ca. 185, ca. 8 mm long; anthers ca. 0.8 mm long, with ca. 10 glands in connective; ovary 3-locular; ovules 15–19 per locule, ± multiseriate; style 7–10 mm long, glabrous. Fruit globose, probably ca. 1 cm diam.; seeds ca. 12 per fruit, ca. 4 mm long, the seed coat lustrous, ca. 1 cell thick across distal wall, the cells nearly isodiametric.

Additional specimen examined. Venezuela. Bolívar: entre Guaniamo y Perro de Agua, ca. 100–280 m, 9 June 1984 (young fr), *S. Lopez-Palacios, A. Carabot & C. Rosquete 4521* (NY).

Calycolpus bolivarensis is most similar to *C. cochleatus*. The differences are summarized in the key below.

1a. Leaves oblong-lanceolate, sessile to subsessile, the petiole 0–1 mm long; lateral veins prominent below; peduncles borne in the axils of bracts, clustered in bracteate shoots at the tips of young branches; hypanthium densely puberulent ..... *C. bolivarensis*

1b. Leaves elliptic to obovate, petiolate, the petiole 1–6 mm long; lateral veins indistinct to scarcely visible below; peduncles borne in the axils of leaves or bracts, solitary or clustered in axillary bracteate shoots along the length of young branches; hypanthium densely lanate ..... *C. cochleatus*

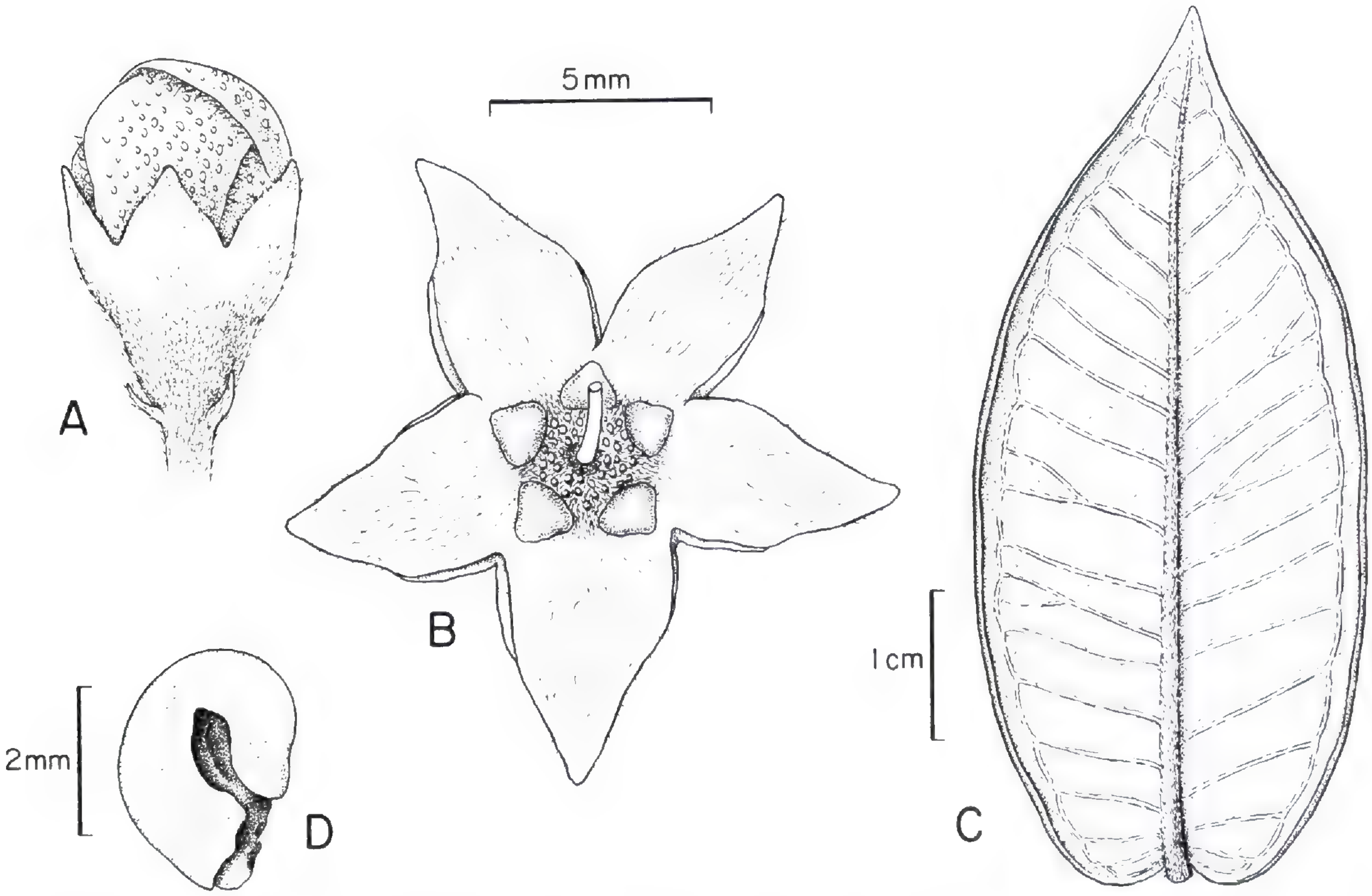

FIGURE 1. *Calycolpus bolivarensis*. A. Flower bud. B. Flower after anthesis, showing subtriangular petal scars, stamen scars, and tears between calyx lobes.—C. Leaf from below.—D. Lateral view of seed. A, C from *Fernandez 3068* (MY); B, D from *Lopez-Palacios et al. 4521* (NY). Drawn by Bobbi Angell.

I am grateful to Bruce Holst for discovering and sending me the specimen of *Calycolpus bolivarensis* from MY that I have used as the type.

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CHROMOSOME NUMBER IN *PHENAKOSPERMUM* AND *STRELITZIA* AND THE BASIC CHROMOSOME NUMBER IN STRELITZIACEAE (ZINGIBERALES)

Chromosome counts are available for most Afro-Madagascan members of Strelitziaceae but until now the neotropical *Phenakospermum* has been unknown cytologically. Chromosome cytology of the small southern African genus *Strelitzia* is comparatively well known. The two acaulescent species *S. reginae* Ait. (syn. *S. parvifolia* Ait.) and *S. juncea* Link (possibly only a form of *S. reginae*) have diploid numbers of $2n = 14$; in contrast, the caulescent *S. alba* (L.f.) Skeels (syn. *S. augusta* Thunb.) has $2n = 22$ (Table 1). The closely related *S. nicolai* Regel & Koern., also caulescent, has been reported by Satô (1948, 1960) as having $2n = 14$. The remaining species, *S. caudata* R. A. Dyer, is unknown cytologically.

It has seemed puzzling that the chromosome number of *S. nicolai* corresponded with the two acaulescent species rather than with the allied caulescent *S. alba*, particularly as the merit of maintaining the two species as separate (Geldenhuys, pers. comm.) is in some doubt. We have now established that at least one Transkeian population of *S. nicolai* has the same chromosome number, $2n = 22$, as *S. alba*. The chromosome number in *Phenakospermum* is also $2n = 22$.

Materials and Methods

Seeds collected in the wild were germinated in the greenhouse. Actively growing root tips were harvested at mid morning into saturated aqueous mono-bromo-naphthalene and left at room temperature for four hours before fixation in 3:1 absolute ethanol-glacial acetic acid for two minutes. After hydrolysis in 10% HCl for six minutes at 60°C, the apical portions of the tips were squashed in FLP orcein (Jackson, 1972). Voucher data are as follows: *Phenakospermum guianensis* Aublet, Guyana: *DeFilipps s.n.* (US); *Strelitzia nicolai* (L.f.) Skeels, South Africa. Transkei: coastal bush at Mkambati Nature Reserve, *P. Goldblatt 7603a* (MO).

Observations and Discussion

The diploid chromosome number of *P. guianensis* and *S. nicolai* is $2n = 22$. The chromo-

Table 1. Chromosome numbers in Strelitziaceae.

Species	Haploid Number *n*	References
Phenakospermum		
guianensis Aublet	11	this paper
Ravenala		
madagascariensis Sonn.	11	Cheesman & Larter (1935); Simmonds (1954); Sharma & Bhattacharyya (1959); Satô (1948, 1960)
Strelitzia		
alba (L.f.) Skeels	11	Cheesman & Larter (1935); Simmonds (1954); Chakravorti (1960); Satô (1948, 1960)
nicolai Regel & Koern.	11[1]	this paper
reginae Ait.	7	Cheesman & Larter (1935); Chakravorti (1960); Satô (1948, 1960); Mahanty (1970); Small et al. (1980)
juncea Link	7	Mahanty (1970, as *S. parvifolia* var. *juncea* and as *S. parvifolia*); Small et al. (1980)
×*kewensis* (*S. reginae* × *S. alba*)	17	Cheesman & Larter (1935)

[1] Reports by Satô (1948, 1960) of $n = 7$ in this species are presumed to be incorrect and hence are excluded from the table.

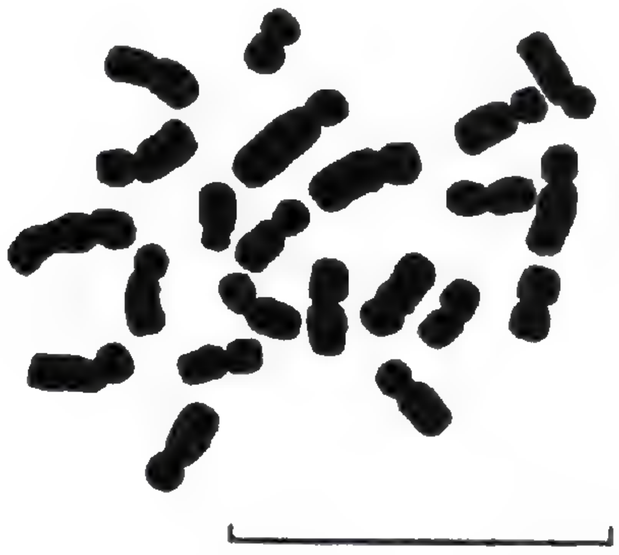

FIGURE 1. Mitotic metaphase in *Strelitzia nicolai*. Scale bar = 10 μm.

somes are of moderate size, ranging 1.5–3.5 μm in the method used. The chromosomes are mostly acrocentric, but four of the smaller pairs are submetacentric (Fig. 1). The karyotypes are comparable to those illustrated by Small et al. (1980) for *S. reginae* and *S. juncea* except for the difference in the number of chromosomes.

It is likely that Satô's count of $2n = 14$ for *Strelitzia nicolai* is incorrect. Our count provides additional evidence that the caulescent species of *Strelitzia* have $x = 11$. This corresponds with the number in the Madagascan *Ravenala*, also $x = 11$ (Table 1), the least specialized member of the family according to Lane (1955). All the arborescent members of Strelitziaceae thus have $x = 11$.

The families most closely related to Strelitziaceae—Musaceae and Heliconiaceae—have $x = 11$ and 12 respectively (Goldblatt, 1980). This makes it reasonable to hypothesize that $x = 11$ is basic for Strelitziaceae, as Mahanty (1970) suggested. If this is correct, it follows that the arborescent members of the family have retained the ancestral base number while the acaulescent species of *Strelitzia* have a derived chromosome number. This implies that the acaulescent condition in the family is secondary, which is consistent with the conclusions of Lane (1955) and Tomlinson (1960).

The alternative, that $x = 7$ is basic, seems to us less likely, although Chakravorti (1960) has suggested that $x = 11$ in Musaceae (including Strelitziaceae and Heliconiaceae) is derived from $x = 7$ by fragmentation across eight secondary constrictions in the *S. reginae* karyotype. This process is mechanically unlikely (Jones, 1977). In light of the predominance of decreasing over ascending aneuploidy in plants (Stebbins, 1950; Jones, 1977 & pers. comm.; Goldblatt, 1981), we assume that the chromosome number in the acaulescent species of *Strelitzia* was achieved by chromosome fusion leading to the reduced base number. Critical measurement of the quantity of DNA in *Strelitzia* may help solve this question.

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ENCEPHALARTOS VOIENSIS (ZAMIACEAE), A NEW EAST CENTRAL AFRICAN SPECIES IN THE *E. HILDEBRANDTII* COMPLEX

In the past 30 years, several locally endemic species of *Encephalartos* have been described for Central Africa. Most are from Mozambique (Dyer & Verdoorn, 1969; Lavranos & Goode, 1985), Zimbabwe (Dyer & Verdoorn, 1969), and, to a lesser extent, Zaire (Devred, 1959; Malaisse, 1969). All of these taxa are located west and southwest of a line connecting Lake Victoria, Lake Tanganyika, and Lake Niassa (Fig. 1). Little work has taken place on *Encephalartos* east of this line. In fact, the distribution map in the most thorough and recent work on African *Encephalartos* (Melville, 1957) shows no collections between the line and the east coast of Africa other than two locally endemic species he described: *E. bubalinus* Melville and *E. tegulaneus* Melville. Heenan (1977) repeated Melville's (1957) descriptions and included a discussion of three undescribed and imperfectly known, presumably new taxa from this area.

One of us (JPS) has recently collected material of *Encephalartos* in the central border region of Kenya and Tanzania. In these collections there is

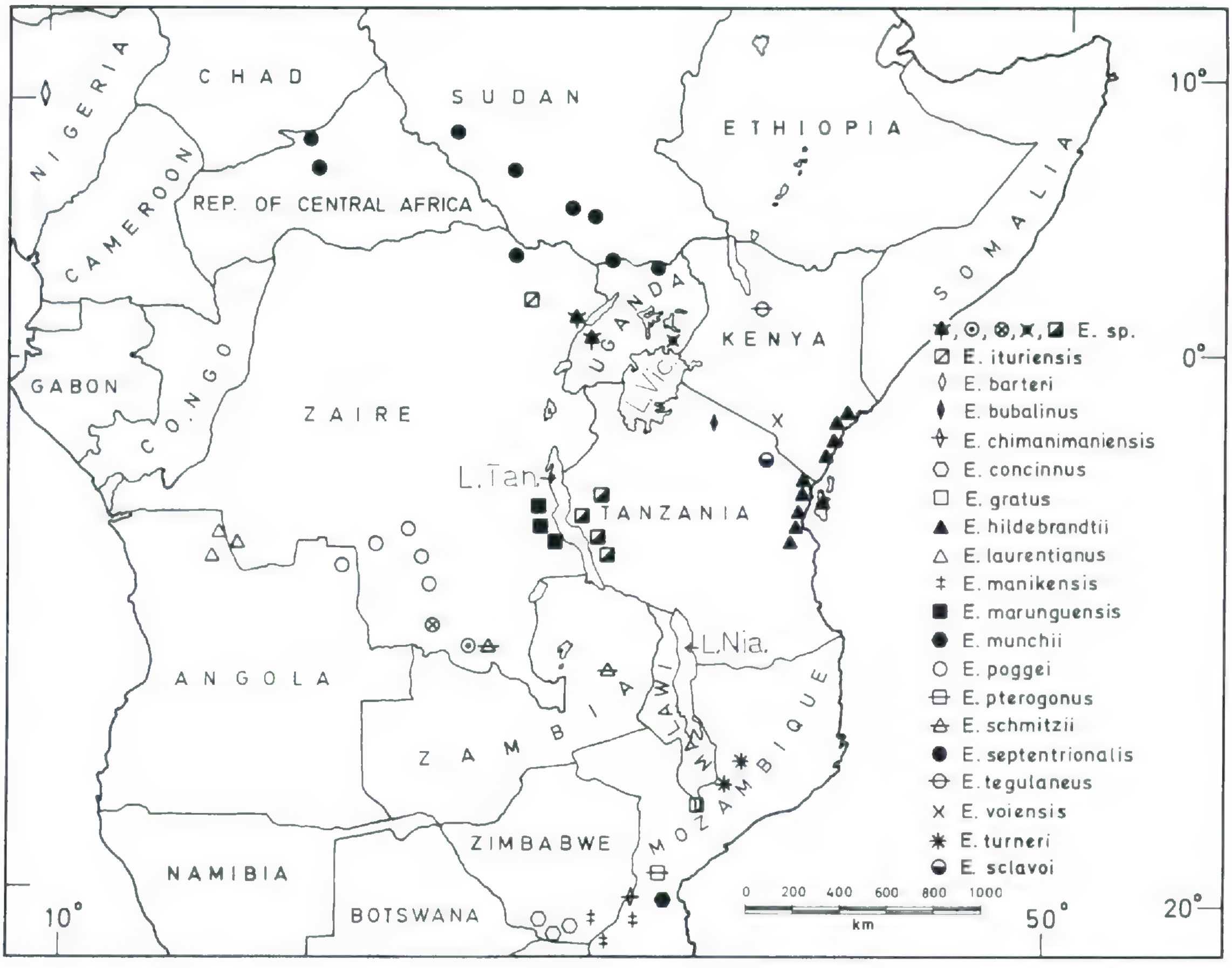


FIGURE 1. Distribution map of *Encephalartos* species in Central Africa. Derived, in part, from Melville (1957) and Devred (1959). L. Nia. = Lake Niassa, L. Vic. = Lake Victoria, L. Tan. = Lake Tanganyika.

at least one new species, which is known to us from two localities near Voi, Kenya. This species appears in many respects, including locality, to correspond to Heenan's (1977) *Encephalartos* "sp. B." This species is described below and is followed by a discussion of its relationships and affinities to neighboring congeners.

Encephalartos voiensis Moretti, D. Stevenson & Sclavo, sp. nov. TYPE: Kenya: Voi, 2 Jan. 1986 (♀), *Sclavo 1* (holotype, K). Figure 2.

Truncus erectus, ad 2.5 m altus, 35–70 cm diam. Cataphylla acuminato-lanceolata vel linearia, dense tomentosa. Folia 2–4 m longa, oblonga, ad basin abrupte attenuata; rachis glabra duobus sulcis superne praedita. Foliola mediana alternata vel subopposita, oblanceolata, subfalcata, sensim acuminata, pungentia, marginibus calloso-dentatis, dentibus 1–5, basi abrupte cuneata superne 1–5 infereque 0–1 spinosa, 25–40 cm longa, 4 cm lata; foliola inferiora abrupte diminuta, bifurcata; foliola infima in spinas mutata. Strobilus ♂ lineare-cylindricus, 45–50 cm longus, 10 cm diam.; pedunculus ebracteatus, 5–7 cm longus, 3–5 cm diam.; microsporophylla ad axin perpendicularia, deltoideo-cuneata, 35–40 mm longa, 22–25 mm lata, bulla deflexa praedita. Strobilus ♀ cylindricus vel ovoideo-cylindricus, 50–60 cm longus, 15–20 cm diam.; pedunculus ebracteatus, 5–7 cm longus, 3–5 cm diam.; megasporophylla mediana rhomboidea, 35 mm longa, 40 mm lata; pedicellus 10 mm longus, tribus abaxialibus faciebus praeditus; bulla rhomboidea, 40 mm lata, 18 mm alta, 24 mm profunda; bullae terminalis facies hexagona atque vulticulo praedita; adaxialis facies ex tribus trapezoideis partibus constituta atque tuberculata crista tuberculatoque margine praedita; lateralis bullae lobi 7–9 mm longi, 2–4 mm lati, ad latera complanati.

Trunk erect, to 2.5 m tall, 35–70 cm diam., straight to slightly tapering towards apex, leaf bases persistent. *Leaves* 2–4 m long, oblong, gradually tapered basally and becoming abruptly spinose in the lower ⅕. *Petiole* bulbous and tomentose. *Rachis* glabrous and with 2 shallow longitudinal adaxial grooves between leaflet insertions. *Median leaflets* alternate to subopposite, coriaceous, adaxially concave, blue-green, inserted at a right angle to the rachis and slightly oblique in the ab-adaxial plane, oblanceolate, subfalcate, 25–40 cm long, 4 cm wide, gradually acuminate apically and pungent, abruptly attenuate and strongly inequilateral basally, superior margin with 1–5 strong spinose teeth on the basal curve and with 1–5 barely discernible callose teeth along the rest, inferior margin with 0–1 small teeth basally and 1–5 barely discernible callose teeth along with the rest. *Lower leaflets* exhibiting an abrupt transition from those with 1 basal spinose tooth on the superior margin to those with bifurcate apices to completely reduced and pungent lower leaflets. *Microsporangiate strobilus* long-cylindric, greenish yellow when young, yellow to tan when shedding pollen, 45–50 cm long, 10 cm diam.; peduncle without bracts, glabrous, 5–7 cm long, 3–5 cm diam. *Median microsporophylls*, 35–40 mm long, 22–25 mm wide, perpendicular to the strobilus axis, cuneate to deltoid, bulla deflexed, terminal facet triangular to pentagonal. *Megasporangiate strobilus* cylindrical to ovoid-cylindrical, green to yellow when young, yellow to tan when mature, 50–60 cm long, 15–20 cm diam.; peduncle ebracteate and glabrous, 5–7 cm long, 3–5 cm diam. *Median megasporohylls* pedicellate with rhomboid bulla, 35 mm long, 40 mm wide; pedicel with 3 abaxial facets, the median facet inconspicuous and triangular, 10 mm long. *Bulla of megasporophyll* rhomboidal, 40 mm wide, 18 mm high, 24 mm deep; the terminal facet slightly concave and hexagonal, 15–17 mm wide, 6–8 mm tall; adaxial face with 2 lateral trapezoidal facets, a median rectangular to trapezoidal facet, and a short median lobe 2–4 mm wide and long, the margin and seminal fringe tuberculate; abaxial face with 2 lateral trapezoidal facets and a median rectangular to trapezoidal facet with obtuse lateral sagittal ridges, the inferior ridge and sagittal crest tuberculate; lateral lobes 7–9 mm long, 2–4 mm wide, flattened laterally.

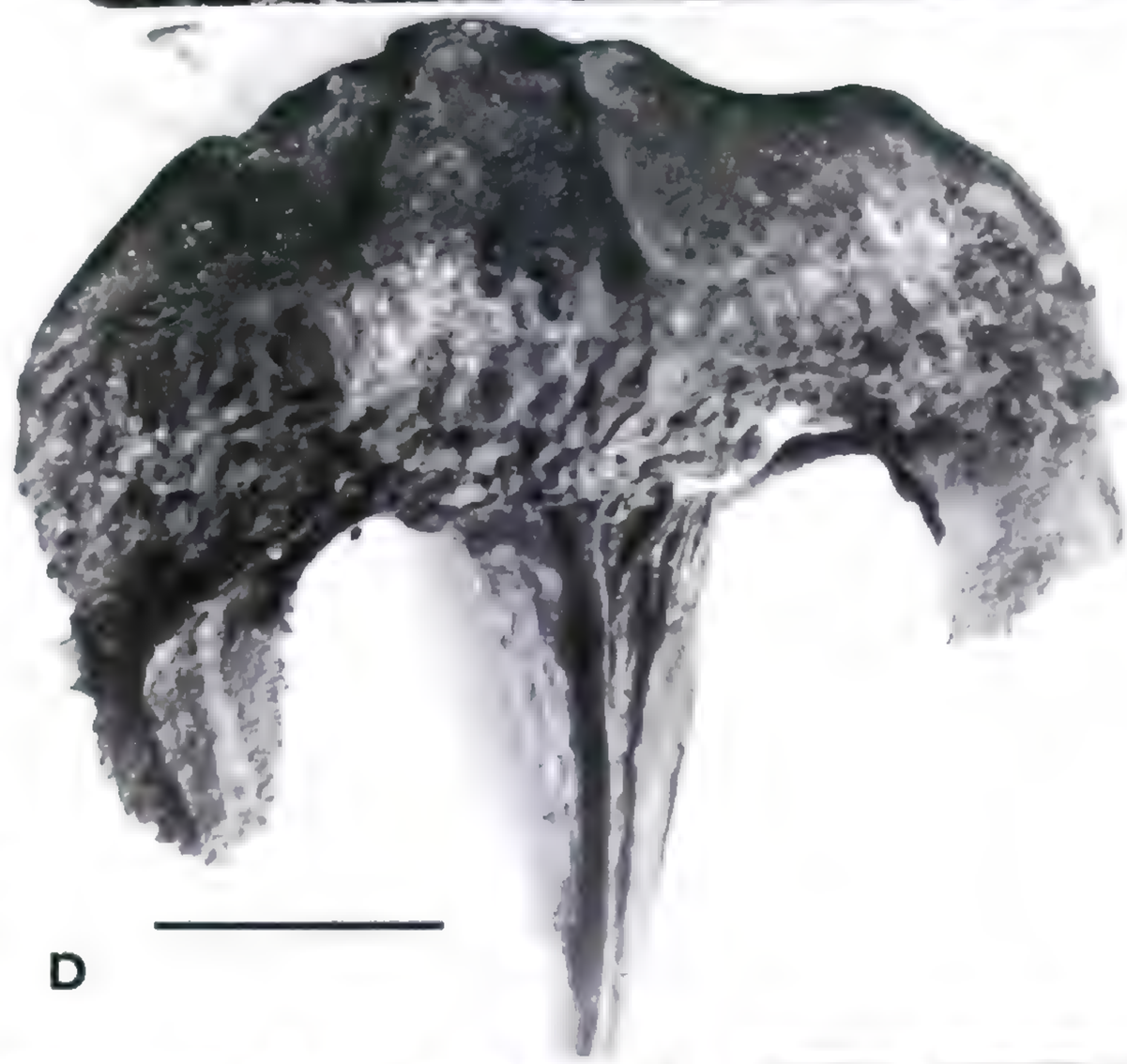
Additional specimens examined. KENYA: near Voi, Mlilonyi Hill, 4 Jan. 1986 (♂), *Sclavo 2* (EA, K, MO, NAP).

Encephalartos voiensis lives in isolated mountains surrounded by dry savanna in which species of *Encephalartos* do not occur. The new species occurs on steep rocky slopes in cloud forest at 1,500–1,800 m elevation as an understory plant. It also grows in partial shade and full sun areas of forest clearings.

Encephalartos voiensis shares some characters with *E. bubalinus*, *E. gratus* Prain, *E. hildebrandtii* A. Br. & Bouché, and *E. tegulaneus*, which are all found in the same general vicinity (Fig. 1); and, to a lesser extent, it resembles *E. manikensis* (Gilliland) Gilliland and its allies in Central Mozambique and in Zimbabwe. *Encephalartos voiensis* shares different features with each of these taxa. For example, foliage characteristics are closest to *E. bubalinus* and (especially) *E. hildebrandtii* in that 1–5 spinose teeth are present on the basal curve of the superior margin of the median pinnae, and at least one spinose tooth is present near the basal portion of the inferior margin. *Encephalartos voiensis* differs from these two species by having subfalcate, very abruptly cuneate basally, very dark green to blue-green leaflets, and the transition to

A

C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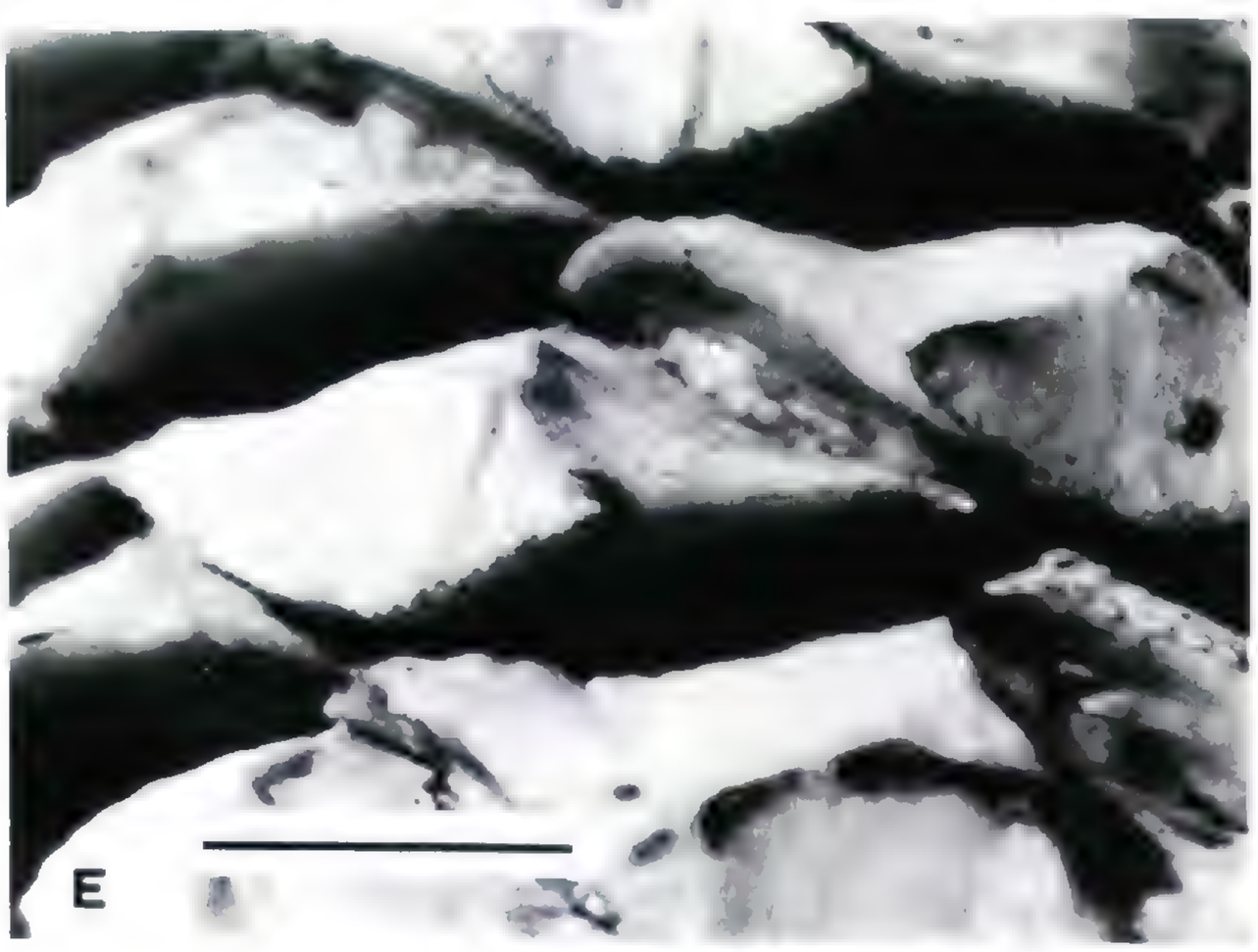
E

reduced leaflets in the lower ⅕ of the rachis is abrupt rather than gradual. *Encephalartos voiensis* can be distinguished further from *E. bubalinus* because the former has median leaflets 4 (vs. 1–2) cm wide, 25–40 (vs. 10–20) cm long, and gradually acuminate (vs. acute) apices. In general, in *E. hildebrandtii*, the median leaflet apices are either bifurcate or trifurcate; in *E. voiensis*, by contrast, they are always pungent. Moreover, the median leaflets of *E. hildebrandtii* have up to nine spinose teeth along each margin; in *E. voiensis* these teeth are reduced to barely discernible callose bumps.

The mega- and microsporangiate strobili of *E. voiensis* resemble those of *E. bubalinus*, *E. gratus*, *E. hildebrandtii*, and *E. tegulaneus* with respect to overall size, shape, and color. There are, however, significant differences in mega- and microsporophyll characters. As in vegetative characters, *E. voiensis* shares individual characters with each of the aforementioned species, but none that is common to all except perhaps the presence of inferior and sagittal crest tubercles. For example, only *E. gratus* and *E. voiensis* have a rectangular to trapezoidal adaxial median lobe. This median lobe is 5–12 mm long in *E. gratus* but only 2–4 mm long in *E. voiensis*. *Encephalartos tegulaneus* has a unique abaxial tuberculate facet that replaces the abaxial angle of the pedicel of its megasporophylls. This feature also occurs in *E. voiensis*, but here the facet is narrower, usually does not extend the full length of the pedicel, is barely discernible in herbarium material, and is nontuberculate. The ab- and adaxial margins of the bulla of the megasporophylls of *E. voiensis* and *E. hildebrandtii* are tuberculate and without ridges, whereas those of *E. bubalinus*, *E. gratus*, and *E. tegulaneus* always have some distinct ridges. The overall appearance of the megasporophylls of *E. voiensis* in shape and arrangement of the bulla facets is most similar to those of *E. hildebrandtii*. Compared with the previously discussed taxa, the lateral lobes of the bulla of *E. voiensis* are uniquely smaller and thinner and appear laterally compressed in the ab-adaxial plane.

The deltoid to cuneate microsporophylls of *E. voiensis* are more similar to those of *E. bubalinus* than to the oblong microsporophylls of *E. gratus*, *E. hildebrandtii*, and *E. tegulaneus*. In addition, only *E. voiensis* and *E. bubalinus* have their microsporophylls inserted at a right angle to the strobilus axis at pollen shedding, whereas in the other species they are either ascendant as in *E. gratus* and *E. hildebrandtii* or descendant as in *E. tegulaneus*. *Encephalartos voiensis* has a median facet on the ab- and adaxial bulla faces; these median facets are not present in *E. gratus*.

Encephalartos voiensis exhibits little variability except that some leaflet characters appear to be associated with habitat differences. The leaflets of plants growing in deep shade are thinner in texture and barely subfalcate, and they generally have fewer and smaller marginal spinose teeth. Only shade plants exhibit these features, and they would most likely change under exposure to higher light intensities, as Stevenson et al. (1986) observed in *Ceratozamia latifolia* under otherwise similar conditions.

Even though the relationship of *E. voiensis* is not completely clear, it is our opinion, based on vegetative morphology, that *E. voiensis* is most closely related to *E. hildebrandtii*. This is because in the cycads, in general, vegetative characters are more useful in separating species as, for example, in *Ceratozamia* (Stevenson et al., 1986), *Dioon* (Sabato & De Luca, 1985), and *Macrozamia* (Johnson, 1959). There are several reasons for this. First, vegetative characters are always present and often exhibit more obvious macroscopic diversity than do reproductive characters. Secondly, most data concerning reproductive characters are either fragmentary or nonexistent, and herbarium material is highly unreliable because of the vast amount of distortion of size and shape induced by drying. Thirdly, because all cycads are dioecious, we think it is important to establish vegetative characters that can be correlated with reproductive characters to establish a common denominator. In the case of the species discussed in this work, microsporophyll and megasporophyll characters do help corroborate the species delimitations indicated by vegetative characters. Finally, cycads often exhibit extreme changes in vegetative morphology between species of different habitats and or localities while at the same time exhibiting only subtle differences in reproductive morphology. These vegetative changes

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FIGURE 2. *Encephalartos voiensis*. A, B. Leaf and leaflet characters. —A. Leaf with characteristic abrupt transition to reduced spinose leaflets in lower portion. Scale bar = 20 cm. —B. Subfalcate leaflets of holotype with spinose teeth. Scale bar = 10 cm. C. End view of megasporophylls. Scale bar = 5 cm.—D. Adaxial view of megasporophyll of the holotype. Scale bar = 1 cm.—E. End view of a microsporophyll. Scale bar = 1 cm.

are stable and remain so even when the species are brought together and cultivated through successive generations in a uniform environment.

The high incidence of locally endemic species of *Encephalartos* in Central Africa appears to be related to habitat preference and physical geography in this region. That is, in general, *Encephalartos* here prefers steep wooded slopes, and this habitat occurs in isolated areas surrounded by savanna in which this genus does not occur. Even *E. hildebrandtii* (Fig. 1) occurs at the top and on the sides near the top of coastal cliffs and on the sides of river valleys. With the appropriate habitats isolated from each other, there is the opportunity for locally endemic taxa to differentiate. *Encephalartos voiensis* fits this pattern because it also occurs on steep slopes of isolated mountains surrounded by savanna. As more areas of Central Africa are explored for *Encephalartos* populations, more new taxa will certainly be discovered.

Keys to East Central African Species of *Encephalartos*

KEY TO VEGETATIVE PLANTS

1a. Median leaflet apices bi- or trifurcate ..... *E. hildebrandtii*
1b. Median leaflet apices sharply pointed, ending in a spikelike tip.
  2a. Median leaflets subfalcate ..... *E. voiensis*
  2b. Median leaflets linear to oblanceolate.
    3a. Median leaflets linear, narrower than 2 cm ..... *E. bubalinus*
    3b. Median leaflets lanceolate or oblanceolate, wider than 2 cm.
      4a. Median leaflets oblanceolate, margins reflexed, distinctly striate below ..... *E. tegulaneus*
      4b. Median leaflets lanceolate, margins flat, indistinctly striate below ..... *E. gratus*

KEY TO MEGASPORANGIATE PLANTS

1a. Microsporophylls oblong, either ascendant or descendant at pollen shedding.
  2a. Bulla puberulent ..... *E. gratus*
  2b. Bulla glabrous.
    3a. Microsporophylls ascendant ..... *E. hildebrandtii*
    3b. Microsporophylls descendant ..... *E. tegulaneus*
1b. Microsporophylls deltoid to cuneate, at right angles to strobilus axis at pollen shedding.
  4a. Lateral ridges of bulla acute ..... *E. bubalinus*
  4b. Lateral ridges of bulla subacute to obtuse ..... *E. voiensis*

KEY TO MEGASPORANGIATE PLANTS

1a. Median lobe of bulla well developed, 7–12 mm long, bulla puberulent ..... *E. gratus*
1b. Median lobe of bulla absent or if present shorter than 5 mm, bulla glabrous or nearly so.
  2a. Median lobe of bulla 2–4 mm long ..... *E. voiensis*
  2b. Median lobe of bulla absent.
    3a. Bulla subtriangular, abaxial angle of pedicel absent ..... *E. tegulaneus*
    3b. Bulla rhomboid, abaxial angle of pedicel present.
      4a. Adaxial margin of bulla with radiating ridges ..... *E. bubalinus*
      4b. Adaxial margin of bulla with tubercles ..... *E. hildebrandtii*

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A NEW SPECIES OF *PERSEA* (LAURACEAE) FROM SURINAM, WITH A DISCUSSION OF ITS POSITION WITHIN THE GENUS

In a shipment of Lauraceae recently received from the University of Surinam, Paramaribo, I encountered a specimen of *Persea* that turned out to represent a new species, differing from all other neotropical *Persea* species by its deciduous and strongly unequal tepals.

Persea julianae van der Werff, sp. nov. TYPE: Surinam: Wilhelmina Mountains, Juliana Peak, small tree, 7 m tall, flowers very pale yellow, axes of inflorescence reddish, *Schulz 10234* (holotype, MO; isotype, BBS). Figure 1.

A congeneribus tepalis deciduis et valde inaequalibus differt.

Tree, 7 m tall. Very young shoots and buds densely appressed-pubescent, the twigs soon becoming glabrous. Leaves alternate, elliptic, 10–14 × 3.5–5 cm, ± coriaceous, the base acute, the tips acute or shortly acuminate, the upper surface glabrous, the lower surface with scattered appressed hairs, the midvein clearly impressed and the lateral veins weakly impressed on upper surface, both of these vein types clearly raised on lower surface; tertiary venation weakly raised on lower surface. Petioles 1–1.5 cm long, glabrous, canaliculate. Inflorescences 4–6 cm long, in axils of deciduous bracts or leaves, paniculate, appressed-pubescent, the axes reddish (fide collector). Pedicels ca. 4 mm long. Flowers very pale yellow. Tepals 6, strongly unequal, united at the very base and falling off in old flowers as a unit, with stamens and staminodia attached. Outer tepals broadly ovate, ca. 2 mm long, appressed-pubescent outside, glabrous inside. Inner tepals elliptic, ca. 6 mm long, appressed-pubescent on both surfaces. Fertile stamens 6, these representing the outer 2 whorls, ca. 5 mm long, the filament slender, ca. 4 mm long, densely pubescent, the anther glabrous, 4-celled, the cells introrse. Stamens of the third whorl about as long as the outer stamens, the filament similarly pubescent, the anther as wide as the filament and devoid of anther cells; glands present, sub-basal. Outer 9 stamens with widened bases. Staminodia (whorl IV) ca. 2.5 mm long, widened at base, filament densely pubescent, inside of the anther glabrous except for an apical tuft of hairs, the outside sericeous, the base cordate. Ovary ellipsoid, ca. 1 mm long, glabrous or with few hairs near the apex; style ca. 2.5 mm long, glabrous. Fruit unknown; tepals deciduous in very early fruiting stage.

The distinctive characters of *P. julianae* make it difficult to place in the most recent infrageneric classification. In her revision of the neotropical species of *Persea*, Kopp (1966) recognized two subgenera. Subgenus *Persea* is characterized by its equal tepals that are pubescent on inner and outer surfaces, usually puberulous ovary, and tepals deciduous at the fruiting stage. This subgenus includes the type species of *Persea*, *P. americana* Mill., and three other Central American species. Subgenus *Eriodaphne* is characterized by its strongly unequal tepals with the outer tepals internally glabrous, usually glabrous ovary, and persistent tepals in the fruiting stage. This subgenus includes about 70 neotropical species and is further divided by Kopp (1966) into four sections. Section *Mutisaea* includes the species with a corymbiform inflorescence; section *Hexanthera* includes species with only six fertile stamens (representing the outermost whorls), section *Aurataea* includes species with a (sometimes slightly) pubescent ovary; and section *Eriodaphne* includes the remaining species, with a glabrous ovary. The species with partly or entirely two-celled stamens belong to section *Eriodaphne*. Thus, the two subgenera can be readily identified in flower (tepals equal vs. unequal) and fruit (tepals deciduous vs. persistent).

The usefulness of this classification of the neotropical *Persea* species is undercut by several species with characters of both subgenera. Several Central American species (for example *P. albida* Kostermans, *P. rigens* Allen, and *P. sylvatica* van der Werff) have equal tepals, which are persistent in the fruiting stage. These species were included in section *Eriodaphne* by Kopp, but the equal tepals

FIGURE 1. *Persea julianae*.—A. Habit.—B. Flower.—C. Detail of flowers showing two outer tepals (small), each with a fertile stamen (whorl I) and a tall staminode (whorl III), and one inner tepal (long) with a fertile stamen (whorl II) and a short, sagittate staminode (whorl IV).—D. Staminode of whorl III, with sub-basal glands.—E. Stamen of whorl I/II.—F. Pistil.—G. Staminode of whorl IV.—H. Old flower, showing dehiscence of tepals and stamens.

do not support this placement. Kopp's (1966) infrageneric classification is weakened further by the unequal tepals deciduous in the fruiting stage of *P. julianae*.

If it were not for the deciduous tepals, *P. julianae* would be immediately placed in subg. *Eriodaphne* section *Hexanthera*, which is represented in Amazonian Brazil and Venezuela by *P. fastigiata* Kopp, *P. pseudofasciculata* Kopp, and *P. hexanthera* Kopp. These species are compared in Table 1.

Persea julianae, named after the Queen Mother of the Netherlands, is only known from the type collection from the Juliana Peak in Surinam at an elevation of 1,050 m. It was collected in a 20-m-tall forest, rooting in a thick humus layer on sandy clay.

Kostermans (1936) recorded three species of

TABLE 1. Selected characters of *Persea julianae*, *P. pseudofasciculata*, *P. fastigiata*, and *P. hexanthera*, based on MO type specimens, with exception of *P. hexanthera*, where data are based on the protologue and the collection *Bernardi s.n.*, annotated by Kopp.

	Tepals	Length of Inflorescence	Pubescence	Lengths of Inner Tepals	Lengths of Pedicels	Twigs	Lengths of Petioles
P. julianae	deciduous	⅓–½ leaves	sparse, appressed	6 mm	4 mm	solid	1.0–1.5 cm
P. pseudofasciculata	persistent	+ ½ leaves	dense, appressed	7 mm	3 mm	hollow	2.5 cm
P. fastigiata	persistent	longer than leaves	sparse, appressed	4 mm	3 mm	solid	1.0–1.5 cm
P. hexanthera	persistent	longer than leaves	sparse, appressed	8.5 mm	5 mm	hollow	2.5 cm

Persea from Surinam, *P. americana* Miller, P. *benthamiana* Meissner, and *P. coriacea* Kostermans. As noted, the strongly unequal tepals, glabrous ovary, and number of fertile stamens separate *P. julianae* from the cultivated *P. americana*. Specimens treated by Kostermans (1936) as *P. benthamiana* were included by Kopp (1966) under *P. nivea* Mez and are characterized by having nine fertile stamens, persistent tepals, and glaucous whitish lower leaf surfaces.

Persea coriacea is an enigmatic species known only from the type collection, from the Hendrik Peak in the Emma Chain, not far from the Juliana Peak. This species is described as having subequal tepals ± 1.75 mm long and nine fertile stamens; these details separate it clearly from *P. julianae*. Kostermans (1936) also mentioned that the fruit was subtended by a small, flat cupule with an entire margin, a character not found in any other *Persea* species. This was probably one reason why Kopp (1966) excluded *P. coriacea* from *Persea* without suggesting an alternative generic placement. The MO isotype of *P. coriacea* does not solve these difficulties. The label states that flower buds and fruits were collected. Presence of floral buds and fruits on the same specimen is very unusual for Lauraceae and is often the result of a disease in which galls, developed from buds, are mistaken for fruits. The buds on the MO isotype *are* diseased, which explains Kostermans's observation that frequently a staminode of the fifth whorl is present. The papillose lower leaf surface is against its inclusion in *Persea*. Papillose lower leaf surfaces are common but not restricted to *Aniba*, but *P. coriacea* does not match any *Aniba* species I know. I regard *P. coriacea* as a name based on a monstrosity, different from the other *Persea* species reported from Surinam; for correct placement, additional specimens are needed.

I thank Dra. M. Werkhoven for making the specimen available. J. Myers drew the illustration.

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THE PUBLICATIONS OF EDGAR ANDERSON: ADDITIONS

Eisendrath (1972) published a bibliography of the writings of Edgar Anderson, botanist at the Missouri Botanical Garden and Professor of Botany at Washington University for most of his career, spanning the years from 1922 until his death in 1969. For biographical information on Anderson, see Finan (1972).

The Missouri Botanical Garden Library is gathering for binding and cataloging the collected works of the curatorial staff, past and present. The following additions to the Eisendrath bibliography of Edgar Anderson have turned up:

1934. A chromosomal interchange in maize involving the attachment to the nucleolus. Amer. Naturalist 68: 345–350.

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FINAN, J. J. 1972. Edgar Anderson 1897–1969. Ann. Missouri Bot. Gard. 59: 325–345.

—Sally Erickson, *Volunteer, Missouri Botanical Garden Library, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.*

BOOK REVIEW

Flora of Australia, Volume 19. Myrtaceae—*Eucalyptus*, *Angophora*. By G. M. Chippendale, including an introduction and appendix, with contributions by D. J. Chippendale & S. G. M. Carr, A. S. George, K. D. Hill, L. A. S. Johnson, and P. J. Lang. Australian Government Publishing Service, Canberra. 1988. xvi + 543 pp., 111 figs. (38 color), 564 maps. ISBN 0-644-05866-8. Paper, price unknown.

This recently published volume of the *Flora of Australia* is the first of three that will cover that large group of trees and shrubs, the Myrtaceae. It is beautifully illustrated with numerous line drawings and seven pages of color photographs, is printed on high-quality paper, and has a good paperback binding. The volume includes a family description by A. S. George and treatments by G. M. Chippendale of the diverse genus *Eucalyptus* L'Hér. (513 species) and the much smaller *Angophora* Cav. (7 species). George calculates that there are about 75 genera and over 1,500 species of Myrtaceae in Australia. Thus, *Eucalyptus* accounts for about one third of the family there. As stated in the introduction, "more than any other group, these plants [the eucalypts] give a distinctive character to the Australian landscape." Of course, species of *Eucalyptus* are also planted around the world for ornamental and forestry purposes. Chippendale's contribution is very welcome indeed.

An informative introduction relates some of the taxonomic history of *Eucalyptus*. The last complete account was that of Blakely, *A Key to the Eucalypts* (1934), with updated editions appearing in 1955 and 1965. Until the late 1950s taxonomy was based on macroscopic characters of buds, fruits, and anthers, but since then a variety of anatomical and inflorescence features have been investigated by various workers. Presently, studies of *Eucalyptus* are appearing at an explosive rate. A quick look at the 18 issues of the *Australian Journal of Botany* for the period 1984–1986 shows that not one issue was without at least one article with *Eucalyptus* in the title and that 59 articles on *Eucalyptus* appeared, 18 of which were systematic. Thus, Chippendale's treatment is necessarily a synthesis of knowledge of *Eucalyptus* as it was in the mid 1980s, and it will soon be out-of-date. In fact, 24 species published while the book was being typeset could not be included. But considering the history of *Eucalyptus*, we cannot expect another comprehensive work soon.

Chippendale briefly reviews some of the features that have been used in systematic studies of *Eucalyptus*, viz., stamens and anthers, cotyledons, operculum, ovules, leaf waxes, oil glands, trichomes, and stigma and style morphology. However, his key to species depends on "readily-observable characters of habit, bark, leaf arrangement and form, inflorescence, buds and fruit."

Near the beginning of the volume are color photographs illustrating types of bark, habit, and various species in flower. Labeling the photographs of the various bark types would have made them more useful.

There are 60 pages of keys for *Eucalyptus*, first one dividing the species into 20 groups and then a key to the species in each group. For systematic treatment the species are divided into 92 series, but these have no close relationship to the 20 groups of species in the key. A description of each series is provided with an accompanying citation of type and notes on size, distribution, and distinguishing characteristics. There is no key to or synopsis of the series, but they are divided into groups in the introduction of the genus under the discussion of some of the systematically important characters. For each species are provided: a description of ca. 8 lines; citation of types, synonyms, and published illustrations; a figure illustrating buds and fruits; a short list of representative specimens; and notes on distribution and distinguishing characteristics. Distribution maps for all species are found on 38 pages at the end of the systematic treatment.

The style of the keys is very brief. Usually only one character comparison is made in each couplet and the alternatives can sometimes seem rather arbitrary, e.g., on page 8, lines 8 and 9 "adult leaves more than 12 cm long" versus "adult leaves less than 12 cm long"; or lines 1 and 2 on page 9—"leaves green" versus "leaves glaucous or grey green or yellow green." The very first character used in the key is bark type, and bark characters are utilized at other points in the key. I experimented by attempting to "identify" three species I know and was able to run them through the key without problem. I was less successful with identified specimens of three other species I did not know, even when I allowed myself knowledge of the bark by looking it up in the descriptions. In

my quick look at the key, I ran into one contradiction: if one takes lead "3:" on page 7, "operculum ± equal to or longer than hypanthium," one may later come to lead "100:" in group 9 on page 31, "operculum ± equal in length to, or shorter than, hypanthium."

In an appendix, Chippendale describes as new or lectotypifies several series, and nine new species included in the flora are formally published by D. J. Carr & S. G. M. Carr, L. A. S. Johnson & K. D. Hill, and P. J. Lang.

Chippendale's impressive treatment of *Eucalyptus* is sure to be a vital reference for botanists, foresters, and horticulturists. It obviously represents many years of careful study and deep familiarity with the genus. I am very happy that it has been published and recommend it to anyone with an interest in *Eucalyptus*.

— L. R. Landrum, *Department of Botany, Arizona State University, Tempe, Arizona 85287, U.S.A.*

Volume 76, Number 2, pp. 365–625 of the ANNALS OF THE MISSOURI BOTANICAL GARDEN was published on June 22, 1989.

Works on Orchids from the Missouri Botanical Garden

Orchids of Panama

L. O. Williams & P. H. Allen

A facsimile of the Orchidaceae, Flora of Panama, which originally appeared in four separate issues of the Annals of the Missouri Botanical Garden from 1940 to 1949. A checklist of Panama's 800 species of orchids has been prepared by R. L. Dressler and appears as an appendix. viii + 484 + xxvi pp., illustrated. 1980. $20.00.

Icones Pleurothallidinarum I: Systematics of the Pleurothallidinae (Orchidaceae)

Carlyle A. Luer

The 29 genera of this subtribe, which contains about 4,000 species, are discussed and illustrated. The introduction contains a detailed discussion of pleurothallid morphology and a key to the genera. 81 pp., color frontispiece, illustrated. 1986. $7.50.

Icones Pleurothallidinarum II: Systematics of Masdevallia (Orchidaceae)

Carlyle A. Luer

Masdevallia contains about 350 species. This overview is at the infrageneric level and includes 29 plates illustrating a representative species of each infrageneric taxon recognized. In addition, each infragenus is described and its constituent species listed. 63 pp., illustrated, color frontispiece. 1986. $6.50.

Icones Pleurothallidinarum III: Systematics of *Pleurothallis* (Orchidaceae)

Carlyle A. Luer

This work provides a guide to the genus *Pleurothallis* with keys to the subgenera, keys to the sections and subsections, and lists of representative species for each infrageneric taxon. A black and white illustration of a representative species of each genus, section, and subsection is included. 109 pp., color frontispiece, illustrated. 1986. $8.50.

Icones Pleurothallidinarum IV: Systematics of *Acostaea*, *Condylago*, and *Porroglossum* (Orchidaceae)

Carlyle A. Luer

The 33 taxa included in these pleurothallid genera are not closely related, but each has developed an actively motile labellum. In each, a stimulus by the pollinator causes the lip to rise quickly, temporarily trapping the pollinator between the lip, column, and petals. Escape requires the pollinator to brush past the stigma, rostellum, and anther. 91 pp., illustrated. 1987. $8.00.

Thesaurus Dracularum, 1 & 2

Carlyle A. Luer with Rodrigo Escobar R. German translations by Fritz Hamer. Illustrations by Stig Dalström.

Thesaurus Dracularum is a popular monograph of the genus *Dracula*. Each of the 80-odd known species is illustrated by a watercolor painting accompanied by descriptions, discussions, and distributions in both English and German, with distribution maps and black and white line drawings. In elephant-size format. Standing orders available. The first two of six fascicles. $40.00 each, postpaid.

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FLORA OF THE VENEZUELAN GUAYANA—VII CONTRIBUTIONS TO THE FLORA OF THE CERRO ARACAMUNI, VENEZUELA[1]

Julian A. Steyermark†, *Bruce K. Holst*,[2] *and Collaborators*

Abstract

A preliminary checklist of the vascular plant flora of Cerro Aracamuni, an isolated sandstone massif of the Roraima Shield in southern Territorio Federal Amazonas, Venezuela, is presented. The list is based on collections from five expeditions to the area. Brief comments on geography and affinities of its flora are included. Twenty-seven new taxa, including one genus, 24 species, and two subspecies are described from the massif, and three new combinations are made. The new taxa include *Ilex aracamuniana* (Aquifoliaceae); *Philodendron roraimae* subsp. *aracamuniense* (Araceae); *Pochota aracamuniana* (Bombacaceae); *Navia carnevalii*, *N. iosothrix*, *N. patria*, *N. platyphylla*, *N. terramarae* (Bromeliaceae); *Hexapterella steyermarkii* (Burmanniaceae); *Symbolanthus aracamuniensis* (Gentianaceae); *Licaria trinervis* (Lauraceae); *Tococa liesneri* (Melastomataceae); *Sauvagesia guianensis* subsp. *aracamuniensis* (Ochnaceae); *Aracamunia liesneri* (Orchidaceae); *Piper mosaicum* (Piperaceae); *Rapatea aracamuniana* (Rapateaceae); *Cephalodendron aracamuniensis*, *Coussarea liesneri*, *Neblinathamnus aracamunianus*, *Remijia reducta* (Rubiaceae); *Bonnetia liesneri*, *Ternstroemia guanchezii*, *T. maguirei* (Theaceae); *Abolboda scabrida*, *Xyris aracamunae*, *X. liesneri*, and *X. prolificans* (Xyridaceae). The three new combinations are: *Paepalanthus sulcatus* (Eriocaulaceae); *Senefeldera yutajensis* (Euphorbiaceae); and *Persea perseiphylla* (Lauraceae).

Of the sandstone massifs of the Roraima Shield, Cerro de la Neblina, on the Venezuelan–Brazilian border, to date has yielded the highest number of endemic genera and species of vascular plants. Thus its neighbors to the north and northeast, Cerro Avispa and Cerro Aracamuni, have emerged as especially interesting for botanical exploration. The first botanical collections from the summits of Cerro

[1] We thank Paul Berry, Germán Carnevali, and George Rogers for carefully reviewing the manuscript, and Luther Raechal for assistance in preparing the text. John Myers prepared several of the plates. Part of this work was supported by National Science Foundation grant BSR 8515205. We also thank the specialists who supplied determinations and descriptions. Their names are listed after each of the families whose treatments they contributed. The illustration and Latin diagnosis of *Aracamunia* were done by Bruno Manara.

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† Dr. Steyermark died on October 15, 1988. For recollections on him and a record of much of his work see the *Annals* issue 76-3.

Avispa, and apparently from Cerro Aracamuni, were made by Félix Cardona Puig and G.C.K. & E. Dunsterville on a trip with the Venezuelan Border Commission in 1972. Coordinates used by them for what they called the "Aracamuni section of Cerro Avispa" (01°30′N, 65°51′W) match very closely with those from the most recent expedition to Cerro Aracamuni. Charles Brewer Carias gathered several plants during a stop to the summit by helicopter in 1983. Small gatherings of plants from the base and slopes of Aracamuni were made on two other occasions, in 1959 from a 900-m-tall granitic outlier of Cerro Aracamuni by John Wurdack and Lincoln Adderley, and from an eastern escarpment of Aracamuni at 750 m by Otto Huber and Ernesto Medina in 1981.

Cerro Aracamuni is the largest of the table mountains closest to Cerro de la Neblina, so exploration of its summit was considered essential to help verify that the high degree of endemism reported from Neblina was not an artifact of incomplete collecting. Although the summit of Cerro Aracamuni attains an elevation of only 1,500 m, contrasted with 3,040 m on Neblina, most of the summit of Neblina lies between 1,800 and 2,200 m.

In 1987, the Terramar Foundation of Venezuela provided Ronald Liesner of the Missouri Botanical Garden and Germán Carnevali and Francisco Delascio of the Herbario Nacional de Venezuela the opportunity to explore the summit and slopes of Cerro Aracamuni between October 15 and November 3, 1987. They gathered a total of 1,018 collections (including some bryophytes and fungi, which are not considered in this paper) from the summit and slopes.

Cerro Aracamuni lies near the southern tip of Territorio Federal Amazonas, Venezuela, in Dept. Río Negro, approximately 125–140 km northeast of Cerro de la Neblina (Fig. 1). It is a small to medium-sized massif for the Guayana region, rather long and narrow with a north-to-south orientation, extending from 01°24′N, 65°47′W to 01°32′N, 65°49′W. Vertical sandstone escarpments flank some of the sides, and a few rock outcrops appear on the upper edges. From its summit, streams drain into the Matapire and Siapa rivers on the east, north, and south, and into the Río Yatúa on the west. Several kilometers of lowland rainforest extend on the Río Siapa side to the base of the massif. The large rapids, Raudal and Salto Gallineta, are prominent topographic features on the igneous outcrops along the Río Siapa. Most of the massif is believed to be of Roraima sandstone.

A close relationship with the flora of Cerro de la Neblina is expected on Cerro Aracamuni due to the proximity of the two massifs. Four of the genera previously known only from Cerro de la Neblina, *Neblinanthera*, *Celiantha*, *Cephalodendron*, and *Neblinathamnus*, are now known from Cerro Aracamuni as well. Species (and subspecies) previously known only from Neblina, and now recorded from Aracamuni, are: *Sobralia speciosa* C. Schweinf., *Endlicheria vinotincta* Allen, *Spathelia neblinaensis* R. Cowan & Briz., *Diacidia glaucifolia* (Maguire) W. R. Anderson, *Philacra auriculata* Dwyer, *Tyleria silvana* Maguire, *Maieta neblinensis* Wurd., *Neblinanthera cumbrensis* Wurd., *Tococa pachystachya* Wurd., *Orthaea wurdackii* Maguire, Steyerm. & Luteyn, *Celiantha bella* Maguire & Steyerm., *Faramea boomii* Steyerm., *Ferdinandusa neblinensis* Steyerm., and *Pagameopsis maguirei* subsp. *neblinensis* Steyerm.

Two additions to the Venezuelan flora from the Aracamuni expeditions are *Tyleria silvana* Maguire, previously known from the Brazilian side of Cerro de la Neblina and Serra Pirapucú, and an as of yet unidentified species of the genus *Jacqueshuberia*, previously known only from Amazonian Brazil and Colombia.

Vegetation of the Summit

The summit is covered mostly by 0.5–1-m-high, dense savanna (non-Poaceae) and low shrub vegetation, and small forested areas occur in depressions and along streams. The savanna is inhabited mostly by Eriocaulaceae, Rapateaceae, Bromeliaceae, Xyridaceae, Liliaceae, and Sarraceniaceae. Common shrubs and small trees of the savanna include *Poecilandra retusa*, *Pagameopsis maguirei* subsp. *neblinensis*, *Bonnetia tristyla*, *Distictella monophylla*, *Emmotum glabrum*, and *Gongylolepis huachamacari*. The patches of forest and gallery forest include *Neblinanthera cumbrensis*, *Aegiphila roraimensis*, *Clusia* sp., *Diacidia glaucifolia*, *Phyllanthus vacciniifolius*, *Psychotria duricoria*, *P. tapajozensis*, and *Tyleria silvana*.

The remainder of this paper is divided into two sections, descriptions of new taxa and presentation of new combinations, and the preliminary checklist of the flora of Cerro Aracamuni.

New Taxa and Combinations from Cerro Aracamuni

Aquifoliaceae—contributed by Julian Steyermark

Ilex aracamuniana Steyerm., sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, summit, Proa

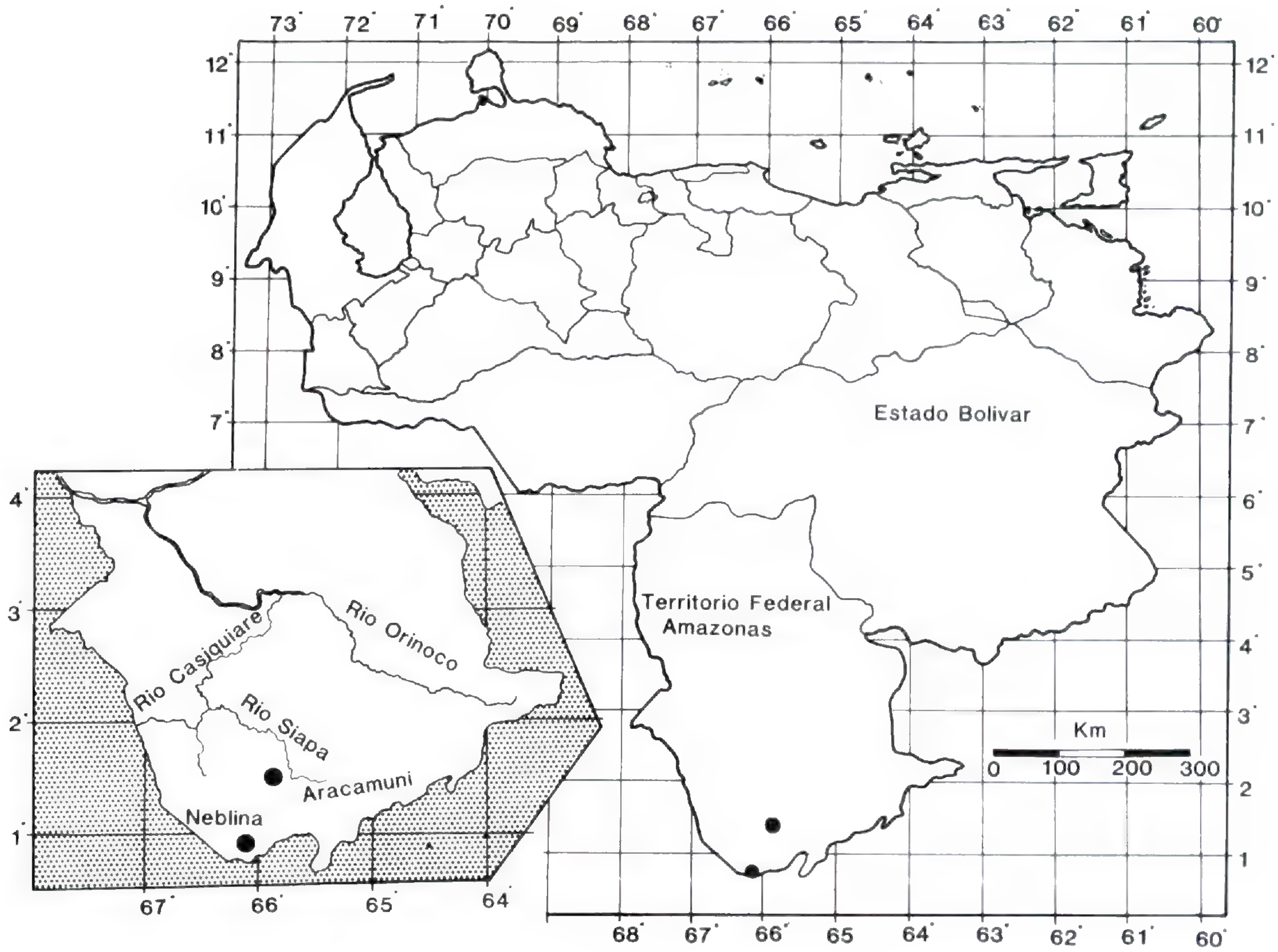

FIGURE 1. Map of Venezuela with détail of southern Territorio Federal Amazonas.

Camp, medium height, semi-open forest, 01°32′N, 65°49′W, 1,400 m, 26 Oct. 1987, *R. Liesner & G. Carnevali 22473* (holotype, MO; isotype, VEN). Figure 2.

Arbor 6–10-metralis; foliorum laminis lanceolato- vel oblongo-ellipticis apice obtuse acutis basi acutis 6.5–10 cm longis (1.7–)2–3.5(–4) cm latis ubique glabris subtus atropunctatis, valde decurrentibus, nervis lateralibus utroque latere 5–7 subtus impressis haud conspicuis, venatione tertiaria tenuiter reticulatis; petiolis 6–12 mm longis; inflorescentia foeminea solitaria axillari lateralique; pedicellis foemineis maturis 13–16 mm longis; calycis lobis breviter suborbicularibus apice acutis vel acuminatis; fructu subgloboso maturo 8–10 × 8–10 mm; pyrenis quinque trigonis 6 mm longis dorsaliter unisulcatis.

Tree 6–10 m tall, glabrous throughout. Leaf blades coriaceous, lance- to oblong-elliptic, obtusely acute at apex, acute at base, 6.5–10 cm long, (1.7–)2–3.5(–4) cm wide, dark punctate below, strongly decurrent on the petiole; midrib narrowly sulcate above, elevated below; lateral nerves 5–7 each side, slightly sulcate above, impressed but not strongly conspicuous below, ascending at 45–50°, inconspicuously anastomosing 2–4 mm from the margin; tertiary venation subimpressed and grossly reticulate above, finely reticulate below with impressed venation. Petioles 6–12 mm long, winged by the decurrent leaf bases. Pistillate inflorescence solitary, axillary and lateral; pedicels in post-anthesis 7–11 mm long, 13–16 mm long in fruit. Calyx lobes in anthesis triangular, acuminate or slenderly acute, in fruit broadly ovate and abruptly acute at apex. Fruit subglobose at maturity, 8–10 × 8–10 mm; pyrenes 5, 6 mm long, trigonal, unisulcate dorsally. Stigmatic lobes in post-anthesis prominent, discoid-capitate, 1 mm high, 1 mm diam.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp, edge of tepui in ravine, 01°26′N, 65°42′W, 1,550 m, 19 Oct. 1987, *R. Liesner & F. Delascio 22181* (MO, VEN); *R. Liesner & F. Delascio 22060* (MO, VEN).

This species is related to *Ilex sipapoana* Edwin and *I. huachamacariana* Edwin. It differs from the former in the longer mature pedicels; prominently decurrent leaf bases; and leaf blades with an obtusely acute apex, less conspicuous reticulation of the abaxial tertiary venation, and fainter

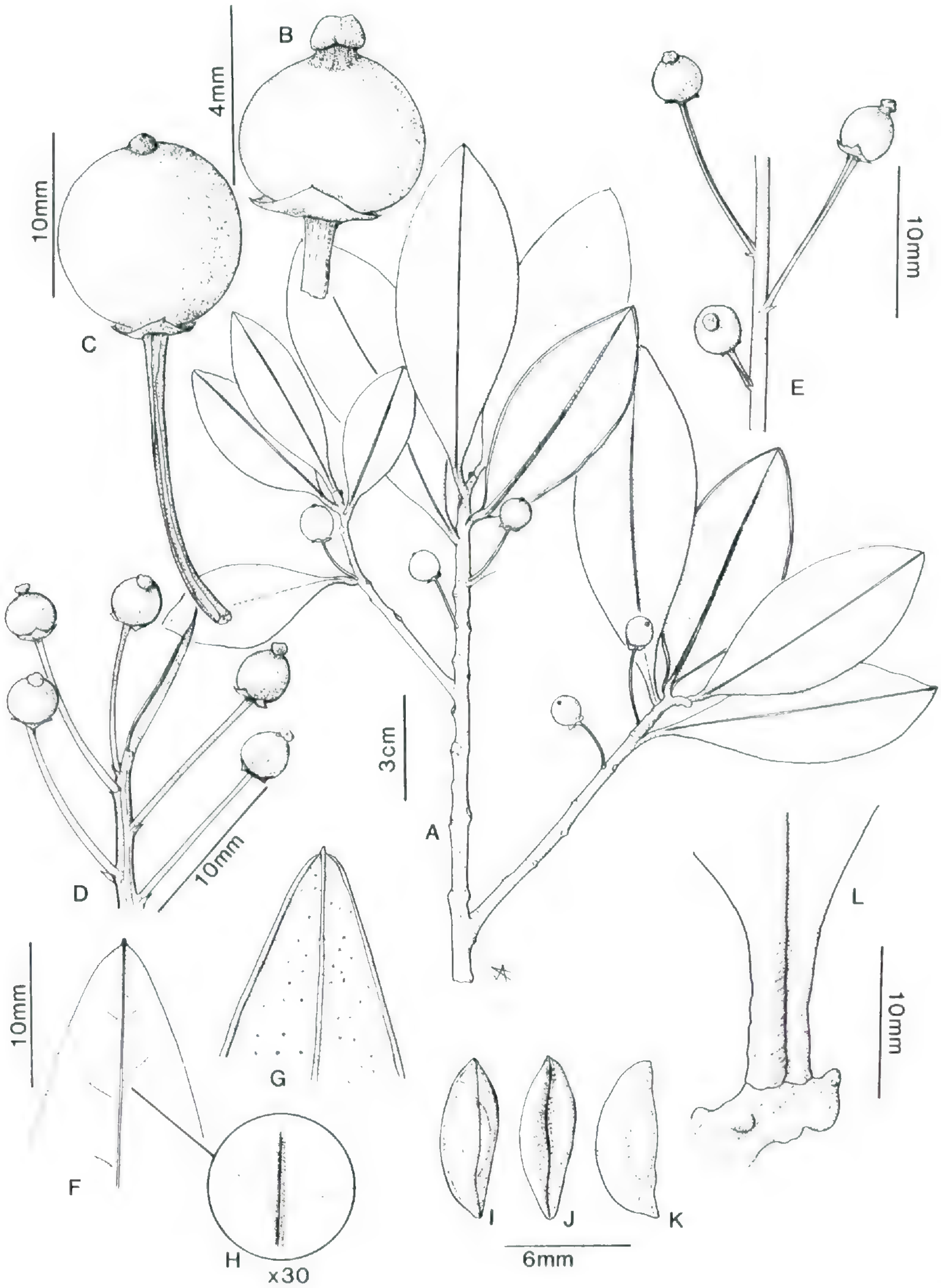

FIGURE 2. *Ilex aracamuniana*.—A. Habit.—B. Immature fruit.—C. Mature fruit.—D, E. Fertile stem.—F. Leaf tip, upper surface.—G. Leaf tip, lower surface.—H. Detail of upper leaf surface.—I, J, K. Seed.—L. Detail of petiole. (A, C–L, from *Liesner & Carnevali 22473*; B, from *Liesner & Delascio 22181*.)

lateral nerves of the lower surface. The new species differs from *I. huachamacariana* by having longer petioles and broader leaf blades not retuse at the apex.

ARACEAE—contributed by George Bunting

Philodendron roraimae K. Krause subsp. **aracamuniense** Bunting, subsp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, Proa Camp, in medium height semi-open forest, 01°32′N, 65°49′W, 1,400 m, 26 Oct. 1987, *R. Liesner & G. Carnevali 22510* (holotype, MO). Figure 3.

A subspecies typica foliorum lamina aliquantum minore et minus crassa et proportione angustiore, petiolo tereti (fide collectorum) abhorret.

Climbing herb. Stem to 5 m long, terminal part

FIGURE 3. *Philodendron roraimae* subsp. *aracamuniense* (*Liesner & Carnevali 22510*).

hidden by mass of coarsely fibrous cataphyll remains. Cataphyll broad, to 24 cm long, marcescent. Petiole stout, terete, 50–57(–68?) cm long in vivo with many lines of small gray dots. Leaf blade coriaceous though easily fracturing along veins, ovate (narrowly triangular in juvenile shoots), 44–54 cm long, 27–ca. 40 cm wide (1.4–1.6 times longer than wide), apex obtuse and abruptly acuminate, 1–1.5 cm long; posterior lobes introrse, rounded at apex or somewhat angular but very blunt, slightly overlapping and enclosing a subrhombic space 5 cm long, or separated by a ± mitriform sinus 14–18 cm long; margins undulate; midrib wide and prominent, primary lateral veins adaxially sulcate and abaxially raised, ca. 6–7 per side arising at angles of ca. 55–65°; lesser veins all manifest and abaxially raised; posterior lobes with 2 primary lateral veins on each side of basal ribs, the latter nude in sinus for ca. 2–3.5 cm. Inflorescence solitary. Peduncle 4.5 cm long. Spathe

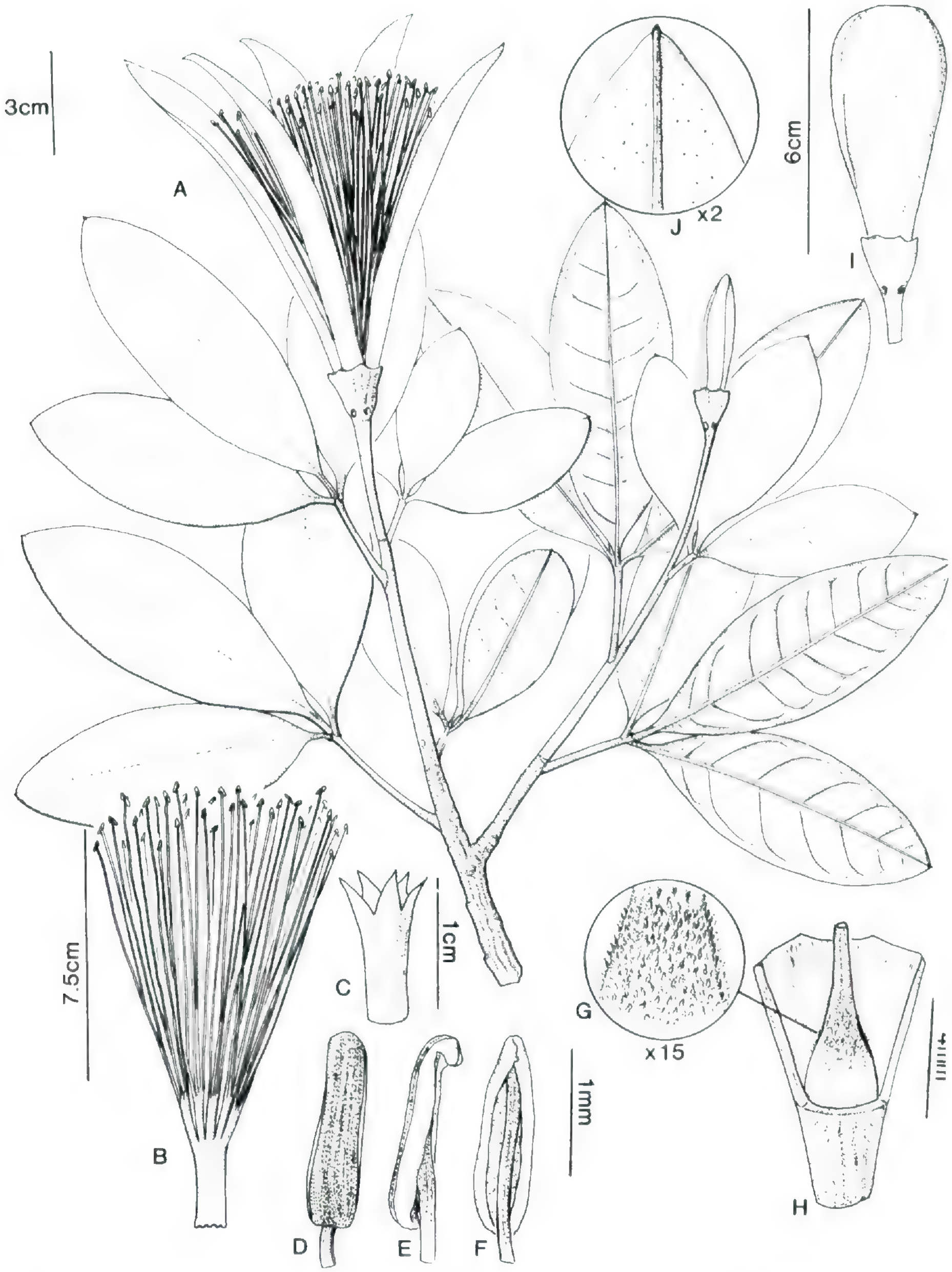

FIGURE 4. *Pochota aracamuniana*.—A. Habit of branch.—B. Androecium.—C. Staminal tube.—D, E, F. Anther.—G. Detail of style base, ovary summit.—H. Ovary and base of style.—I. Fruit.—J. Detail of lower leaf surface. (A–H, J, from *Liesner & Carnevali 22559*; I, from *Liesner & Carnevali 22577*.)

stout, 15–17 cm long, not constricted, outside with tube red and limb yellowish. Spadix 12.5–14.5 cm long, pistillate part 4 cm long and 2–2.5 cm thick, staminate part 8.5–10 cm long with sterile part to 4.5 cm and fertile part to 5.5 cm long. Ovary 3–5-locular, locules each with 6–8 or more ovules apparently superposed from bottom to top.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Cerro Aracamuni, Popa Camp, savanna with small to large patches of forest and stream, 01°26′N, 65°47′W, 1,550 m, 16 Oct. 1987, *R. Liesner & F. Delascio 21956* (MO).

The characters that separate the two subspecies of *P. roraimae* are few, yet the specimens seem quite distinct at first glance, chiefly because of the proportionally narrower leaf blade of subsp. *aracamuniense*. Even the juvenile leaves of both taxa have a similar, narrow blade outline. An important difference may prove to be petiole shape, said to be terete in the Aracamuni collections; in the ma-

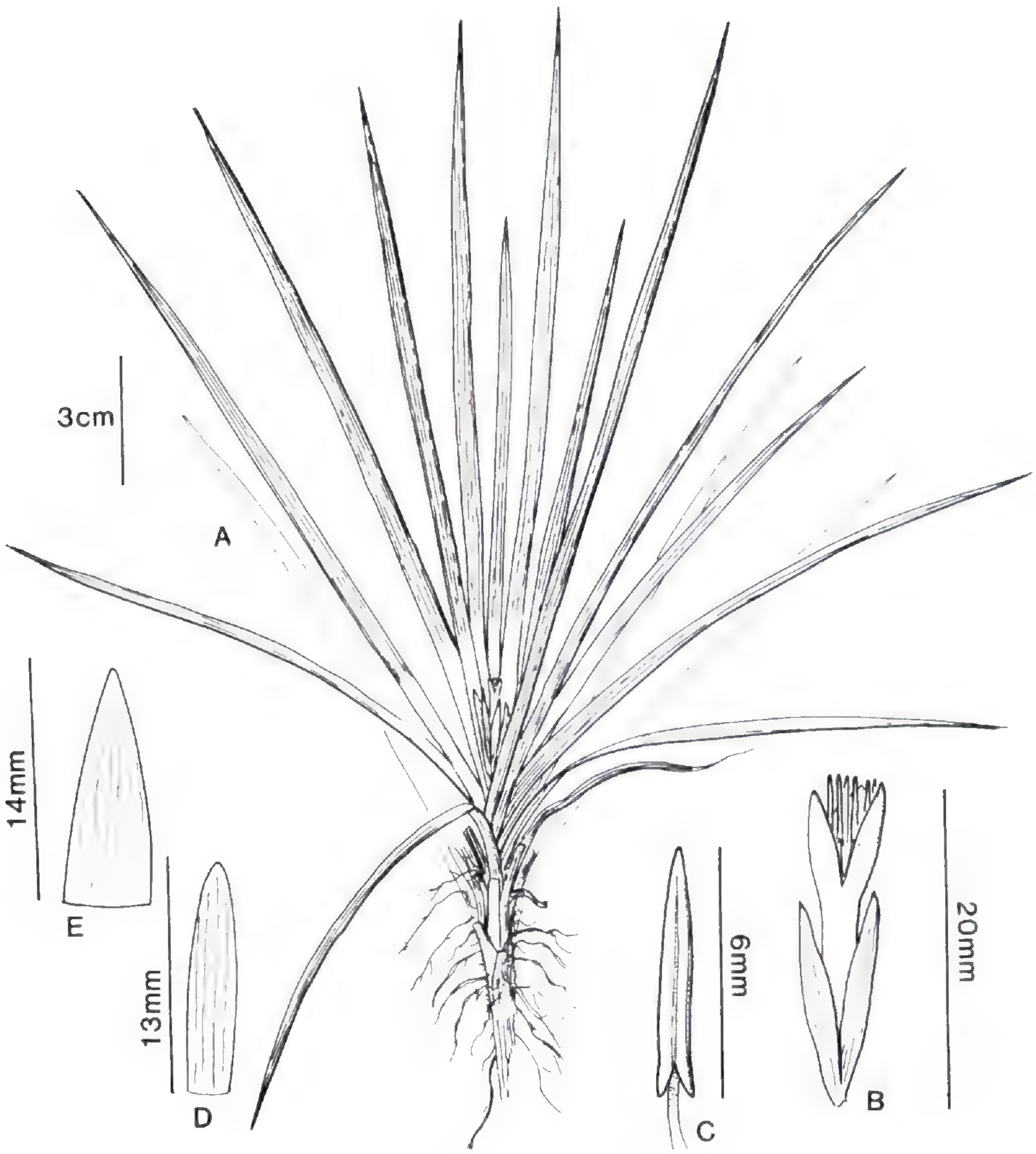

FIGURE 5. *Navia carnevalii.*—A. Habit.—B. Flower.—C. Anther.—D. Sepal.—E. Floral bract. (From *Liesner & Delascio 22322.*)

terial of subsp. *roraimae* from the Gran Sabana, it is rounded abaxially, while the adaxial surface has a median, longitudinal, obtuse angle (ridge) and two plane faces.

This is the common *Philodendron* growing on the summit of Cerro Aracamuni, climbing up tree trunks. Its relation to *P. nebulense* Bunting (described from Cerro de la Neblina) remains to be determined when fertile material of the latter becomes available.

BOMBACACEAE—contributed by Julian Steyermark

Pochota aracamuniana Steyerm., sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, summit, Proa Camp, semi-open forest at edge of forest, 01°32′N, 65°49′W, 1,400 m, 28 Oct. 1987, *R. Liesner & G. Carnevali 22559* (holotype, MO; isotype, VEN). Figure 4.

Arbor 3–6-metralis; foliis (1-)3-foliolatis, foliolis elliptico-oblongis vel lanceolato-ellipticis apice obtusis vel subobtusis minute mucronatis basi acutis vel subacutis, majoribus 6–10.5 cm longis 2–3.7 cm latis subtus atrolepidotis; petiolis 1.5 2 cm longis, petiolulis 4 8 (–13) mm longis; petalis 8–11 cm longis 7–15 mm latis; tubo staminali 10–11 mm longo praeter basin versus minute papillatum glabro; filamentis 6–7.5 cm longis; stylo basi lepidoto parte inferiore 4.2 cm atroglandulari parte superiore 4 cm glabro.

Tree 3–6 m tall. Leaves (1-)3-foliolate, leaflets coriaceous, elliptic-oblong to lance-elliptic, obtuse or subobtuse at apex with a minute mucro, acute to subacute at base, 6–10.5 cm long, 2–3.7 cm wide, densely dark brown lepidote beneath; midrib sulcate above, elevated below; lateral nerves impressed and manifest above, conspicuously impressed below, anastomosing 2–3 mm from margin; tertiary venation impressed above, subreticulate below. Petioles 1.5–2 cm long; petiolules 4–8(–13) mm long. Pedicel 2–3.5 cm long. Receptacle dark glandular. Calyx campanulate, 5–8 mm long (dried), to 12 mm (living), 10–12 mm wide at summit in anthesis, subundulate, minutely mucronate at sum-

mit, dark glandular-lepidote without, sericeous within. Petals linear-ligulate, 8–11 cm long, 7–15 mm wide, canescent-lepidote on both sides. Stamens ca. 110, in 5 principal phalanges. Staminal tube 10–11 mm long, glabrous except for minute papillation basally; filaments 6–7.5 cm long; anthers 1–2.5 mm long. Style 8.2 cm long, sparsely dark glandular-lepidote in lower 4.2 cm, lepidote at very base, glabrous in the upper 4 cm. Ovary ovoid-deltoid, 4 × 3.5 mm, glabrous below, lepidote above. Fruit narrowly obovate, truncate-rounded at summit, 6 cm long, 2.5 cm wide at summit, minutely dark lepidote.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Cerro Aracamuni, summit, Proa Camp, edge of savanna, 01°32′N, 65°49′W, 1,400 m, 28 Oct. 1987 (ft), *R. Liesner & G. Carnevali 22577* (MO, VEN); Cerro Aracamuni, summit, Popa Camp, savanna at edge of forest, 01°26′N, 65°47′W, 1,550 m, 19 Oct. 1987, *R. Liesner & F. Delascio 22174* (MO, VEN).

This species is related to *Pochota robynsii* Steyerm., but differs by having broader petals; generally obtuse, elliptic leaflets with a mucronulate apex; and conspicuous secondary nerves and tertiary venation.

BROMELIACEAE—contributed by Lyman B. Smith & Julian Steyermark

Navia carnevalii Lyman B. Smith & Steyerm., sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, Quebrada Camp, laja area, 01°24′N, 65°38′W, 600 m, 22 Oct. 1987, *R. Liesner & F. Delascio 22322* (holotype, US; isotypes, MO, VEN). Figure 5.

A *N. umbratile* Lyman B. Smith, cui valde affinis, foliorum laminis subintegris glabris, bracteis florigeris anguste oblongis vel oblongo-lanceolatis glabris differt.

Plant shortly caulescent, the stem variable in length, 1–6 cm long. Leaf sheaths brown, 1.5–2 cm long, 5–10 mm wide, many ribbed. Leaf blades white at base, suberect, linear, attenuate, not contracted at base, coriaceous, 9–21 cm long, 3–5 mm wide, glabrous above, minutely inconspicuously lepidote below, margins thickened, subinvolute, subentire. Inflorescence 2–3-flowered, enclosed within the bracts, narrowly lanceolate, 2.5 cm long, 2–3 cm wide. Outer bracts foliaceous, linear, to 6 cm long, 1–2 mm wide. Floral bracts membranous, narrowly oblong or oblong-lanceolate, acuminate, about equaling the sepals, 13–14 mm long, 4 mm wide. Sepals free, keeled, conduplicate, lanceolate, 12–13 mm long, 3 mm wide, glabrous, obtusely narrowed to a slightly incurved, slightly mucronate tip. Corolla white, 20 mm long, with a narrow cylindric tube, 12 mm long, the lobes lanceolate, subacute, 6–7 mm long, 2–2.5 mm wide. Ovary superior.

The subentire leaves and the narrowly oblong or oblong-lanceolate, acuminate floral bracts distinguish this species from *N. umbratilis* Lyman B. Smith of Cerro Yutajé.

Navia iosothrix Lyman B. Smith & Steyerm., sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, riverbank in shade of forest, Quebrada Camp, in area of rapids flowing over laja, 01°24′N, 65°38′N, 600 m, 20 Oct. 1987, *R. Liesner & F. Delascio 22203* (holotype, US; isotypes, MO, VEN). Figure 6.

A speciebus omnibus adhuc cognitis a conjunctione inflorescentiae parvi globosae pauciflorae, bracteae primariae valde reductae haud foliaceae, sepalorum minimorum lateralium verisimiliter librorum cucullatorum differt.

Plant caulescent with a short thickened stem 5–7 cm long, in a dense spreading rosette. Leaf sheaths oblong-ovate, slightly broader than and merging into the leaf blades, 13–20 mm long, 13–15 mm wide, many-nerved. Leaf blades divaricately spreading, with a median stripe, linear, long-attenuate, 15–23 cm long, 10–13 mm wide, minutely serrulate throughout with teeth ca. 0.2 mm long, minutely and sparsely lepidote on both surfaces, especially beneath. Infructescence simple, sessile, subglobose-ovoid, many-flowered, 1.5–1.8 cm high, 1.5–1.7 cm diam., ferruginous-tomentellose. Outer bracts few, not foliaceous, strongly reduced, 2.5–3 cm long, 4–5 mm wide, serrulate. Smaller lateral sepals apparently free, cucullate. Ovary superior. Capsule broadly ovate, 6.5 mm long; seeds blackish brown, 0.8 mm long, verruculose, costate, finely reticulate.

The strongly reduced, nonfoliaceous primary bracts, together with the smaller, free, cucullate lateral sepals and ferruginous tomentose infructescence distinguish this species. The specific name refers to the rusty-colored hairs of the infructescence.

Navia patria Lyman B. Smith & Steyerm., sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp, crevice of bluff at edge, savanna with small to large patches of forest and stream, 1°26′N, 65°47′W, 1,550 m, 17

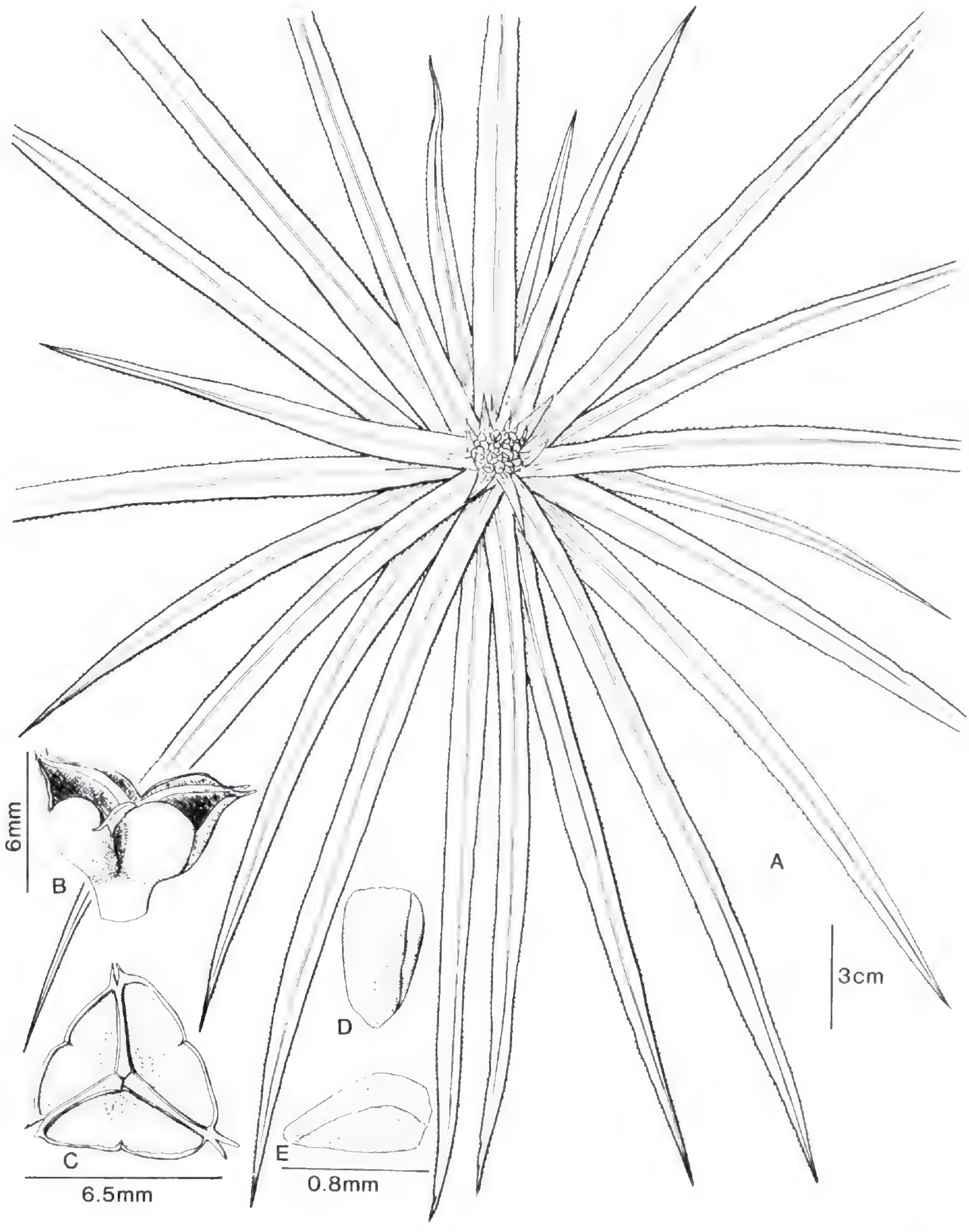

FIGURE 6. *Navia iosothrix.*—A. Habit.—B. Fruit, lateral view.—C. Fruit, view from above.—D, E. Seed. (From *Liesner & Delascio 22203.*)

Oct. 1987, *R. Liesner & F. Delascio 22041* (holotype, US; isotypes, MO, VEN). Figure 7.

A *N. crispa* Lyman B. Smith, cui valde affinis, foliorum laminis haud crispatis, bracteis primariis paulo reductis basi pallidis, bracteis florigeris acutis, multo majoribus differt.

Plant in dense spreading rosette, subacaulescent. Leaf sheaths brown, membranous, 15–17 mm long, 15–17 mm wide at base. Leaf blades widely spreading, with a broad white median stripe, linear, acuminate, 11–16 cm long, 8–10 mm wide, densely serrulate, not crisped on margins, both surfaces pilosulous, especially beneath. Inflorescence sessile, subglobose, digitately bipinnate from many short spikes, 2.5 cm high, 3.5–4 cm diam. Outer bracts foliaceous, somewhat reduced, sparsely puberulous without, strongly carinate, entire. Floral bracts broadly lanceolate, acute, somewhat longer than the sepals, 15 mm long, 5 mm wide below the middle, entire, glabrous. Sepals lanceolate, acuminate, the outer two carinate, 13 mm long, ca. 3 mm wide, entire, glabrous. Corolla white, 10 mm long. Ovary superior.

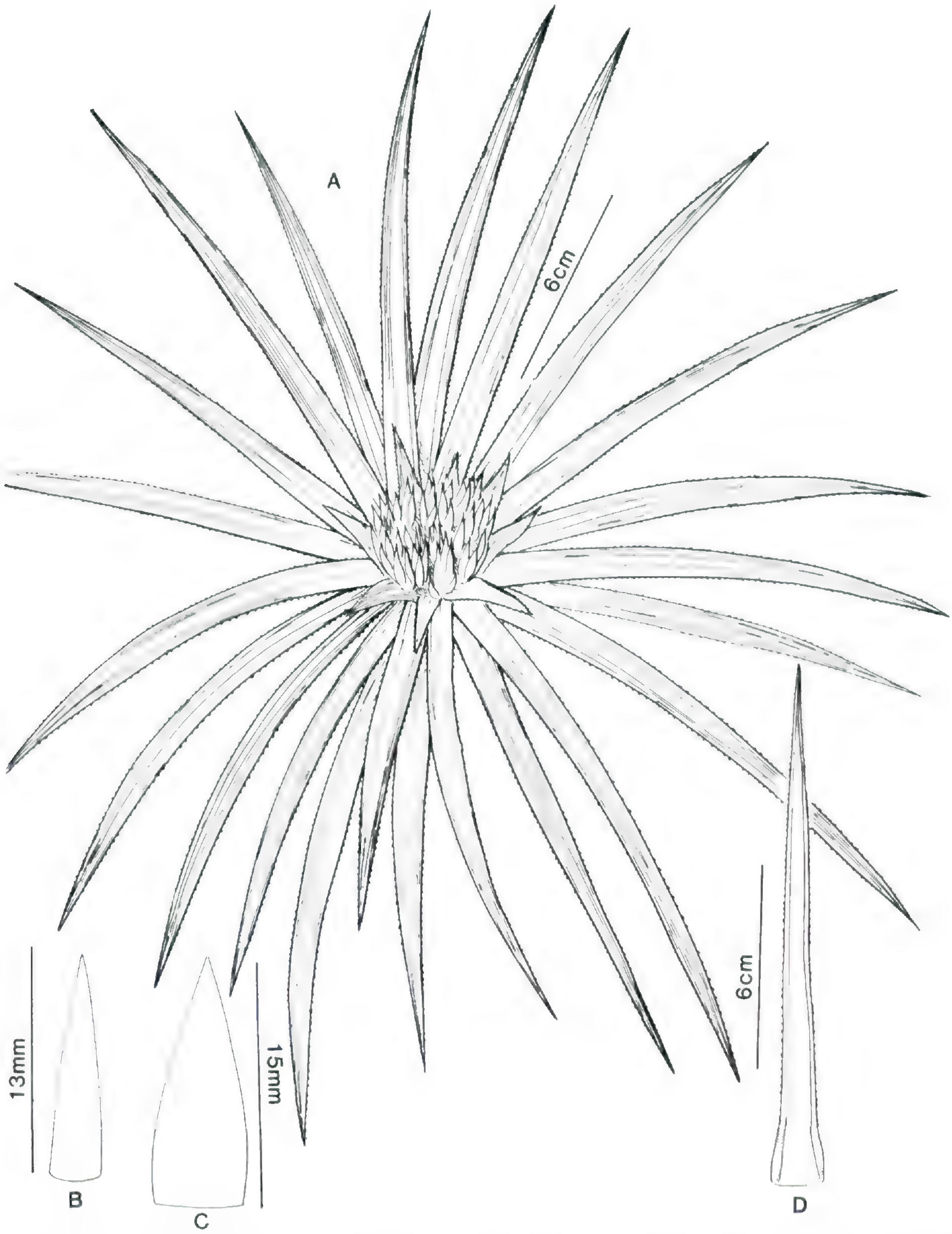

FIGURE 7. *Navia patria.*—A. Habit.—B. Sepal.—C. Floral bract.—D. Leaf. (From *Liesner & Delascio 22041.*)

This species differs from *N. crispa* Lyman B. Smith in having the outer primary bracts pale and only slightly reduced basally, the floral bracts larger, and the leaf margins noncrispate.

Navia platyphylla Lyman B. Smith & Steyerm., sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp, steep slope of ravine forest at edge of tepui, 01°26′N, 65°47′W, 1,550 m, 17 Oct. 1987, *R. Liesner & F. Delascio 22062* (holotype, US; isotypes, MO, US). Figure 8.

A *N. diffusa* Lyman B. Smith, cui valde affinis, foliis latioribus spinis longioribus, inflorescentia quadripinnata atra; floribus juvenilibus et alteris reflexis differt.

Terrestrial plant, 2 m tall when fruiting. Sheaths not seen. Leaf blades coriaceous, linear-ligulate, attenuate, 1.3–1.5 m long, 4–4.5 cm wide, strongly spinose in the lower ¼–⅓ with black, broad-based spines 3 mm long, obscurely and sparsely lepidote beneath, mostly glabrous above. Inflorescence laxly 4-pinnate, 2 m tall, longer axes 9–14 cm long, the ultimate axes 3–11 cm long, glabrous, the flowers 3–4 mm apart. Primary bracts broadly triangular, long-attenuate, shorter than the sterile

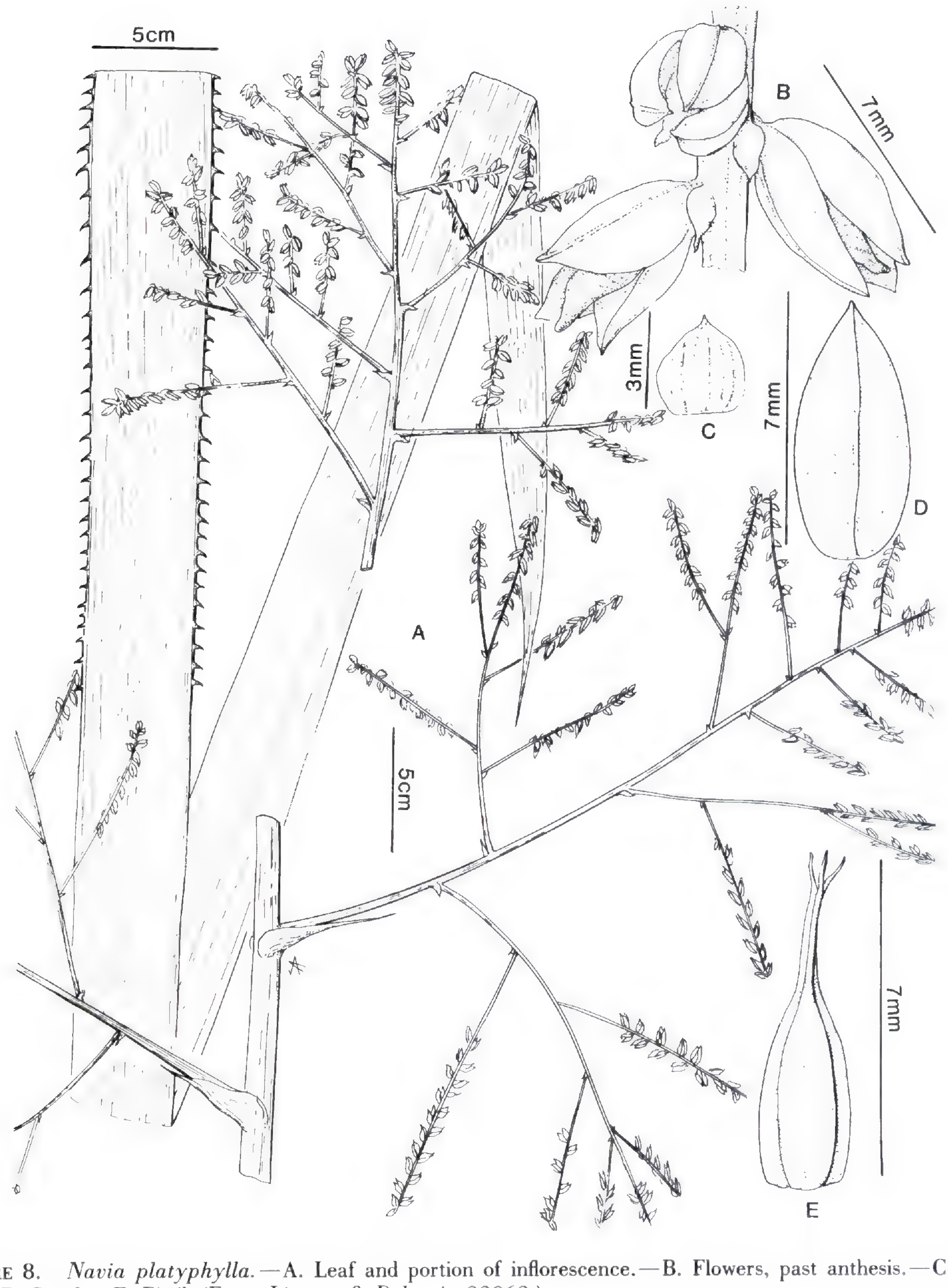

FIGURE 8. *Navia platyphylla.*—A. Leaf and portion of inflorescence.—B. Flowers, past anthesis.—C. Floral bract.—D. Sepal.—E. Pistil. (From *Liesner & Delascio 22062.*)

bases of the main axes, 3.5–4.5 cm long, scarious margined. Bracts subtending the secondary axes broadly ovate, abruptly attenuate, 3–7 mm long. Flowers reflexed. Floral bracts broadly suborbicular-deltoid, subamplexicual, acuminate, 3–5 mm long, about ⅜ length of the sepals. Sepals oblong-ovate or ovate, subobtuse, 4–7 mm long, the posterior strongly carinate. Petals (past anthesis) 9 mm long. Ovary superior, ovoid, 4 mm long.

This species differs from *N. diffusa* by having reflexed flowers (even when young), larger sepals, and much broader leaves with longer, stouter spines. The four-pinnate inflorescences are also characteristic. It is distinguished from *N. hechtioides* Lyman B. Smith by having shorter sepals, the posterior ones nonalate. From *N. brocchinioides* Lyman B. Smith, it is differentiated by the non-digitate, solitary, shorter spikes.

Navia terramarae Lyman B. Smith & Steyerm., sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Araca-

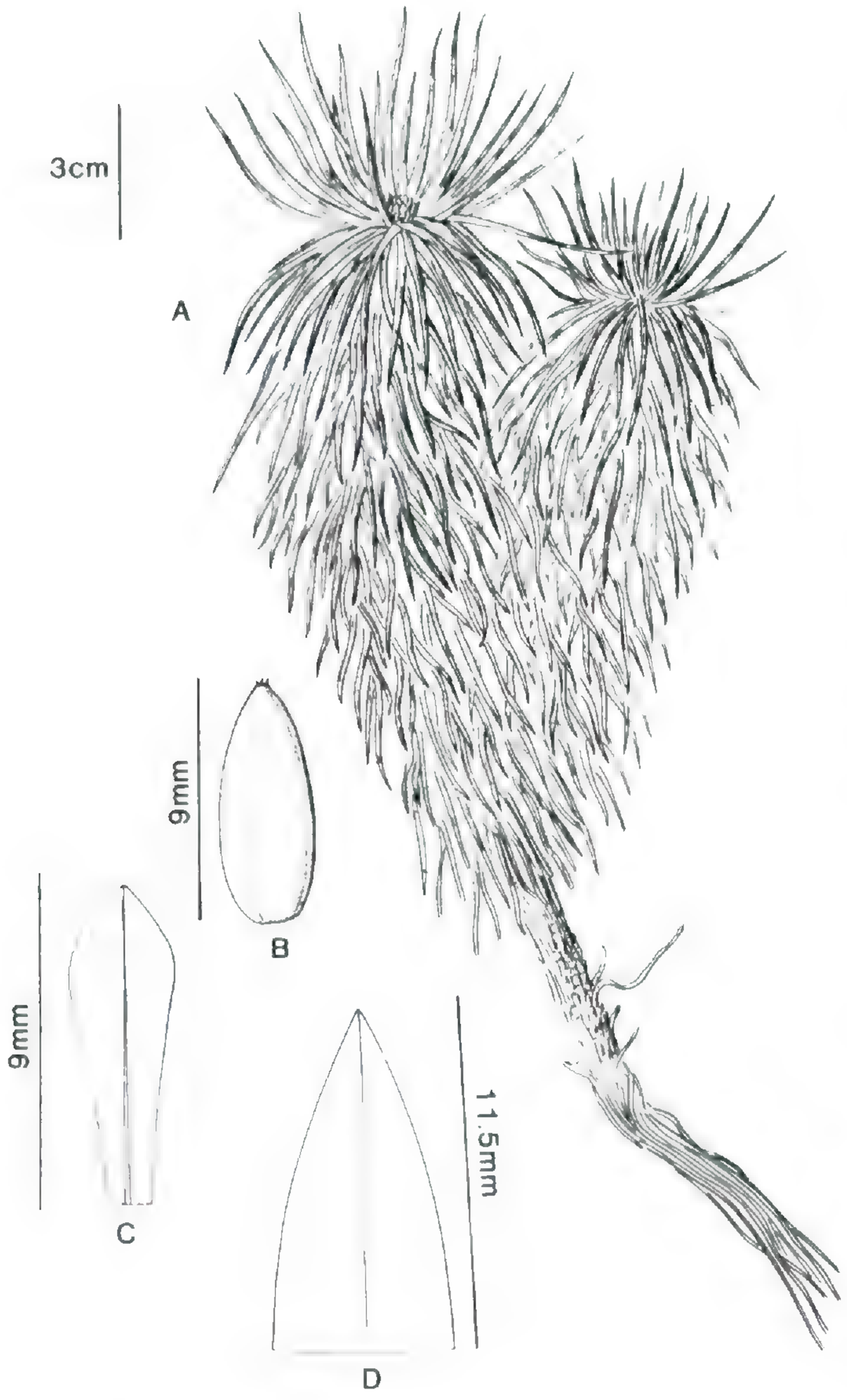

FIGURE 9. *Navia terramarae*.—A. Habit.—B. Fruit.—C. Sepal.—D. Floral bract. (From *Liesner & Delascio 21998, 22599.*)

muni, summit, Popa Camp, savanna with small to large patches of forest and stream, stream bank, 01°26′N, 65°47′W, 1,550 m, 16 Oct. 1987, *R. Liesner & F. Delascio 21998* (holotype, US; isotypes, MO, VEN). Figure 9.

A. *N. liesneri* Lyman B. Smith, Steyerm., & H. Robinson, cui valde affinis, foliorum laminis interioribus ad basin versus albis et a *N. delascionis* Lyman B. Smith, Steyerm. & H. Robinson, item valde affinis, foliorum laminis obscure serrulatis laxe minuteque obscure serrulatis, et ab ambabus caulibus elongatis, ramosis subterraneis, foliis omnino glabris differt.

Caulescent plant with elongated, simple or dichotomously branched stems 10–20 cm long, 0.7–1.5 cm wide. Leaf sheaths brown, membranous, 5–6 mm wide, striate. Leaves crowded in a dense rosette, the older ones strongly reflexed, the interior leaves white basally; leaf blades narrowly linear-triangular, 4.5–6 cm long, 1.5–2 mm wide, glabrous, terminating in a slender apiculum, laxly and minutely spinulose, the spinules ascending, 0.2–0.25 mm long, 1–1.5 mm apart. Inflorescence simple, sessile, glomerate. Outer bracts linear, 1.7–2.5 cm long, minutely serrulate. Floral bract uniformly membranous, ca. 6-striate, broadly oblong-lanceolate, acute, 10–12 mm long, 5.5 mm wide at base. Sepals free, linear-oblanceolate, obtusely acute, 8.5–9 mm long, 1–2 mm wide. Ovary superior. Capsule lance-oblong, slightly narrowed at summit, 9 mm long, 3 mm wide at middle.

This species is closely related to the recently described *Navia liesneri* and *N. delascionis*. The interior leaves are white at the base as in *N. delascionis*, but the more conspicuous teeth resemble those of *N. liesneri*. The leaf blades are narrower than in either *N. liesneri* or *N. delascionis*. The lower margins of the leaf blades are shortly white ciliate in *N. delascionis* and conspicuously floccose-ciliate, whereas in *N. terramarae* the leaf blades are completely glabrous.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Cerro Aracamuni, summit, Proa Camp, semi-open forest, 01°32′N, 65°49′W, 1,400 m, 28 Oct. 1987, *R. Liesner & G. Carnevali 22599* (MO, US, VEN).

The new species is named for the Terramar Foundation of Venezuela in recognition of the invaluable assistance provided on the expedition to Cerro Aracamuni.

BURMANNIACEAE—contributed by Paul J. M. & H. Maas

Studying the material available of Burmanniaceae for Steyermark's *Flora of the Venezuelan Guayana*, we came across an undescribed species of the saprophytic genus *Hexapterella*. We name it after Julian Steyermark to honor his lifelong dedication to the Venezuelan flora.

Hexapterella steyermarkii P. Maas & H. Maas, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, summit, Proa Camp, 01°32′N, 65°49′W, 1,400 m, 29 Oct. 1987 (fl, fr), *R. Liesner & G. Carnevali 22622* (holotype, MO; isotype, U). Figure 10.

Herba saprophytica. Flores hypocrateriformes sex-costati. Perianthium ad maturitatem fructus persistens. Tepala exterioria integra. Tepala interioria tepalibus exterioribus mensura formaque dissimilia. Antherae sessiles tubum floralem non excedentes.

Saprophytic herbs 12–21 cm high. Rhizomes unknown. Stems lavender, unbranched, or sometimes branched at the base of the plant, upper part of stem and inflorescence papillate (papillae ca. 0.02 mm long). Leaves narrowly triangular to tri-

FIGURE 10. *Hexapterella steyermarkii.*—A, B. Habit. C. Old flower with dehiscing capsule.—D. Flower.—E. Leaf.—F. Inner side of flower showing outer and inner tepals, and stamens.—G. Detail of stamen.—H. Seed. (B, from *Maguire et al. 42251*; G, from *Steyermark 105202*; A, C, D, E, F, and H, from *Liesner & Carnevali 22622.*)

angular-ovate, 2–4 mm long, 0.8–2 mm wide, base auriculate, apex acuminate. Inflorescence a bifurcate or single cyme, cincinni 2–6-flowered, 8 25 mm long, flowers 1.8–11 mm apart, or plant having a solitary, terminal flower. Bracts narrowly triangular to triangular-ovate, 1.8–3.5 mm long, 0.6–1.9 mm wide, base often auriculate, apex acuminate. Pedicels 2–4(–5.5) mm long. Flowers pale purple to lavender, or white with purple to lavender lobes, (4.5–)6.5–9.5(–11) mm long. Tepals per-

sistent, papillate on both sides. Outer tepals 3, narrowly triangular(–ovate), 3.0–4.3 mm long, 0.8–1.4 mm wide, margins involute. Inner tepals 3, obcordate to spathulate, 0.6–1.3 mm long, 0.5–0.8 mm wide. Floral tube 2.5–4.9 mm long, 0.8–1.5 mm diam., 6-ribbed. Thecae sessile. Style 3.5–4.6 mm long, branches 0.6–0.9 mm long. Ovary (transversely) obovoid-ellipsoid, 1.2–2.7 mm long, 1–2.5 mm diam., upper part 1-locular, basal part 3-locular. Capsule globose to transversely broadly ellipsoid, 1.5–3.2 mm long, 2–3.5 mm diam., crowned by the persistent perianth, dehiscing by transverse slits and irregularly withering of the wall between the ribs. Seeds irregularly globose to ovoid, 0.3–0.5 × 0.2–0.3 mm.

Distribution. Known only from the Venezuelan Guayana (Territorio Federal Amazonas and Estado Bolívar); (470–)1,100–1,800 m; often along rivers or on dry rock ledges.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro de la Neblina, Río Yatúa, slopes of Cañon Grande below Cumbre Camp, 1,100–1,800 m, 26 Nov. 1957 (fl, fr), *B. Maguire et al. 42251* (NY); Cumbre del Cerro Autana, 1,230–1,270 m, 21–22 Sep. 1971 (fl, fr), *J. Steyermark 105202* (U, VEN). BOLÍVAR: Chimantá Massif, along Río Tirica (Río Apapurén) just above Techiné-Merú, 410 m, 16 Jan. 1955, *J. Steyermark & J. Wurdack 113* (VEN).

Hexapterella steyermarkii is only the second species described in this genus. The other species, *H. gentianoides* Urban, is a fairly common saprophyte in Guyana and Surinam, and has been collected once in Venezuela—at Cerro de la Neblina, between 1,100 and 1,800 m. *Hexapterella steyermarkii* is known from three collections in Territorio Federal Amazonas (Cerros Aracamuni, Neblina, and Autana) and one from Estado Bolívar (Chimantá Massif).

The two species of *Hexapterella* can be distinguished by the following key:

1a. Anthers on long filaments slightly exceeding the floral tube; upper part of perianth caducous; inner tepals narrowly ovate-triangular ..... *H. gentianoides*

1b. Anthers sessile, not exceeding the floral tube; perianth persistent on fruit; inner tepals obcordate ..... *H. steyermarkii*

ERIOCAULACEAE—contributed by Nancy Hensold

Paepalanthus sulcatus Hensold, nom. et stat. nov. *Paepalanthus stegolepoides* var. *acutalis* Moldenke, Phytologia 15: 463. 1968.

Selected specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp, 01°26′N, 65°47′W, 1,550 m, 15 Oct. 1987, *R. Liesner & F. Delascio 21940* (MO, VEN).

EUPHORBIACEAE—contributed by Grady Webster

Senefeldera yutajensis (Jabl.) Webster, comb. nov. *Sapium yutajense* Jabl., Mem. New York Bot. Gard. 17: 184. 1967, fig. 24. TYPE: Venezuela. Territorio Federal Amazonas: Caño Yutajé, *B. Maguire & C. Maguire 35261* (holotype, NY).

Jablonski noted that the leaf venation and inflorescence of this species suggested *Senefeldera*, but he placed it in *Sapium* because of the staminate flower with a two-lobed calyx and two connate stamens. However, the branched inflorescence, caducous stipules, and especially the non-arillate seeds of the type collection are quite incompatible with *Sapium*. The small stamen number is shared with *Senefelderopsis*, but that genus has unbranched inflorescences and leaves with the veinlets not prominulous. Surprisingly, there is a resemblance to *Mabea*, especially to *Mabea pohliana* (Benth.) Muell. Arg. in sect. *Apodae* Pax & Hoffman (Pflanzenr. 147. V: 39. 1912). That species of *Mabea* has a branched inflorescence, an androecium of only two or three stamens, and an indumentum of dendritic hairs. Yet *Mabea pohliana* differs by having serrulate, short-petiolate leaves without prominulous venation, discrete staminate sepals and stamens, pedicellate pistillate flowers, and an elongated stylar column. In its subsessile pistillate flowers, elongated stylar column, and entire leaves with prominulous venation, *Senefeldera yutajensis* agrees with other species of *Senefeldera*, and this seems the best generic placement despite the indumentum of dendritic hairs. Along with *Senefeldera triandra* Pax & Hoffman (Pflanzenr. 147. XIV: 55. 1919) and possibly *Mabea paraguensis* Muell. Arg. (Fl. Brasil 11(2): 527. 1874), *Senefeldera yutajensis* may represent a phyletic branch intermediate between the genera *Senefeldera* and *Mabea*.

Additional specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Cerro Aracamuni, summit, Proa Camp, 01°32′N, 65°49′W, 1,400 m, 29 Oct. 1987, *R. Liesner & G. Carnevali 22625* (DAV, MO, VEN).

GENTIANACEAE—contributed by Julian Steyermark

Symbolanthus aracamuniensis Steyerm., sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp, savanna, 01°26′N, 65°47′W, 1,550 m, 17 Oct. 1987, *R. Liesner*

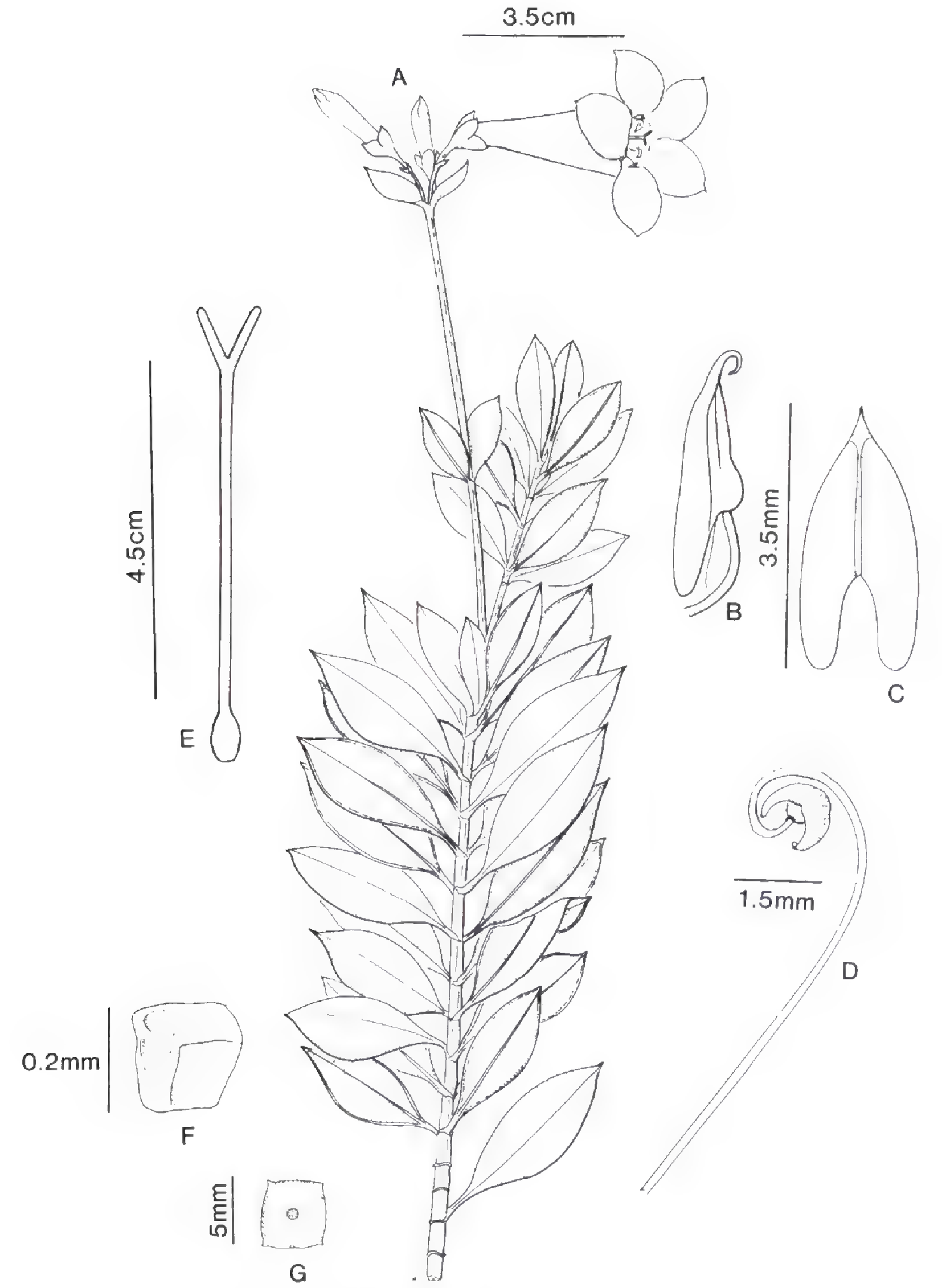

FIGURE 11. *Symbolanthus aracamuniensis.* —A. Habit of branch.—B, C. Anther.—D. Stamen.—E. Pistil. —F. Seed. —G. Cross section of stem. (From *Liesner & Delascio 22079.*)

& F. Delascio 22079 (holotype, MO; isotype, VEN). Figure 11.

A *S. huachamacarensis* et *S. yaviensis* calyce valde reducto, 7 8 mm longo, lobis 5–6 mm longis differt.

Glabrous herb, 0.3–0.8 m tall. Stem 4-angled, 3–3.5 mm diam. Leaves short-petiolate, blades lance- to oblong-elliptic, the apex acute, the decurrent base acute to cuneate, silvery abaxially, the larger lower and middle blades 4–6.5 cm long, 1.5–2.2 cm wide, faintly plinerved above, obsoletely nerved below; petiole 2–7 mm long. Inflorescence terminal, cymosely 3–4-flowered; pedicel slender, 0.5–2 cm long. Calyx 7–8 mm long, 8–9 mm wide, 5-lobed; lobes ovate, obtuse, nearly divided to the base, 5 6 mm long, 4 mm wide, scarious-margined. Corolla lavender-pink, pink, or whitish, infundibuliform, 5–5.5 cm long; tube 3–3.8 cm long, 3–3.5 mm wide at base, 2–3 cm wide at summit; lobes 5, broadly ovate, 2.2–2.5 cm long, 2–2.2 cm wide, broadly curved above to an obtuse mucronulate apex. Stamens 5, subequal, as high as or higher than the orifice of the corolla. Filaments coiling, attached to corolla tube 5 mm above its base, 4 cm long; anthers suboblong, dorsifixed, lance-oblong, sagittate at base, narrowed to a revolute aristate tip, 3.5–5 mm long, 1.5 mm wide, the sagittate lobes 1–1.5 mm long; thecae with a dorsal basal enlargement. Capsule oblong, 13 mm long, 6 mm wide. Seeds quadrangular,

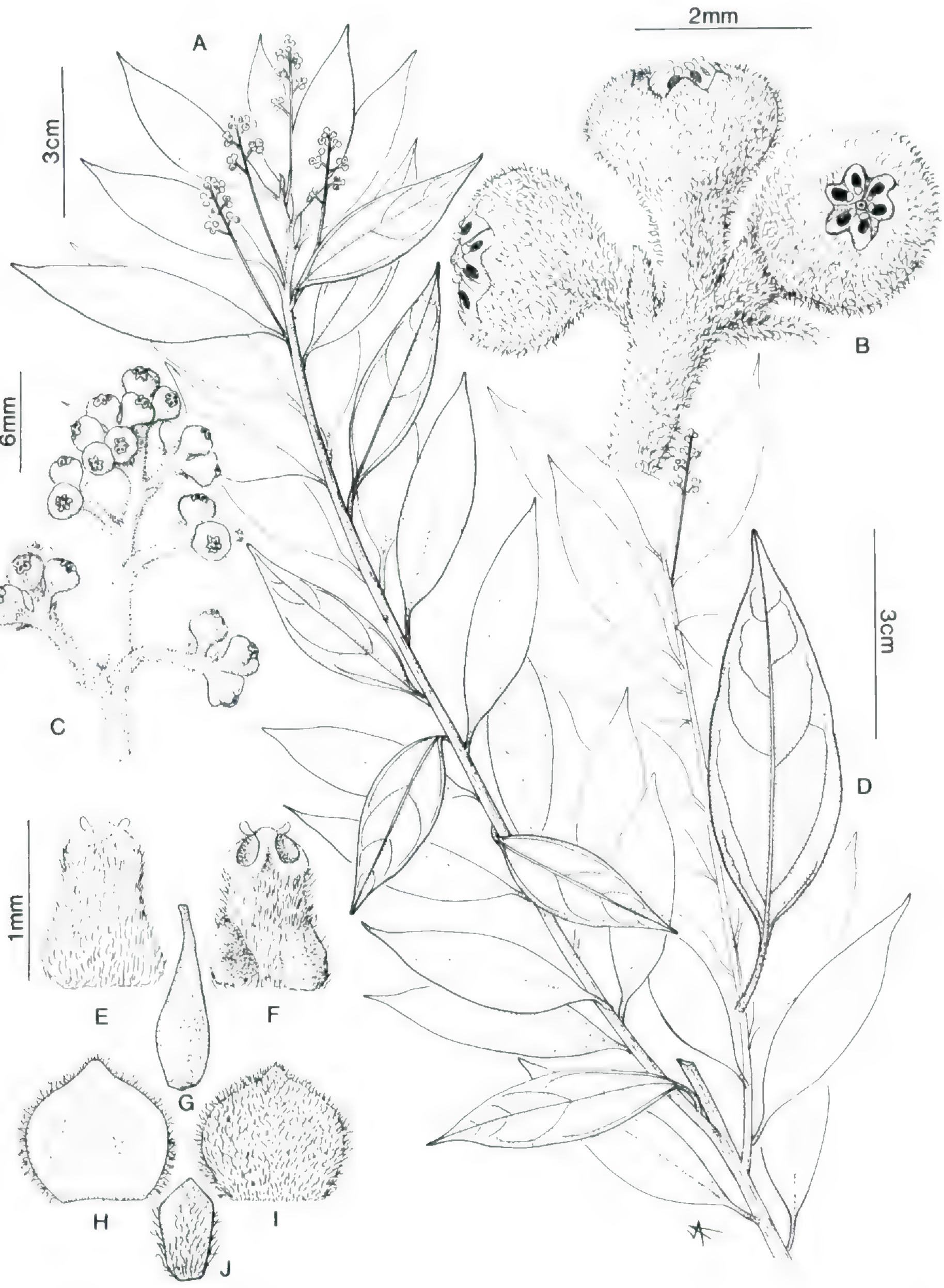

FIGURE 12. *Licaria trinervis*.—A. Habit of branch.—B. Flowers.—C. Part of inflorescence.—D. Leaf.—E, F. Ventral and dorsal views of stamen.—G. Ovary.—H, I. Ventral and dorsal views of tepal.—J. Staminode. (From *Liesner & Delascio 22161*.)

broader than long, 0.2 mm long, 0.3 mm wide, depressed at the summit, the surface plane with a microscopic cellular appearance.

This species differs from *S. yaviensis* Steyerm. and *S. huachamarensis* Steyerm. in its much shorter calyx. Other distinctive characters of the new species are the anthers with revolute, aristate tips and a dorsal enlargement at the junction of the anther with the filament.

LAURACEAE—contributed by Henk van der Werff

Licaria trinervis van der Werff, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, summit of Cerro Aracamuni, 01°26′N, 65°47′W, 1,550 m, 19 Oct. 1987, *R. Liesner & F. Delascio 22161* (holotype, MO; isotypes, HBG, NY, VEN). Figure 12.

Frutex vel arbor parva. Ramuli teretes, juvenales fusco-tomentosi, velustiores glabri. Folia alterna, 4–10 × 1.5–3 cm, anguste elliptica, fortiter chartacea, basi apiceque acuta, super glabra (juvenalissima sparse tomentosa), subtus fusco-tomentosa (vetera glabrescentia). Nervi utroque costae latere 4–5, marginem versus arcuati et connati;

super immersi, subtus elevati, precipue costa et nervi basales. Petioli 0.5–1 cm, fusco-tomentosi, glabrescentes. Inflorescentiae axillares, fusco-tomentosae, paniculatae, foliis breviores, 2–3 cm longae. Pedicelli ad 1 mm longi. Flores fusco-tomentosi, depresse globosi, ca. 1.5 mm longi, ca. 2.2 mm lati; stamina fere tepalis obtecti, solum apicibus expositis. Tepala 6, aequalia, fusco-tomentosa, incurvata, ca. 1 mm longa et 1.2 mm lata. Stamina 3, ca. 1 mm longa, 2-locellata; filamentis liberis, pubescentibus, basi 2 glandulis praeditis; locellis parvis, fere apicalibus. Staminodia 6, 0.5–0.6 mm longa, basibus pubescentia. Ovarium glabrum, ellipsoideum, ca. 0.6 mm longum; stylo gracili, ca. 0.6 mm longo. Fructus ignotus.

Shrubs or small trees, to 5 m tall. Twigs terete, rather slender, brown tomentose when young, glabrescent with age. Leaves alternate, 4–10 × 1.5–3 cm, narrowly elliptic, evenly distributed along the twigs, base acute, apex acuminate, firmly chartaceous, upper surface glabrous or loosely tomentose along the midrib when very young, lower surface brown tomentose when young, tomentum wearing off with age and the oldest leaves occasionally glabrous; lateral veins 4–5 pairs, the basal pair much more strongly developed than the others, all laterals arching upwards and becoming loop-connected; veins immersed above, raised below (especially the midvein and the basal laterals). Petioles 0.5–1 cm long, flattened above, brown tomentose when young, glabrescent with age. Inflorescence in axils of leaves or deciduous bracts, brown tomentose, paniculate, shorter than subtending leaves, 2–3 cm long. Pedicels to 1 mm long, brown tomentose. Flowers brown tomentose, depressed-globose, 1.5 mm long, ca. 2.2 mm wide, the stamens nearly enclosed by the tepals with only their tips exposed. Tepals 6, equal, incurved, ca. 1 mm long, 1.2 mm wide, brown tomentose. Stamens 3, ca. 1 mm long; the filaments free, with 2 glands near the base, pubescent, about as wide as the anthers; anther cells small, nearly apical, opening towards the tip of the anther. Staminodia 6, representing the two outer whorls, ca. 0.5–0.6 mm long, their bases pubescent. Ovary glabrous, ellipsoid, ca. 0.6 mm long; style slender, ca. 0.6 mm long. Fruit unknown.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, summit of Cerro Aracamuni, Proa Camp, 01°32′N, 65°49′W, 1,400 m, 25 Oct. 1987, *R. Liesner & G. Carnevali 22451* (MO, VEN), 2 Nov. 1987, *R. Liesner & G. Carnevali 22714* (MO, VEN).

Licaria trinervis belongs to subg. *Licaria*, as defined by Kurz (1983). It does not seem to have close relatives within this subgenus; among its striking characters are the brown tomentose pubescence on the young parts, depressed-globose flower shape, strongly developed basal pair of lateral veins on the leaves. Another distinction is that no other *Licaria* species in the Venezuelan Guayana is known from the tepui summits, although *L. macrophylla* (A.C. Smith) Kostermans is known from slopes of Cerro Huachamacari at 600 m, *L. tomentosa* van der Werff occurs on the slopes of the Chimantá Massif.

Persea perseiphylla (Allen) van der Werff, comb. nov. *Ocotea perseiphylla* Allen, Mem. New York Bot. Gard. 10: 109. 1964.

This species was known to Allen only from the holotype (*Schultes & Lopez 10103*, US), a specimen in young bud. Characters necessary for correct generic placement were not discernible at this young stage, and Allen mistakenly placed the species in *Ocotea*. Fruiting specimens show clearly that this species belongs in *Persea*. Inspection of the holotype also showed that the tepals of the buds are unequal, with the outer three shorter than the inner ones, a character found in most neotropical *Persea* species but never in *Ocotea*. Hence *Ocotea perseiphylla* is transferred to *Persea*. Because open flowers have not yet been collected, *P. perseiphylla* cannot be placed in any of the sections of subg. *Eriodaphne* Nees; the general resemblance to *P. maguirei* L. Kopp and *P. croatii* van der Werff suggests that it belongs in sect. *Aurataea* Kopp. It has nine four-celled stamens and therefore does not belong to sect. *Hexanthera* Kopp.

Additional specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp, 01°26′N, 65°47′W, 1,550 m, 18 Oct. 1987 (fr), *R. Liesner & F. Delascio 22099* (MO); 19 Oct. 1987 (fr), *R. Liesner & F. Delascio 22169* (MO); vertiente sur de la Sierra de Unturán, cabeceras del Río Mavaca, 01°32′N, 65°11′W, 550–650 m, 26 Feb. 1981 (fr), *F. Guánchez 809* (MO, TFAV).

MELASTOMATACEAE—contributed by John J. Wurdack

Tococa liesneri Wurd., sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, summit, Proa Camp, savanna with small to large patches of forest, 01°32′N, 65°49′W, 1,400 m, 1 Nov. 1987, *R. Liesner & G. Carnevali 22700* (holotype, MO 3502486; isotype, US).

T. obovata Gleason affinis, foliorum laminis (3-nervatis) et petiolis minoribus, calycis dentibus exterioribus vix eminentibus, petalis minoribus differt.

Shrub 0.4–0.5 m tall, the terete branchlets moderately puberulous with dendritic hairs ca. 0.2 mm long and sparsely glandular-setose with smooth hairs 1–2 mm long. Petioles 0.5–1 mm long; blade 1.5–

2.5 × 0.8–1.4 cm, ovate-oblong, apex rounded-acute, base cordulate, subcoriaceous and entire, ciliate with loosely appressed and in part gland-tipped hairs, above sparsely loose-strigose with smooth hairs 1.5–2.5 mm long, below sparsely loose-strigulose with gland-tipped hairs on the primary veins and very sparsely puberulous with short dendritic hairs but esetulose on the surface, 3-nerved (excluding the tenuous incomplete inframarginals), with obscure lax venule reticulation. Flowers 5-merous, solitary or ternate at branchlet ends, pedicels 2–7 mm long and (as the hypanthium) moderately dendritic-puberulous and glandular-setulose, the persistent bracteoles 2–2.5 × 0.7 mm and usually inserted ca. 0.5 mm below the ca. 5–5.4-mm-long hypanthium; calyx tube ca. 0.6 mm long, the oblong interior lobes ca. 3–3.5 × 2 mm, the glandular-setulose external teeth not or barely projecting (to 0.2 mm); torus glabrous within. Petals 10–11 × 8–9 mm, obovate-oblong with rounded-truncate apex, pink and glabrous. Stamens essentially isomorphic, glabrous; filaments ca. 6.5–7 mm long; anthers ca. 5 × 0.6 × 0.5 mm, oblong-subulate with ventrally inclined pore and with short blunt-basal spur. Stigma not expanded; style ca. 11–12 × 0.3–0.5 mm; ovary 3-celled and ca. 3 mm inferior, the truncate glabrous apical cone 1.4–1.5 mm long.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp, savanna, 01°26′N, 65°47′W, 1,550 m, 16 Oct. 1987, *R. Liesner & F. Delascio 22007* (MO, US).

Tococa obovata has distinctly five-nerved leaf blades measuring mostly 4–8 × 2–5 cm, petioles 0.3–0.7 cm long, external calyx teeth projecting 1–2 mm, and petals 15–21 × 7–9 mm; its interior calyx lobes are similarly developed, and both species have glabrous petals. In general vegetative aspect, *T. liesneri* resembles the typical subspecies of *T. bolivarensis* Gleason, which has broadly deltoid calyx lobes ca. 0.5 mm long and densely pruinose-granulose petals. The collection *Pires & Marinho 15708* (US, in fruit, from Brazil. Amazonas: alto Río Negro, São Gabriel da Cachoeira) bears a strong resemblance to *T. liesneri* except for completely eglandular vegetative setae.

OCHNACEAE—contributed by Julian Steyermark

Sauvagesia guianensis (Eichl.) Sastre subsp. **aracamuniensis** Steyerm., subsp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp, savanna, 01°26′N, 65°47′W, 1,550 m, 17 Oct. 1987, *R. Liesner & F. Delascio 22075* (holotype, MO; isotype, VEN).

A subsp. *guianense* squamulorum laminis suborbicularibus apice late rotundatis, foliorum glandulis marginalibus utroque latere 1–3 adpressis recedit; a subsp. *guaiquinimensis* petalis apice rotundatis, squamulorum lami a subsp. *sipapoensis* atque subspeciebus alus foliorum glandulis marginalibus paucis differt.

Subligneous plant 0.5–1 m tall. Leaves linear-oblanceolate, 9–10 mm long, 1.8–2 mm wide, remotely appressed serrulate with 1–3 appressed glandular teeth on uppermost 1.5–2 mm of margins, obtusely acute at apex with a blunt, glandular protuberance; lateral nerve depressions obliquely ascending. Pedicels 2 mm long, flowers hidden in the upper leaves. Petals pink, obovate, rounded at apex, 6.5 mm long, 3.8–4 mm wide at the middle. Staminodia 9–10 mm long, the lamina suborbicular, 0.3–0.5 × 0.3–0.5 mm, stipitate portion 0.6–0.7 mm long.

This subspecies is distinguished from subsp. *guianense* by having the leaf margins remotely appressed serrulate with 1–3 glandular teeth on each side of the uppermost 1.5–2 mm of the margins, and the leaf apex with a blunt, glandular protuberance. From subsp. *sipapoensis* Steyerm. it differs by the relatively few appressed glandular teeth on each of the uppermost margins and the suborbicular rounded lamina of the staminode. It differs from subsp. *guaiquinimensis* Steyerm., which has a similar suborbicular rounded lamina, in the rounded petals.

ORCHIDACEAE—contributed by Germán Carnevali & Ivón Ramírez

The generic revision of the Spiranthinae by L.A. Garay (1982) formed the basis for a better understanding of the spiranthoid complex. A reevaluation of this group for a treatment of the Orchidaceae from the Venezuelan Guayana has revealed the presence of a very distinctive new species that cannot be assigned to any of the genera delimited in Garay's revision.

Aracamunia liesneri Carnevali & I. Ramírez, gen. et sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp, on moss covered streambank in almost closed forest, 01°26′N, 65°47′W, 1,550 m, 16 Oct. 1987, *R. Liesner & F. Delascio 21988* (holotype, VEN; isotype, AMES, MO). Figure 13.

Plantae terrestres, graciles, minutae (vix 4–7 cm altae); radicibus cylindraceis, carnosis, pubescentibus; foliis basalibus vel caulescentibus subpetiolatis, vagina basi appendice liguliformi rigido ascendenti apice irregulariter dilatato pilis minimis breviter pedunculatis instructo; caulibus e rhizomate brevi decumbenti vix erectis; racemo

elongato remote paucibracteato, apice laxe spicato; floribus parvulis. Species singula adhuc nota, venezuelensis. Sepala similia, inter se satis alte connata, nectarium vel tubum amplum formantia, apicibus parallelibus; sepalis extus minute glandulari-papillosis, sepalo postico columnae basi dorsaliter adnato; sepalis lateralibus sepalo dorsali valde similibus, antice valde concavis, sepalo postico partim agglutinata, basi leviter decurrentia. Labellum longe unguiculatum, ungue tubo sepalino omnino adnatum, deinde sagittatum, marginibus in medio utrinque columnae lateribus agglutinatis. Columna erecta, dorsaliter sepalo postico satis alte adnata, apice libera, basi in pedem brevissimum apice ovarii oblique praedita; stigmate transverse elliptico; rostello valido, oblongo, apice truncato, apice structura globulari et papillosa praedito. Anthera ellipsoidea. Pollinia lineari-clavata, viscidio parvulo, rotundo affixa. Ovarium subcilindricum, sessile, haud tortum.

Small terrestrial or muscicolous erect herbs, 4–7 cm high. Roots cylindric, 3–6, fleshy, coarse, pubescent, up to 3 cm long. Stems 5–15 mm long, ca. 3 mm thick, totally enveloped by the leaf sheaths, terete. Leaves glabrous, thinly subfleshy, marcescent, 7–11 per rosette, 4–5 fresh at flowering, sheaths imbricating and invaginating the stem, lamina flat or concave, margins slightly undulate, elliptic or ovate-elliptic, acute or shortly acuminate, 5–9 mm long, 3–4 mm wide, basally contracted into a channeled pseudopetiole 1–1.5 mm long and wide, this merging into the sheath. Sheath ovate to ovate-elliptic, ca. 5 mm long, 4 mm wide when flattened, with 1(2) erect, liguliform structures connected at the center of the sheath base and protruding from it, these 3.8–4.5 mm long, 1–1.2 mm wide, rigid, ± expanded apically where covered by multicellular short-pedunculate, globose hairs ca. 0.05 mm long. Inflorescence a terminal raceme, 35–45 mm long, laxly 3–6-flowered, fertile in the upper ¼, covered (except for the bracts) with sparse, cylindric to subcapitate, unicellular hairs ca. 0.1–0.2 mm long. Peduncle terete, 21–28 mm long, triarticulate, each articulation subtended by one glabrous, lanceolate, long-acuminate bract, this basally enveloping and apically spreading, the lowermost bracts 6.5–7 mm long, 3 mm wide, the apical bracts 5 mm long, 2 mm wide. Rachis 12–17 mm long, straight or slightly fractiflex. Floral bracts 3–7 mm long, 2–2.5 mm wide, identical to the peduncle bracts but somewhat smaller, much longer than the pedicellate ovary. Flowers tubular, not resupinate, white, 7–8 mm long including the ovary, forming an acute angle with the rachis. Ovary subcylindrical, 2–2.2 mm long, 1–1.2 mm thick. Sepals fused in the basal ¾, forming a cylindric, 5–5.5-mm-long tube around the column, petals, and labellum, the free parts concave, triangular-oblong, rounded apically, 2–2.1 mm long, 0.9–1.1 mm wide, minutely glandular-papillose without; dorsal sepal partially adnate to back of column in the basal ⅓ within. Petals membranaceous, connivent with the dorsal sepal along their whole length, uninervate, linear-spathulate, ca. 5 mm long, 0.7 mm wide near apex, 0.1–0.2 mm wide in the attenuated basal half. Labellum connivent with column margins, membranaceous, trinervate, 5.5–6 mm long, ca. 1 mm wide near apex, narrowly oblong in general outline, somewhat dilated in the apical ¼, apex obtuse, thickened and finely papillose-ciliate, base sagittate with 2 retrorse, linear-oblong, apically rounded and thickened lobes 1.3–1.5 mm long, 0.4 mm wide; labellum attached to ovary apex by a relatively long, linear-oblong claw, 0.9–1.2 mm long, 0.4 mm wide, this adnate to the sepaline tube. Column erect, elongate, subcylindric, 4.5 mm long, 0.7–0.8 mm wide at base. Anther ellipsoid, bilocular, obtuse at both extremes, 2 mm long. Rostellum oblong, 1.8 mm long, ca. 1 mm wide, apically truncate and bearing a globular, papillose structure 0.4 mm long and wide. Clinandrium margins narrow, membranaceous, ± erect and slightly enclosing the anther. Stigmatic surface ventral, papillose, transversely elliptic, 0.8 mm wide.

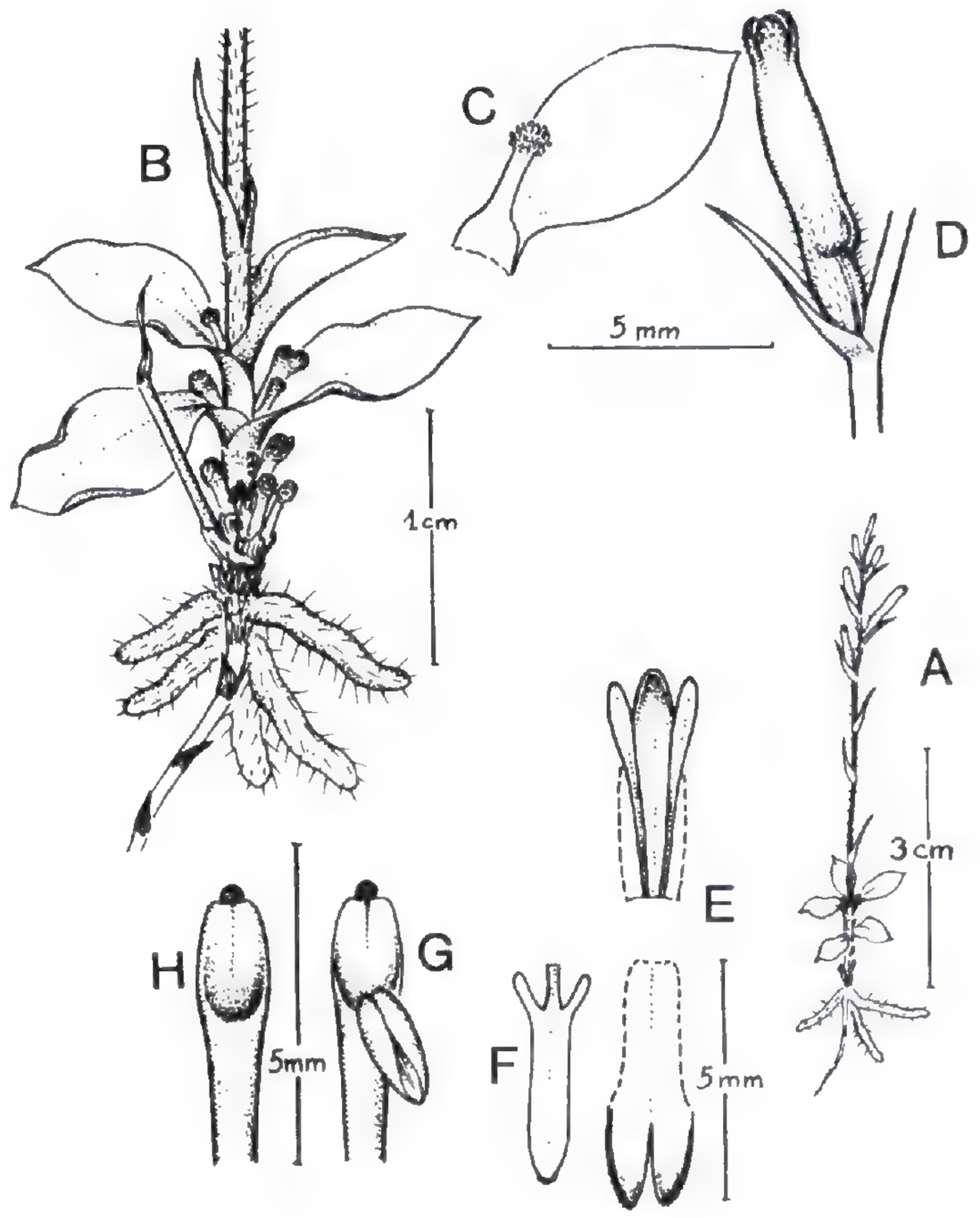

FIGURE 13. *Aracamunia liesneri.*—A. Habit.—B. Detail of plant, showing the ligulelike structures. —C. Leaf with ligulelike structure at leaf sheath.—D. Flower, pedicellate ovary, and floral bract. E. Perianth segments.—F. Labellum.—G. Upper side view of column, with anther retracted. —H. Lower side view of column showing stigmatic surface. (From *Liesner & Delascio 21988.*)

This new genus seems to belong to the *Eury-*

styles Wawra complex, with which it shares the small vegetative habit, nonresupinate flowers, and sepals connate for at least part of their length. However, *Aracamunia* differs from the other genera of the *Eurystyles* complex in its terrestrial habit, eciliate leaves and bracts, presence of ligulelike structures, noncapitate inflorescences, and ecristate sepals connate for about ¾ of their length (vs. up to ½ their length). Within the complex, it seems to be closer to *Eurystyles* as defined by Burns-Balogh et al. (1985), but in *Aracamunia* the stigmas are confluent as in *Pseudoeurystyles* Hoehne.

The most distinctive feature of *Aracamunia* is the presence of the ligular, apparently glandular structures that originate from the bases of the leaf sheaths and persist even after disintegration of the leaf blades and sheaths. These ligular structures are erect, rigid, solitary, or (rarely) in pairs on each leaf sheath. They show traces of vascular axes, with phloem extending farther apically than the xylem, suggesting a glandular function. The apices vary widely in shape: sometimes bifid, lobulate, coarsely dentate, or expanded into a suborbicular blade. The multicellular hairs of the liguliform structures are denser in younger more apical portions, with each of the hair cells containing a large nucleus proportionate to the size of the cells.

The ligular structures have vascular connections with the leaf sheaths and the stem. Further study is required to determine if they are glandular or perhaps have an assimilative function.

Etymology. Generic name for Cerro Aracamuni where the type species was collected, in the Federal Territory of Amazonas in southern Venezuela. The specific epithet honors Ronald Liesner who collected the type material.

PIPERACEAE—contributed by Julian Steyermark

Piper mosaicum Steyerm., sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp, savanna with small to large patches of forest and stream, 01°26′N, 65°47′W, 1,550 m, 16 Oct. 1987, *R. Liesner & F. Delascio 21968* (holotype, MO; isotype, VEN). Figure 14.

Frutex 1 metralis; ramis retrorse pubescentibus; foliis elliptico-lanceolatis apice acute acuminatis, basi aequilateraliter subacutis vel acutis, breviter mucronatis 8.5–14 cm longis 2.5–4 cm latis, conspicue reticulatis argenteo-maculatis ubique rugulosis, praeter squamas farinaceas lepidotas glabris, subtus nervis et costa media adpresso-pubescentibus, squamis farinaceis onustis; totis pinnatim venosis, nervis lateralibus utroque latere 5–8; petiolis 2–7 mm longis adpresso-puberulentis, infra medium vaginatis; spicis erectis 17 mm longis 5 mm latis, pedunculis 4.5 mm longis, breviter retrorse puberulis.

Shrub 1 m tall; stems nodose, minutely and retrorsely subappressed-pubescent, 3–4 mm thick. Leaf blades elliptic-lanceolate, acuminate at the minutely mucronate apex, equilaterally acute to subacute at base, drying gray-silvery and blackish, reticulate-rugulose both sides, 8.5–14 cm long, 2.5–4 cm wide, upper surface glabrous except for farinaceous lepidote scales, the darker areas with more minute scales, lower surface paler, covered with a dense farinaceous lepidote layer with pale stellulate trichomes along the midnerve, pinnately nerved throughout to the upper ¼, the lateral nerves 5–8 each side; midnerve and lateral nerves on lower surface appressed-pubescent. Petioles 2–7 mm long, minutely appressed-puberulent, the petiolar sheath vaginate in lower half. Spikes erect, 17 mm long, 5 mm wide, peduncle 4.5 mm long, shortly retrorsely puberulous. Stigmas sessile, spreading over the summit of the fruit. Fruit depressed-truncate at summit, suborbicular, subquadrangular.

This species differs from *Piper gentryi* Steyerm. by having mottled, smaller leaf blades; shorter petioles with sheaths that are longer, winged; retrorsely pubescent stems and peduncles; and fewer lateral nerves. It is distinguished from *P. holtii* Trel. & Yuncker by having shorter peduncles and spikes and smaller, mottled leaf blades that lack the sulcate nerves on upper leaf surface and lack conspicuously elevated nerves of the lower surface.

RAPATEACEAE—contributed by Julian Steyermark

Rapatea aracamuniana Steyerm., sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, slope, Quebrada Camp, area of rapids flowing over laja, river bank in sun, more common in shade, 01°24′N, 65°38′W, 600 m, 20 Oct. 1987, *R. Liesner & F. Delascio 22197* (holotype, MO; isotype, VEN). Figure 15.

Planta herbacea; foliorum laminis supra omnino minute dense papillato-verruculosis, subtus conspicue fusco-glanduliferis ornatis inter punctos minores dispositis; spiculis (sepalis exclusis) 23 25 mm longis; bracteolis infimis 17 18 mm longis; antheris 10 mm longis; filamentis ciliolatis.

Herb. Leaves petiolate, sheaths 11–13 cm long, 6–8 cm wide, conspicuously many-costate, densely papillate; leaf blades ligulate-lanceolate, falcately acuminate at apex, inequilaterally acute at base, 36–66 cm long, 5–7.4 cm wide at the middle, upper surface densely verruculose-papillate, lower

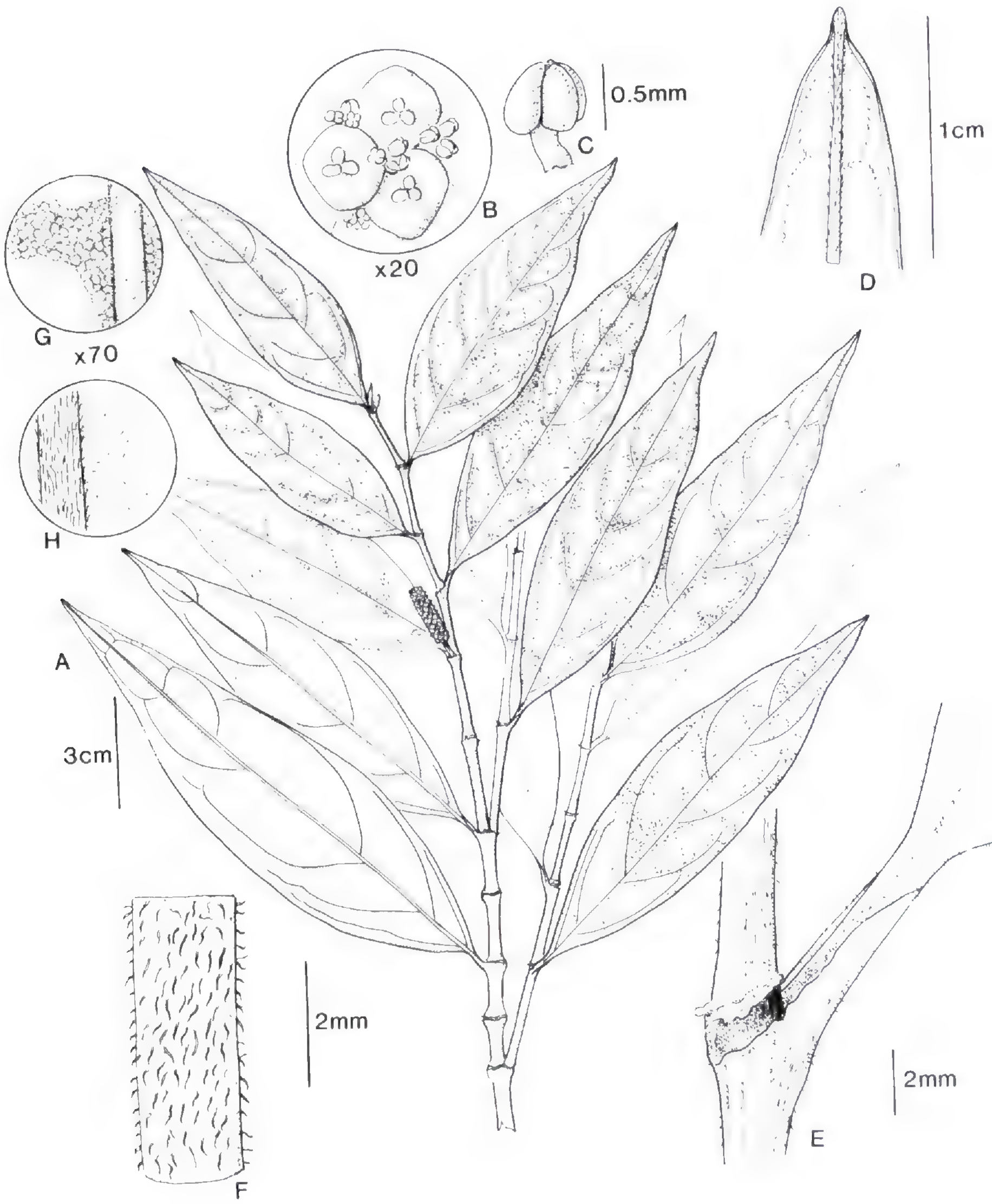

FIGURE 14. *Piper mosaicum.*—A. Habit of branch.—B. Detail of spike.—C. Anther.—D. Leaf tip, lower surface.—E. Detail of stem node.—F. Stem.—G, H. Details of lower leaf surface. (From *Liesner & Delascio 21968.*)

surface with brown glandular punctae regularly distributed between smaller punctate glands, midrib conspicuously impressed on upper surface, elevated on lower surface, bordered by 55–60 finely elevated parallel nerves on each side. Petiole 3–7.5 cm long, 8–9 mm wide. Inflorescence solitary, pedunculate, shallowly hemispherical, 4.5–6.5 cm long, 8–12.5 cm wide, enveloped by 2 broadly deltoid involucral bracts; these cordate at base and acute at apex, 7–12.5 cm long, 9–10 cm wide, minutely brown papillate-verruculose without, minutely pale papillate within. Spikelets numerous, pedicellate; pedicels 10–13 mm long, 1 mm wide, broadened to 1.5 mm wide at summit. Spikelets numerous, (excluding sepals) 23–25 mm long, 5 mm wide, ca. 12-bracteolate. Bracteoles graduate, the lowest 17–18 mm long, 3 mm wide, ¾ length of spikelet, linear-lanceolate, acute, scarious-margined; the innermost (uppermost) 22–23 mm long, 3–4 mm wide, narrowly triangular-lanceolate, acuminate, minutely puberulent without in upper portion, minutely ciliolate. Sepals with free expanded portion broadly lanceolate, acuminate, 12 mm long, 4 mm wide at base, membranous, 5-nerved, the lower portion attached to corolla tube for 15 mm long and 4 mm wide, hyaline throughout. Corolla yellow, 3 cm long; tube 12 mm long, 2.5–3 mm wide; laminate portion rhomboid, abruptly acute, 17 mm long, 9 mm wide at the widest portion, narrowed to claw 9 mm long, 2 mm wide. Anthers linear, bilobate at base, 10 mm long, 0.5 mm wide, prolonged at apex into a linear-oblong gland 1.5–

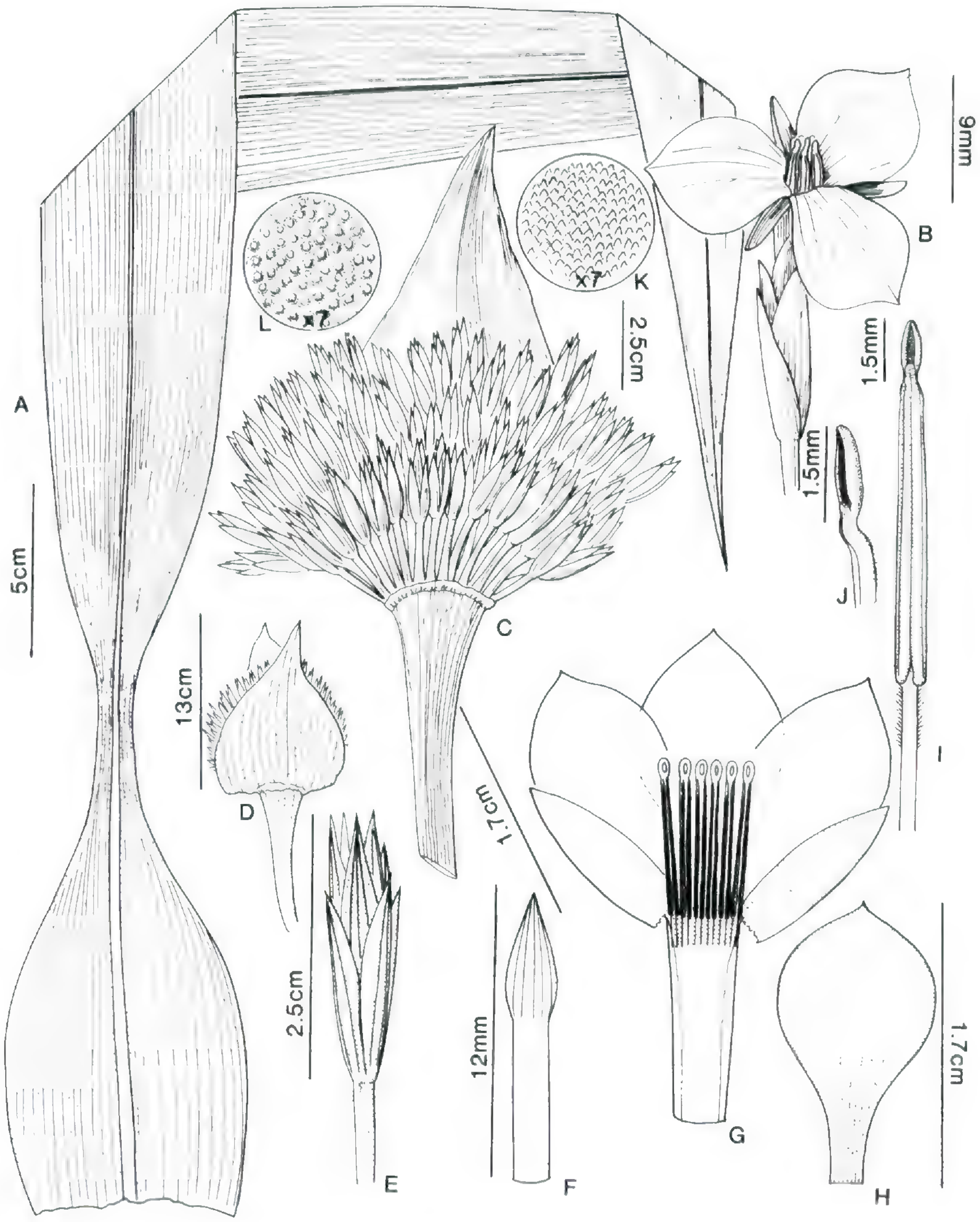

FIGURE 15. *Rapatea aracamuniana*.—A. Leaf.—B. Spikelet with open flower.—C. Inflorescence.—D. Inflorescence with bracts.—E. Fruit.—F. Corolla in bud.—G. Flower with corolla opened.—H. Petal.—I. Stamen.—J. Anther gland.—K. Detail of upper leaf surface.—L. Detail of lower leaf surface. (From *Liesner & Delascio 22197*.)

1.7 mm long, 0.4–0.5 mm wide. Filaments 4 mm long, 0.5 mm wide, pilosulous-ciliolate in the uppermost 2 mm. Style glabrous, 28 mm long, 0.3 mm wide, curved at apex, narrowed to a conical apex.

This species is related to *Rapatea steyermarkii* Maguire of extreme southeastern Venezuela in Estado Bolívar. Although similar in inflorescence, involucral bracts, and leaf shape and size, *R. aracamuniana* has filaments that are ciliolate (vs. glabrous in *R. steyermarkii*). The anthers, lowest bracteoles, and spikelets are longer in *R. aracamuniana*. The upper and lower leaf surfaces of *R. steyermarkii* are densely brown pubescent on the lower surface with elongate, crisp-villosulous, loose multicellular hairs, whereas in *R. aracamuniana* the lower surface has only brown glandular dots between smaller, pale punctations. In *R. steyermarkii* the upper leaf surface has short, divaricate, pointed hairs irregularly scattered on the nerves in addition to a minutely papillate surface, whereas the upper surface in *R. aracamuniana* is densely verruculose-papillate throughout.

Since *Rapatea steyermarkii* was originally described without flowers, the following description (taken from a specimen of *Holst & Liesner 2847* from Río Acanan, Estado Bolívar) is added to provide details lacking from the original description.

RAPATEA STEYERMARKII

Sepalis (parte libera) 19–20 mm longis; antheris 5 mm longis, 0.7 mm latis; filamentis 3 mm longis omnino glabris; stylo 15 mm longo glabro.

RUBIACEAE—contributed by Julian Steyermark

Cephalodendron aracamuniensis Steyerm., sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp, ravine forest at edge of tepui, 01°26′N, 65°47′W, 1,550 m, 17 Oct. 1987, *R. Liesner & F. Delascio 22064* (holotype, MO; isotype, VEN).

Arbor 4–6-metralis; ramulis dense hirsutis pilis divaricatis 2 3 mm longis instructis; foliorum laminis late obovatis apice abrupte acutis basi rotundatis vel subcordatis 32–35 cm longis prope medium 16–26 cm latis, supra ferrugineo-hirsutis pilis 2 3 mm longis onustis; venatione tertiaria supra conspicue rugosa; pedunculo dense ferrugineo-hirsuto pilis 2–3 mm longis patentibus ornato; calyce 15 mm longo dense antrorse adpresso-pubescenti pilis 1 2.5 mm longis praedito, lobis quinque inaequalibus; corolla subhypocrateriformi 35–37 mm longa (tubo 27 mm longo, lobis 8 mm longis), tubo dense pubescenti pilis adpressis retrorsis 0.5 mm longis munito; antheris 7 mm longis.

Tree 4–6 m tall, stems of the branches ferruginous-brown hirsute with spreading hairs 2–3 mm long. Stipules at the stem apex prominent, oblong-obovate, rounded at apex, 5.5–7 cm long, 3–3.5 cm wide, densely ferruginous-brown hirsutulous. Leaf blades subcoriaceous, both sides rugulose, broadly obovate, abruptly acute at apex, rounded-subcordate at base, 32–35 cm long, 16–26 cm wide at or near the base, lower portion of upper surface hirsute with erect to ascending ferruginous hairs 2–3 mm long, becoming more shortly pubescent in age, lower surface densely villous-hirsute with ferruginous-brown hairs, the midrib and main lateral nerves with denser, loosely spreading to subretrorse hairs 2–3 mm long. Lateral nerves 16–20 each side, arcuate-ascending at 35–40°, inconspicuously anastomosing near the margin, elevated below, impressed above; tertiary venation conspicuously rugose on lower surface. Inflorescence capitate, globose, at anthesis 3 cm long, 3.5 cm wide, up to 4 cm long and 4.5 cm wide at postanthesis, enveloped at anthesis by 2 suborbicular rounded bracts 3 cm long, these 3.5–4 cm wide, densely ferruginous hirsute. Peduncle 9–29 cm long, 5–6 mm wide, densely ferruginous hirsute with loosely spreading hairs 2–3 mm long. Bract subtending base of hypanthium lanceolate, acute 5 mm long, 1.5 mm wide. Hypanthium turbinate-oblong, in anthesis 6 mm long, 4.5 mm wide, densely ferruginous hirsute with ascending hairs 2.5–3 mm long. Calyx and hypanthium 19–20 mm long in anthesis. Calyx tubular-cylindric, 15 mm long, 5–6 mm wide, the tube in anthesis 13 mm long, 3.5 mm wide, appressed-pubescent with hairs 1–2.5 mm long; calyx lobes 5, unequal, 4 lobes broadly suborbicular, rounded, 1.5 mm long, 2 mm wide, the 5th lobe broadly subtriangular-ovate with a 0.5–0.6 mm long caudate appendage, densely short-sericeous within. Corolla white, subsalverform, 35–37 mm long, the tube 27 mm long, 3 mm wide in the upper 15 mm, 1.5 mm wide in the lower 10–12 mm, densely pubescent without, with appressed hairs 0.5 mm long; corolla lobes 8 mm long, 2 mm wide, densely antrorsely pubescent without, glabrous within in the basal 2.5 mm, pilose with spreading hairs 0.5–0.7 mm in the adjacent 11 mm, glabrous in the uppermost 12 mm. Stamens inserted in the upper ¾ of the corolla tube; anthers linear, 7 mm long, 0.5 mm wide, slightly bilobate-rounded at base; filaments 1 mm long, glabrous, inserted 10 mm below base of corolla lobes. Style 8.5 mm long, glabrous. Disk glabrous. Fruits not seen.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Cerro Aracamuni, summit, Proa Camp, ravines near edge of tepui, 01°32′N, 65°49′W, 1,400 m, 31 Oct. 1987, *R. Liesner & G. Carnevali 22682* (MO, VEN).

Cephalodendron was known until now as a monotypic genus endemic to the summit of Cerro de la Neblina in Venezuela. The new taxon differs from *C. globosum* Steyerm. in the longer, spreading-hirsute pubescence of stems, peduncles, petioles, and lower leaf surface; longer calyx, corolla, and anthers; and cylindric calyx tube 3¼–3½ times longer than broad.

Coussarea liesneri Steyerm., sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, slope forest, Quebrada Camp, 01°24′N, 65°38′W, 600 m, 21 Oct. 1987, *R. Liesner & F. Delascio 22262* (holotype, VEN; isotype, MO).

Arbor 8-metralis; foliis oblongo-ellipticis apice abrupte acuminatis, acumine usque ad 1.5 cm producto, basi acutis 22–33 cm longis 7–14 cm latis ubique glabris, nervis lateralibus utroque latere 10–12; petiolis 1.5–2 cm longis; inflorescentia paniculata, pedunculo incluso 8–

10 cm longa basin versus 6 cm lata; pedunculo 4–4.5 cm longo puberulento; calyce 4-lobato profunde campanulato 2.5 mm longo superne 2 mm lato extus minute puberulento, lobis inaequalibus squarrosis sublanceolatis apice obtusis 0.5 mm longis puberulento-ciliatis; hypanthio minute puberulento, staminibus basi corollae insertis.

Tree 8 m tall. Leaf blades oblong-elliptic, 22–33 cm long, 7–14 cm wide, glabrous throughout, abruptly acuminate at apex (the acumen up to 1.5 cm long), acute at base; principal lateral nerves 10–12 each side, elevated below, slightly elevated or impressed above; tertiary venation reticulate and elevated below, inconspicuous above. Petiole 1.5–2 cm long, 2.5–3.5 mm wide, glabrous. Inflorescence terminal, paniculately branched, 8–10 cm long including the peduncle, 6 cm broad at the base, with 3 main divaricate tiers of lateral axes. Flowering portion of inflorescence 6 cm long with 7–10 axes, the lower 4 proximate, 1–2 cm long and branched into 3 secondary axes bearing capituliform clusters 7–10 mm broad, each containing 5–10 sessile flowers; the other tiers of axes shorter, 1–3 cm long; rachis and axes minutely puberulent. Peduncle 4–4.5 cm long, 2–2.5 mm wide, puberulent. Calyx 4-lobed, deeply campanulate, 2.5 mm long, 2 mm wide at summit, narrowed below, minutely puberulent without, sparsely puberulent at the summit margin, glabrous within; lobes unequal, squarrose, sublanceolate, obtuse at apex, 0.5 mm long, 0.2 mm wide, puberulent-ciliate; hypanthium turbinate, 1.5 mm long, 1 mm wide at summit, minutely puberulent without. Corolla cylindric, apically narrowed, 6 mm long, 1.5 mm wide (in bud); corolla lobes 3 mm long (in bud). Stamens inserted at base of corolla tube; anthers 2.5 mm long.

This species is related to *Coussarea rudgeoides* Rusby of Bolivia and Peru, from which it differs in the denticulately lobed calyx with pubescent, squarrose lobes; longer peduncle; longer calyx tube exceeding the hypanthium; and insertion of the filaments at the base of the corolla tube. In *C. rudgeoides* the filaments are attached in the lower ¼ of the corolla tube, and the calyx tube is about as long as the hypanthium.

Neblinathamnus aracamunianus Steyerm., sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp, savanna at edge of tepui, 01°26′N, 65°47′W, 1,550 m, 19 Oct. 1987, *R. Liesner & F. Delascio 22153* (holotype, MO; isotype, VEN).

Suffrutex 0.5-metralis; foliis ternatis elliptico-oblongis apice obtusis vel subacutis majoribus 3.5–4.2 cm longis 1.3–2.2 cm latis subtus praeter areolas foveolatas minute albido-pubescentes glabris; calycis lobis spathulato-linearibus apicem versus dilatatis apice subacutis 4 mm longis superne 0.5–0.7 mm latis extus albido-hispidulis, marginibus hispido-ciliatis; corollae tubo 16 mm longo extus glabro intus prope antheras minute papilloso-puberulentoaliter glabro, lobis ovato-oblongis apice late rotundatis 5 mm longis 3 mm latis.

Suffruticose plant 0.5 m tall. Stems slender, densely introrsely hirtellous. Leaves ternate, elliptic-oblong, mainly obtuse to subacute at apex, acute at base, the larger and principal leaf blades 3.5–4.2 cm long, 1.3–2.2 cm wide, glabrous above except for sparse, appressed hairs in the sulcate midnerve, paler and mainly glabrous below except for depressed, minute, white pubescent, foveolate areas within the reticulate venation; principal lateral nerves 4–6 each side, inconspicuous to obsolete above, the midnerve and lateral nerves glabrescent or with sparse, appressed trichomes 0.2–0.5 mm long; tertiary venation obsolete above, finely reticulate below and impressed, the areoles in depressed foveolate areas with circles of minute white trichomes. Petiole 2–3 mm long, moderately to densely appressed-pubescent with pale hairs. Inflorescence terminal or axillary, the flowers solitary or in pairs. Pedicels 1–2 mm long. Hypanthium turbinate, 2 mm long, 1.5 mm wide, densely gray hirtellous. Calyx lobes linear-spathulate, broadened near the subacute apex, subacute at base, 4 mm long, 0.5–0.7 mm wide in upper half, hispidulous without, with gray-white pubescence, glabrous within, the margins hispid-ciliate. Corolla tube red, greenish white on lobes, 16 mm long, slenderly salverform, the tube 12 mm long, 2 mm wide, glabrous without, minutely papillose-puberulent within for 3 mm in the zone of the anthers, elsewhere glabrous; corolla lobes 5, ovate-oblong, rounded at apex, 5 mm long, 3 mm wide. Anthers linear, 2 mm long, inserted ⅔ way up tube; filaments free for 1 mm, attached 3 mm to tube 4 mm above its base. Style 10 mm long, glabrous; stigmas 2 mm long.

The genus *Neblinathamnus* was originally described by Steyermark (1963) with two species known, *N. argyreus* from Venezuela on Cerro de la Neblina and *N. glabratus* from adjacent northern Brazil on Serra Pirapucú. This third species differs from the other two in its shorter corolla; larger leaf blades with subacute or obtuse apices; and shorter, spathulate-linear, subacute calyx lobes, which are more dilated at the apex, dorsally pubescent, and more abundantly ciliolate.

Remijia reducta Steyerm., sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept.

Río Negro, Cerro Aracamuni, summit, Proa Camp, savanna near edge of tepui, 01°32′N, 65°49′W, 1,400 m, 25 Oct. 1987, *R. Liesner & G. Carnevali 22407* (holotype, MO; isotype, VEN). Figure 16.

Frutex 0.5–1-metralis; ramulis juvenilibus dense hirsutis pilis antrorsis; foliis parvis revolutis lanceolato-ellipticis vel elliptico-oblongis apice obtusis vel subacutis, basi acutis 4–10 cm longis 2–3 cm latis, supra tenuiter rugosis subtus dense tomentoso-pilosis; petiolis 2–9 mm longis dense adpresso-hirsutis; inflorescentia valde abbreviata, floribus solitariis; pedunculo 1–2 mm longo dense ferrugineo-hirsuto; calyce 1–2 mm lobis deltoideis minutis; corolla hypocrateriformi, tubo 11 mm longo extus dense hirsuto pilis antrorse adpressis 3 mm longis praeddito, intus glabro; lobis quinque lineari-lanceolatis acutis 10–12 mm longis 2–3 mm latis; antheris 3.5 mm longis; capsulis maturis 13–18(–32) mm longis; seminibus 5–6.5 mm longis, corpusculo suborbiculari 3 mm longo, alis 1–2 mm latis.

Shrub 0.5–1 m tall. Stems antrorsely densely hirsute with appressed to ascending ferruginous hairs; terminal stipule ovate-oblong to broadly ovate, obtuse or rounded, 10–17 mm long, 5–14 mm wide, densely appressed-hirsute with elongate ferruginous-brown hairs 1.5–2 mm long. Internodes 3–6 mm long. Leaf blades coriaceous, drying dark above and ferruginous-brown below, revolute, lance-elliptic to elliptic-oblong, obtuse to subacute at apex, acute at base, 4–10 cm long, 2–3 cm wide, rugulose or bullate and glabrous above at maturity, densely hirsutulous with subappressed to ascending hairs in early stages, densely tomentose below, midrib and lateral nerves with densely appressed, crisp, longer hairs; lateral nerves 10–12 each side, slightly to deeply sulcate above, finely and minutely reticulate and elevated below. Petioles 2–9 mm long, 1–2 mm wide, densely appressed-hirsute. Internodes 3–6 mm long. Inflorescence greatly abbreviated, lateral, the flowers solitary, one on each side. Peduncle at anthesis 1–2 mm long, in fruit 5–7 mm long, densely and antrorsely ferruginous hirsute. Hypanthium at anthesis 2–3 mm long, in fruit cylindric to oblanceolate and elongating to 9 mm long, densely antrorsely ferruginous-hirsute. Calyx 1–2 mm long, subtruncate or with minute, broadly deltoid lobes, glabrous within. Disk equaling the calyx. Corolla white, salverform, tube 11 mm long, 3 mm wide above, 2.5–3 mm wide below the middle, densely buff-brown hirsute with antrorsely appressed hairs 33 mm long, glabrous within; lobes 5, recurved, linear-lanceolate, acutish, 10–12 mm long, 2–3 mm wide, densely antrorse-hirsute without, glabrous within. Stamens attached to tube slightly below the middle; anthers linear, 3.5 mm long, 0.7 mm wide; filaments 4 mm long, attached 6.5 mm above base of tube, glabrous. Style 3 mm long, glabrous; stigmas linear, 2 mm long. Capsule at maturity obovate or broadly oblong, 13–18(–32) mm long; valves conspicuously osseous, bifid at apex, densely brown hirsute without, glabrescent, 8–13 mm wide; seeds few, wings pale buff-brown, body pale brown, finely cellular on surface, oval or subovate, rounded or subtruncate at one or both ends, often more narrowed at the other end, 5–6.5 mm long, 2.7–3 mm wide; wings 1–2 mm wide.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp, low savanna, 01°26′N, 65°47′W, 1,550 m, 17 Oct. 1987, *R. Liesner & F. Delascio 22045* (MO, VEN).

This species differs from other species of *Remijia* by having solitary flowers. It is further distinguished by its small leaf blades, short petioles, densely ferruginous tomentose lower leaf surface with strongly reticulate tertiary venation, finely rugulose upper leaf surface, and relatively small seeds.

THEACEAE—contributed by Julian Steyermark (*Bonnetia*) and Brian Boom (*Ternstroemia*)

Bonnetia liesneri Steyerm., sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp, savanna with small to large patches of forest and stream, 01°26′N, 65°47′W, 1,550 m, 18 Oct. 1987, *R. Liesner & F. Delascio 22105* (holotype, MO; isotype, VEN). Figure 17.

Suffrutex 0.5-metralis; foliis anguste oblanceolatis vel anguste ellipticis apice ut videtur subacutis vel obtusiusculis autem sub microscopio emarginulato-rotundatis 18–30 mm longis 4–8 mm latis; sepalis anguste-elliptico-lanceolatis aristato-oblongis apice rotundatis 11–12 mm longis 3–4 mm latis; style simplice vix 3-lobulato 8 mm longo.

Subshrub 0.5 m tall with spreading branches. Leaves clustered at the tips of the branches, narrowly oblanceolate to narrowly elliptic, seemingly subacute or obtusish at apex, but under 20× magnification rounded with an emarginulate summit, attenuate to the base, 18–30 mm long, 4–8 mm wide, glabrous throughout, leaf margin microscopically repand, cartilaginous, shortly 1–2 mm petiolate; midrib slightly elevated below, obsolete above; lateral nerves and tertiary venation obsolete. Flowers solitary near the summits of the branches. Peduncle ancipital, ebracteolate, mainly 13–15 mm long (sometimes much longer), glabrous. Sepals

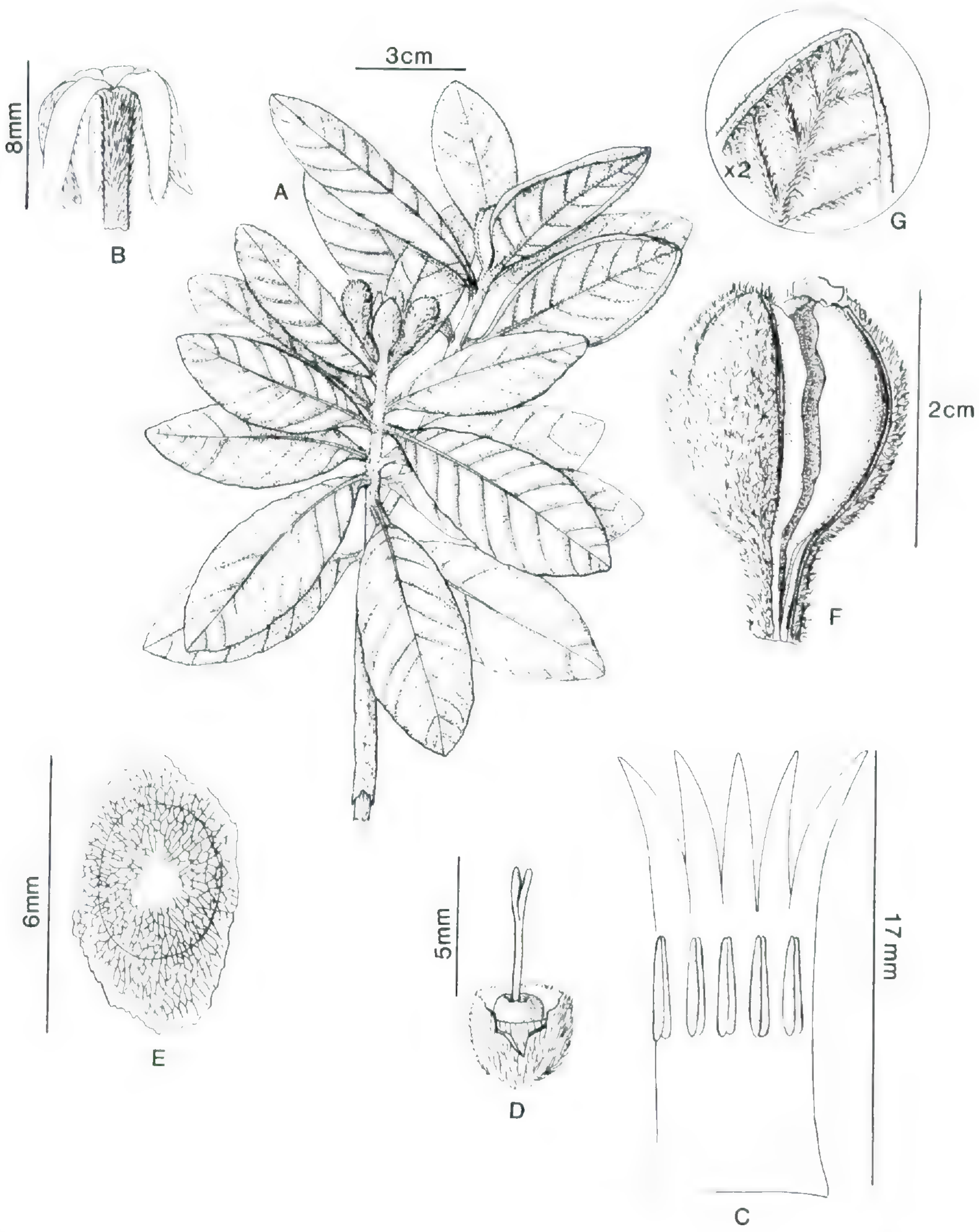

FIGURE 16. *Remijia reducta*.—A. Habit of branch.—B. Corolla.—C. Corolla opened.—D. Pistil with calyx cut away.—E. Seed.—F. Fruit.—G. Detail of lower leaf surface. (From *Liesner & Carnevali 22407*.)

narrowly elliptic-lanceolate to ovate, aristate-acuminate at apex, acute at base, 11–12 mm long, 3–4 mm wide at the middle, entire. Stamens numerous; anthers suborbicular, slightly longer than broad, 0.7 mm long, 0.5 mm broad. Style 8 mm long, undivided, merely shallowly 3-lobulate at the apex. Ovary (post-anthesis) ovoid, 5 mm long, 3 mm wide. Fruit ovoid, 3-celled, tapering to the persistent style, 10 mm long.

This species is most similar to *Bonnetia huberiana* Steyerm. of the Chimantá Massif, Estado Bolívar, but differs by having undivided, shallowly three-lobulate style; larger petals; larger, aristate-acuminate, entire sepals; and microscopically rounded emarginulate leaf apex.

Ternstroemia guanchezii Boom, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Atures, transecto desde matorral ribereño hasta bosque bajo ralo, en la margen izquierda del caño "Cabeza de Manteco," afluente del Río Autana, en el "Raudal Manteco," 04°52′N, 67°27′W, 100–120 m, 10 Nov. 1984, *F. Guánchez & E. Melgueiro 3447* (holotype, NY; isotype, TFAV). Figure 18.

Frutex 2–3 m altus, ramulis oppositis vel suboppositis teretiusculis ravidis; foliis oblanceolatis vel angustis ellip-

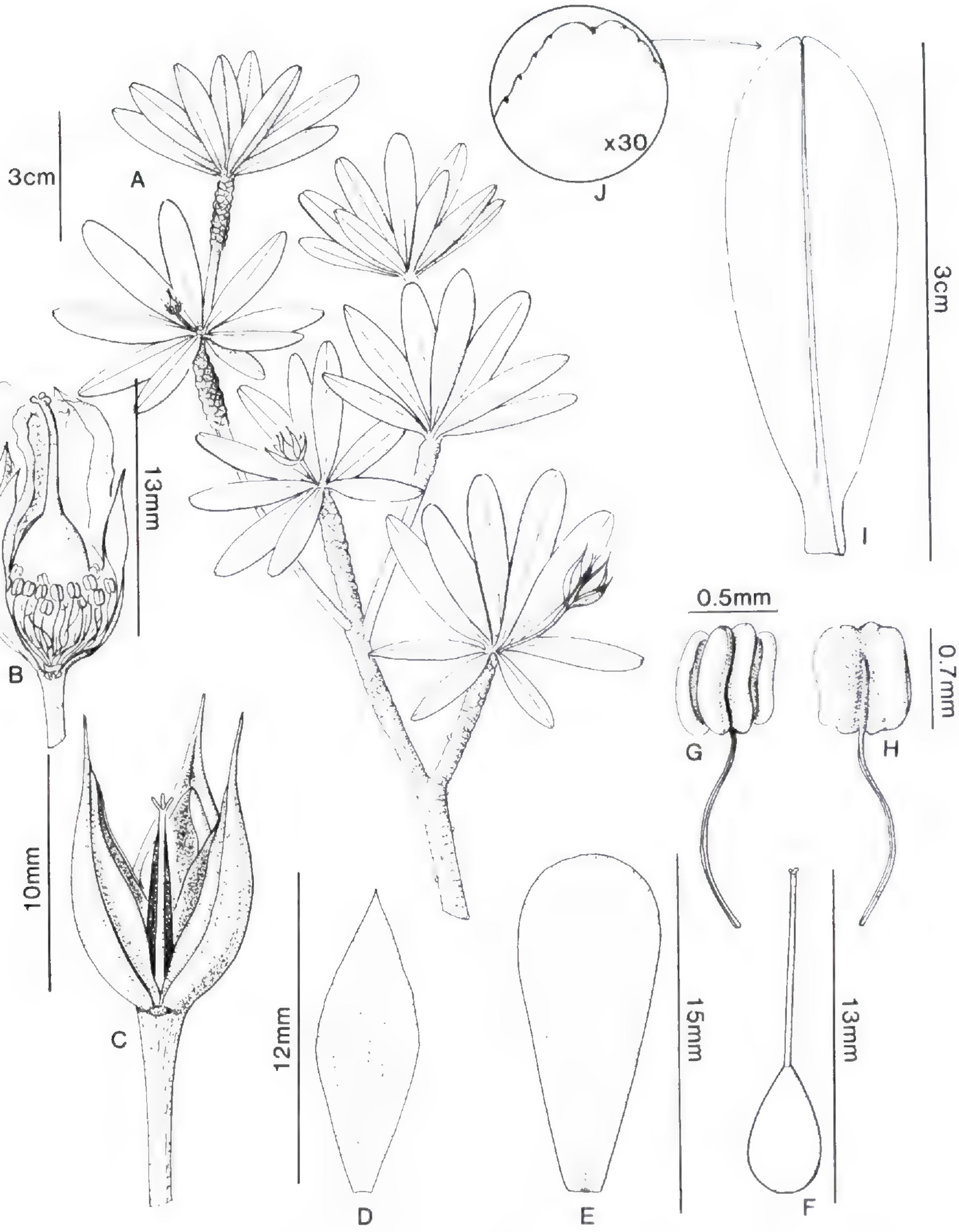

FIGURE 17. *Bonnetia liesneri*.—A. Habit of branch.—B. Flower.—C. Fruit.—D. Sepal.—E. Petal.—F. Pistil.—G, H. Stamen.—I. Lower leaf surface.—J. Leaf apex. (From *Liesner & Delascio 22105*.)

ticis 5–7(–8.5) × 1–1.5(–3) cm aliquantum asymmetricis apice acutis vel acuminatis basi acuminatis vel attenuatis, petiolis 0.2–0.5(–1) mm longis, costa superne canaliculata infra prominula, venis obscuris utrinque; floribus fasciculatis, pedunculo ad 10 mm longo erectiusculo vel pendulo, bracteolis 2 subopppositis cymbiformibus 2.5–3 × 1.5–2 mm apice acutis atroglandulosis, margine apicem versus atroglanduloso-serrulatis, calycis lobis 5 liberis cymbiformibus 3.5–4 × 3–3.5 mm, duobus exterioribus margine atroglanduloso-serrulatis, et tribus intimis eglandosis-integris, corollae lobis 5 liberis ovatis vel lanceolatis 3.5–4 × 1–1.5 mm apice obtusis marginibus integris, staminibus ca. 24 liberis uniserialibus basifixis, filamentis 0.3–1 mm longis, antheris 0.6–1 mm longis thecis parallelis introrsus dehiscentibus, stigmate et stylo teretibus 2.5 mm longis, ovario 1 × 1(–1.2) mm 2-loculari, utroque loculo 2-ovulatis; fructibus incognitis.

Shrub 2–3 m tall; branchlets opposite to subopposite, terete, grayish. Leaves clustered within the apical 3(–5) cm of branchlets, coriaceous, glabrous, oblanceolate to narrowly elliptic 5–7(–8.5) × 1–1.5(–3) cm, slightly asymmetrical, apex acute to acuminate (to rounded), base acuminate to attenuate, petiole 0.2–0.5(–1) mm long, midrib canaliculate above, evident the entire length, prominent below, the veins obscure on both surfaces. Flowers fasciculate, axillary among leaf bases, up to 7 per cluster, peduncles to 10 mm long, suberect to pendulous; bracteoles 2, cymbiform, subopposite, unequal in size, 2.5–3 × 1.5–2 mm, apex acute, black gland-tipped (the gland itself tipped by sev-

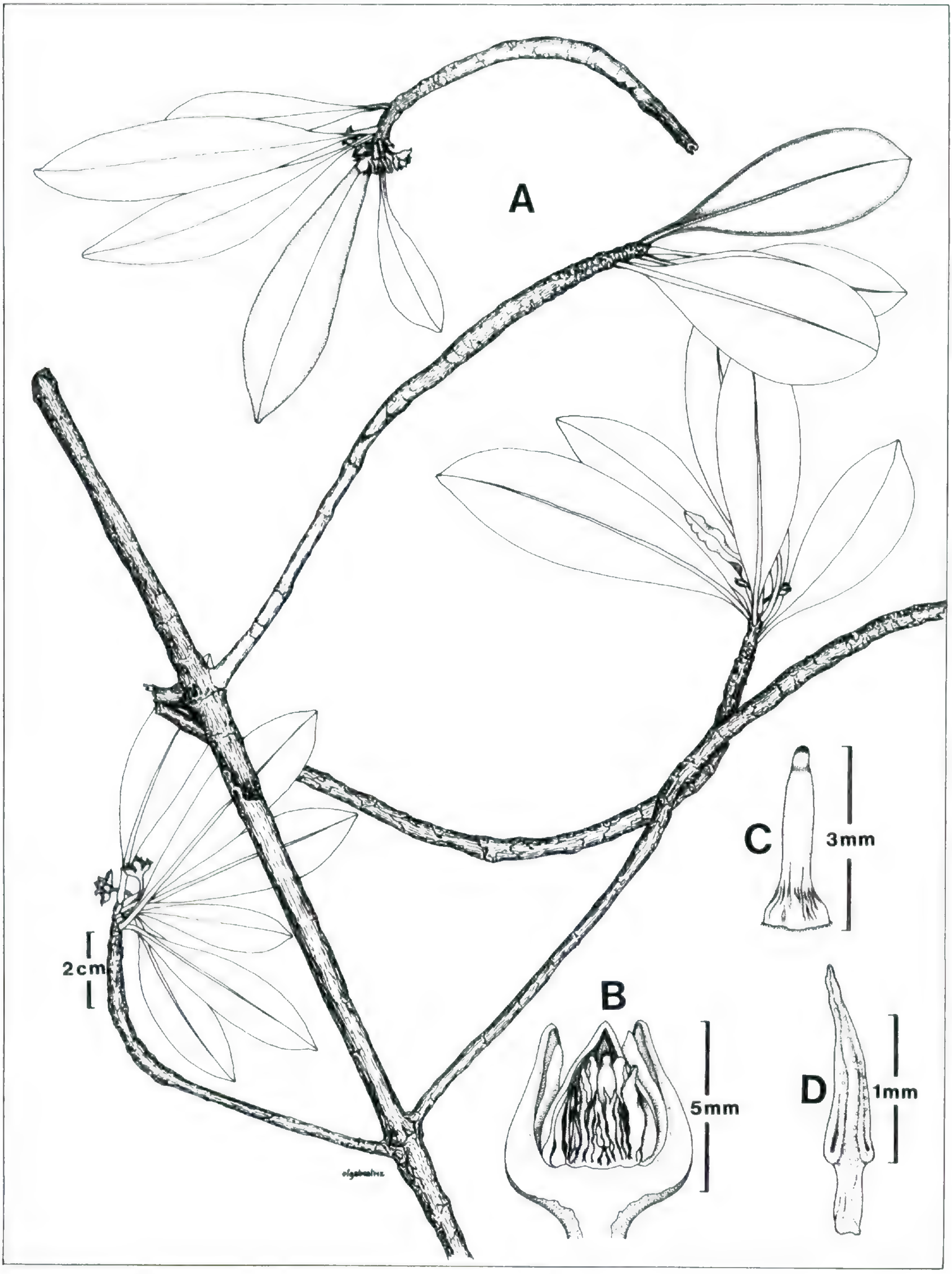

FIGURE 18. *Ternstroemia guanchezii.*—A. Habit.—B. Flower, longitudinal view with two calyx lobes and one petal removed, showing stamens and summit of gynoecium.—C. Gynoecium.—D. Stamen. (From *Liesner & Delascio 22236.*)

eral eglandular cilia), the margin black glandular-serrulate; calyx lobes 5, free, cymbiform, 3.5–4 × 3–3.5 mm, the margin scattered black glandular-serrulate on outer lobes, entire on inner 3 lobes; corolla of 5 free petals, these ovate to lanceolate, 3.5–4 × 1–1.5 mm, apex obtuse, margin entire; androecium of ca. 24 uniseriate stamens, free from corolla; filaments of varying lengths, 0.3–1 mm long; anthers 0.6–1 mm long, basifixed, thecae parallel, dehiscence introrse; gynoecium with terete stigma and style, 2.5 mm long, ovary 1 × 1(–1.2) mm, 2-locular with 2 pendulous ovules per locule, the ovules 0.5–0.6 × 0.1–0.2 mm. Fruits unknown.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Cerro Aracamuni, slope, Quebrada Camp, in area of rapids flowing over laja, 01°24′N, 65°38′W, 600 m, 20 Oct. 1987, *R. Liesner & F. Delascio 22236* (MO, NY, VEN).

This distinctive species, with graceful, subopposite to opposite branchlets and small, fasciculate flowers, is known from lower to middle elevations of the western Venezuelan Guayana in forests along streams running through igneous rocks known locally as "lajas." The new species is named in honor of Francisco Guánchez, former director of the Herbario TFAV in Puerto Ayacucho, who first collected this species in 1984.

Ternstroemia maguirei Boom, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Cerro de la Neblina, south slope of Cumbre Camp, caño toward Cañon Grande, occasional on exposed rock outcrop, 1,500 m, 16 Jan. 1954, *B. Maguire, J. Wurdack & G. Bunting 37347* (holotype, NY; isotype, VEN). Figure 19.

Frutex vel arbor 1–6 m altus, 6 cm diametro, ramulis fasciculatis angularibus ravido-fuscis; foliis ellipticis ad ovatis vel obovatis (7.5–)10–14 × (3.8–)4.5–6.7 mm aliquantum asymmetricis apice acutis vel rotundis basi acutis vel rotundatis, petiolo (5–)8–13(–15) mm longo, costa superne canaliculata infra prominula, venis 10–15(–19)-jugis utrinque vix manifestis, lamina inferne fusco-punctata; floribus geminatis subterminalibus, pedunculo 11–38(–50) mm longo; bracteolis duabus subopppositis cymbiformibus 5.5–6 × 3.5–4 mm apice acutis, margine atroglanduloso-serrulatis, calycis lobis 5 liberis perlate ovatis (5–)7–8.5 × (6.5–)8–9 mm, duabus exterioribus margine atroglanduloso-serrulatis, tribus intimis fere eglanduloso-integris; corollae lobis 5 basi per ca. 3 mm connatis, lobis liberis lanceolatis ca. 5 × 3.5 mm apice acuminatis margine integris; staminibus ca. 37 uniserialis basifixis basi connatis, filamentis 0.8–1 mm longis, antheris 2 mm longis, thecis parallelis 1–1.5 mm longis introrsus dehiscentibus, connectivo ultra thecas producto, stigmatibus et stylis teretibus 8 mm longis; ovario biloculari, ovulis 0.4–0.2 mm; fructibus laevibus perlate ovoideis 2–3-locularibus 15 × 16 mm, stylo persistenti ca. 5 mm longo, parietibus 2.5–3 mm crassis; seminalibus 16, 8–9 × 4.5 mm.

Shrub or small tree 1–6 m tall, 6 cm diam., branchlets fasciculate, angular in cross-section, grayish brown. Leaves distributed along branchlets, coriaceous, elliptic to ovate or obovate, (7.5–)10–14 × (3.8–)4.5–6.7 mm, slightly asymmetrical, apex acute to rounded, base acute to rounded, petiole (5–)8–13(–15) mm long, midrib canaliculate above, evident the entire length, prominent below, the veins 10–15(–19) pairs, scarcely visible above and below, blade below with scattered dark glandular punctations. Flowers subterminal, paired, peduncles 11–38(–50) mm long; bracteoles 2, cymbiform, subopposite, unequal in size, 5.5–6 × 3.5–4 mm, apex acute, black gland-tipped, the margin black glandular-serrulate; calyx lobes 5, free, widely depressed ovate, (5–)7–8.5 × (6.5–)8–9 mm, the margin scattered black glandular-serrulate on outer 2 lobes, entire to slightly glandular on inner 3 lobes; corolla of 5 petals, these fused basally for ca. 3 mm with lanceolate lobes ca. 5 × 3.5 mm, apex acuminate, margin entire; androecium of ca. 37 uniseriate stamens, these free from corolla, connate basally; filaments of varying lengths, 0.8–1 mm long; anthers 2 mm long, basifixed, thecae parallel with apiculate connective, this 1–1.5 mm long, dehiscence introrse; gynoecium with terete stigma and style, 8 mm long, ovary 2.5–3.5 mm, 2-locular with 8 pendulous ovules per locule, the ovules 0.4 × 0.2 mm. Fruits smooth, widely depressed-ovoid, 15 × 16 mm, persistent style 5 mm long, fruit wall 2.5–3 mm thick, 2–3-locular, 16-seeded, the seeds 8–9 × 4.5 mm.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Cerro de la Neblina, Cañon Grande, SSW of Cumbre Camp, 1,200–2,200 m, 25 Dec. 1957, *B. Maguire et al. 42510* (NY, VEN); Cerro de la Neblina, Camp XI, 6 km NNE of Pico Phelps, 00°51′40″N, 65°58′50″W, 1,450 m, 27 Feb. 1985, *M. Nee 31158* (NY, VEN); Dept. Río Negro, Cerro Aracamuni, Popa Camp, 01°26′N, 65°47′W, summit, 1,550 m, 16 Oct. 1987, *R. Liesner & F. Delascio 21985*, same locality, 18 Oct. 1987, *Liesner & Delascio 22117*, 19 Oct. 1987, *R. Liesner & F. Delascio 22158* (MO, NY, VEN); Cerro Aracamuni, Proa Camp, 01°32′N, 65°49′W, summit, 1,400 m, 26 Oct. 1987, *R. Liesner & G. Carnevali 22506* (MO, VEN); Cerro Duida, N escarpment along escarpment above Culebra, 1,400 m, 20 Nov. 1950, *B. Maguire et al. 29570* (NY); Cerro Duida, Caño Negro Basin, N slopes and ridges, 2,000 3,000 m, 23 Nov. 1950, *B. Maguire et al. 29660* (NY); al SE de la comunidad de Culebra, 03°40′N, 65°45′W, 800–900 m, 6 Feb. 1982, *J. Steyermark et al. 126125* (MO, NY, VEN).

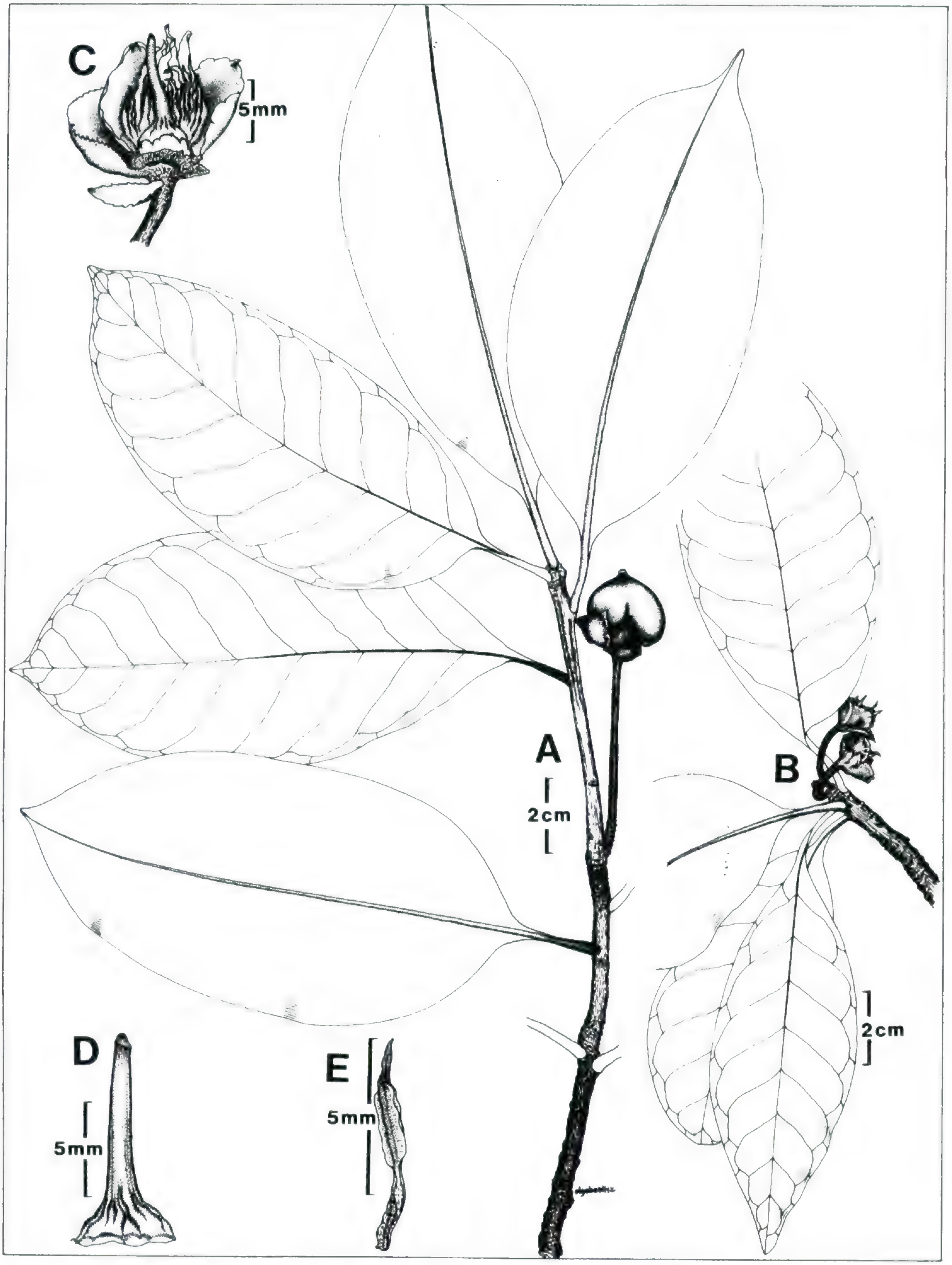

FIGURE 19. *Ternstroemia maguirei.* —A. Habit, showing mature fruit.—B. Habit, showing flowers.—C. Flower, longitudinal view with two calyx lobes and several petals removed, showing stamens and gynoecium.—D. Gynoecium.—E. Stamen. (A, from *Maguire et al. 37347*; B–E, from *Maguire et al. 42510.*)

This new species is notable for its inflorescence of strictly one pair of flowers and its relatively large, smooth capsular fruits that are apparently nondehiscent. It is restricted to elevations above 800 m on sandstone in southern Venezuelan Guayana (Cerros Neblina, Aracamuni, and Duida). It is named in honor of Bassett Maguire, Senior Scientist Emeritus of the New York Botanical Garden and inveterate botanical explorer of the Guayana Highland. Maguire and colleagues first collected this species in 1954, and he first directed my attention to *Ternstroemia* as a genus in need of taxonomic study.

XYRIDACEAE—contributed by Robert Kral (VDB)

Abolboda scabrida Kral, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, summit, Proa Camp, medium height, semi-open forest, 01°32′N, 65°49′W, 1,400 m, 28 Oct. 1987, *R. Liesner & G. Carnevali 22598* (holotype, VEN; isotypes, MO, VDB). Figure 20.

Herba perennis densicaespitosa, praeter inflorescentiam et bases scabrida et scabridorugosa. Radices spongiosae. Caules breves, ascendentes, usque ad 2–3 cm longi, basibus persistentibus veternorumfoliorum obtecti. Folia extima rosularum praesertim vaginalia, anguste triangulata; folia principalia erecta vel expansa, leviter excurvata, 3 6 cm longa, ad basin dilatata, ca. 5-costata, sursum abrupte contracta, 2–3-costata; laminae 0.5–1 mm latae, pallide virides, leviter compressae, transversim irregulariter rugosae et tuberculatae; apices gradatim vel abrupte contracti, incrassati, ad apicem obtusati vel excurvato-mucronati; margo leviter vel valde incrassata, scabra; paginae superiores planae aut leviter convexae, inferiores concavae vel planae aut prominenter 2 3-costatae. Scapi unici, scabrosi, 6 10 cm alti, 0.5–0.7 mm lati, a basin leviter compressi vel tricostati et sulcati, ad apicem teretes. Vaginae scaporum erectae, lineari-lanceolatae, subulatae, convexae, leviter striatae, inaequales, 2-jugatae, pari infimo basali, pari supero ca. ⅔ distanti a basi scaporum, vaginis exterioribus 1–1.5 cm longis, longitudine ¾ ⅘ interiores aequantibus. Spica anguste turbinata, 1.1 -1.4 cm longa, pauciflora (flores vulgo 4); bracteae 2-jugatae, subdecussatae, lanceolatae, incrassato-subulatae, 1 -1.4 cm longae, convexae, a medio ad apicem carinatae, scabridulae, ad apicem obusae, medio virides, marginibus late scarioso-marginatae. Sepala 2, lateralia, subopposita, lanceolata, inaequilateralia, ca. 1 cm longa, curvata, anguste acuta, a medio ad apicem acute carinata scabridula. Corolla azurea, ca. 1 cm longa. Staminodia bibrachiata, brachiis planis, anguste oblongis, ca. 1 mm longis. Antherae oblongae ca. 1 mm longae; filamenta ca. 1.5 mm longa. Appendices stylorum 3, recurvatae, clavatae, 1 reducta. Capsula obovoidea, ca. 2.5 mm longa, obscure trilobata, valvis ad apicem inflexis et erosis. Semina late asymmetrice obovoidea, ca. 0.5 mm longa, longitudinaliter valde 12–14-costata, anthracina.

Perennial, densely cespitose herbs, all but the bases and inflorescence scabrid and scabrid-rugose. Roots spongy. Stems short, ascending, up to 2–3 cm long, the bases covered by old leaves. Outer leaves of a rosette for the most part sheath, narrowly triangular; principal foliage leaves erect to spreading, slightly excurved, 3–6 cm long, dilated at base, ca. 5-costate, then abruptly contracted above, 2–3 costate; blades 0.5–1 mm wide, pale green, somewhat compressed, transversely irregularly rugose and tuberculate; apices gradually to abruptly narrowed, thickened, at tip obtuse or excurved-mucronate; margin slightly thickened to very thickened, scabrid; upper surface flat to somewhat convex, the lower surface concave to flat or prominently 2–3-costate. Scape solitary, scabrous, 6–10 cm high, 0.5–0.7 mm wide, at base somewhat compressed to tricostate and sulcate, terete toward apex. Scape sheaths erect, linear-lanceolate, subulate, convex, slightly striate, unequal, in 2 pairs, the lower pair basal, the upper pair ca. ⅔ way up from scape base, the outer sheaths 1–1.5 cm long, ¾–⅘ as long as the inner sheaths. Spike narrowly turbinate, 1.1–1.4 cm long, few-flowered (flowers usually 4); bracts 2 pairs, subdecussate, lanceolate, thickened-subulate, 1–1.4 cm long, convex, carinate from middle to tip, scabridulous, obtuse at tip, medially green with margins broadly scarious-bordered. Sepals 2, lateral, subopposite, lanceolate, inequilateral, ca. 1 cm long, curvate, narrowly acute, sharply and scabridulously carinate from middle to tip. Corolla blue, ca. 1 cm long. Staminodia bibrachiate, the branches flat, narrowly oblong, ca. 1 mm long. Anthers oblong, ca. 1 mm long; filaments ca. 1.5 mm long. Stylar appendages 3, recurved, claviform, 1 appendage reduced. Capsule obovoid, ca. 2.5 mm long, obscurely trilobed, the valves inflexed and erose at apex. Seeds broadly asymmetrically obovoid, ca. 0.5 mm long, longitudinally strongly 12–14-ribbed, coal black.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp, on edge of tepui in slope savanna, 01°26′N, 65°47′W, 1,550 m, 17 Oct. 1987, *R. Liesner & F. Delascio 22071* (MO, VDB, VEN).

This species is related to *A. acicularis* Idrobo & Smith, particularly var. *granularis* Maguire, but the foliage and scapes are rugose and scabrid (vs. smooth or granular), the sepal keels are scabridulous (vs. smooth or granular), the petals are blue (vs. white), and the seeds are smaller.

Xyris aracamunae Kral, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río

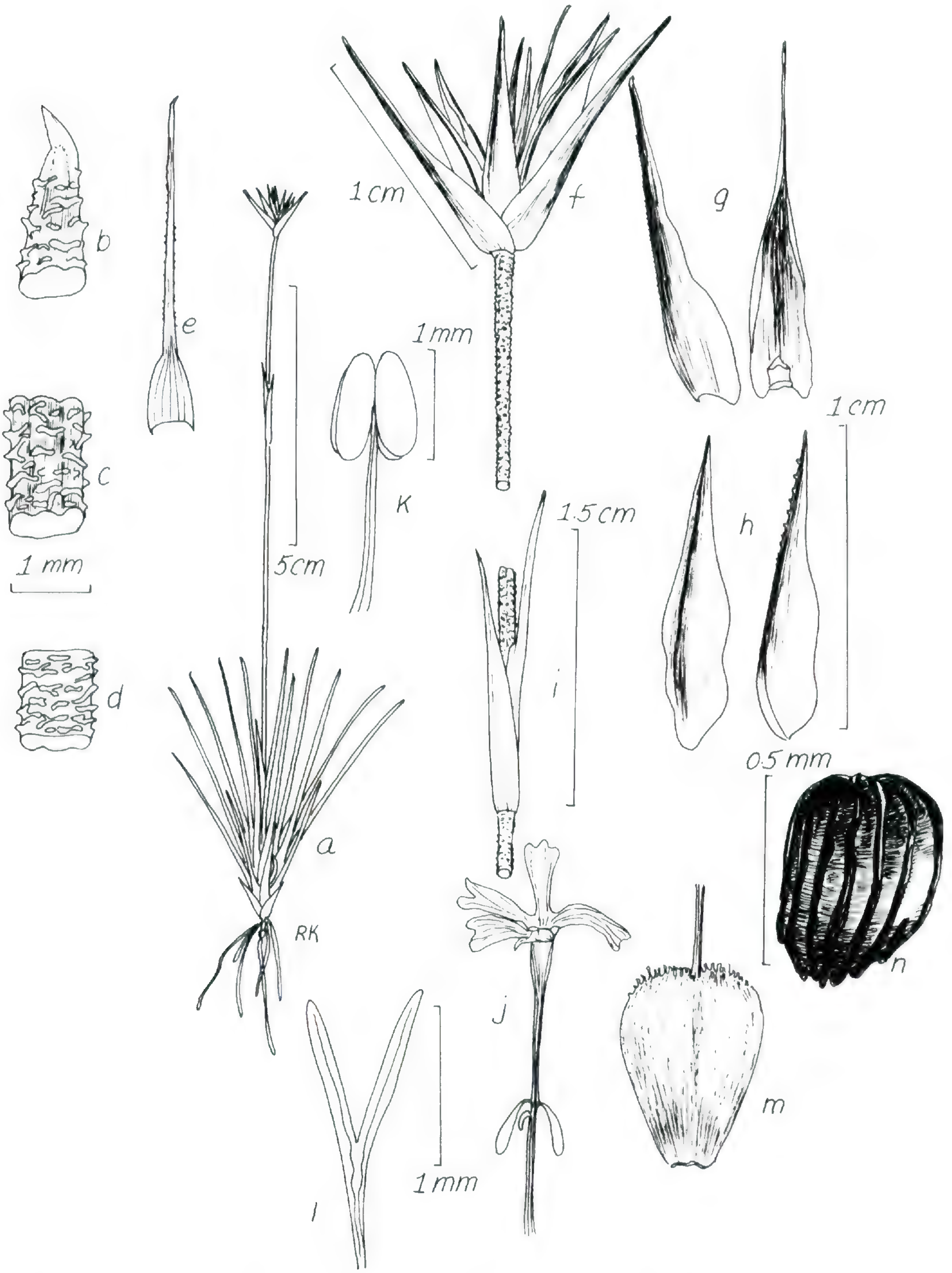

FIGURE 20. *Abolboda scabrida*.—a. Habit.—b. Leaf tip.—c. Sector of leafblade, upper side.—d. Sector of leaf blade, lower side.—e. Leaf.—f. Spike and upper scape.—g. Involucral bract, side view (left), upper side (right).—h. Lateral sepal, outer side (left), side view (right).—i. Scape sheath pair, side view.—j. Style, showing appendages and stigma head. k. Stamen.—l. Staminode.—m. Capsule and style base.—n. Seed. (From *Liesner & Carnevali 22598*.)

Negro, Cerro Aracamuni, summit, Proa Camp, savanna with small to large patches of forest, in savanna, 01°32′N, 65°49′W, 1,400 m, 25 Oct. 1987, *R. Liesner & G. Carnevali 22452* (holotype, VEN; isotypes, MO, VDB). Figure 21.

Herba perennis, densicaespitosa. Radices graciles. Caules breves. Folia rigida, erecta vel leviter expansa, anguste linearia, 30 55 cm longa, valde flexuosa et torta; laminae leviter compressae, in sectione transverssali ellipticae, vaginis 1 2-plo longiores, 2 2.5 mm latae, distincte paucicostatae; apices gradatim contracti, anguste incurvo-acuti, incrassati, ventraliter sulcati; margines leviter incrassatae, dense albotomentosae, a basi ad apicem ventraliter sulcatae; vaginae elongatissimae, convexae, obscure brunneolae, papilloso-rugulosae, valde apertae, a basi ad apicem gradatim contracti, eligulatae, marginibus longe ciliatis, pilis villosis, pallidis. Vaginae scaporum laminis ut in laminis foliorum. Scapi lineares, aliquantum compressi, torti, 4 7 dm alti, dense albotomentosi, in sectione transversali elliptici, ad apicem subteretes, prominenter pluricostati. Spicae late obovoideae vel turbinatae, obtusae, pluriflorae, bracteis convexis, firmis, ferrugineo-fuscis, spiraliter imbricatis, integris; bracteae steriles plures, triangulatae vel ovatae, 3–6 mm longae, subacutae, fertilibus breviores et in eas gradatim transientes, infimis ad apicem acutum retrorse albohirsutae; bracteae fertiles oblongo-ovatae, 7–9 mm longae, humiliter costatae. Sepala lateralia libera, subequilateralia, lanceolata, ca. 6 mm longa, curvata, acuta; ala carinalis fimbriociliata, lata, firma. Laminae petalorum obovatae, ca. 5 mm longae, luteolae, fere integrae. Staminodia bibrachiata, brachiis longe penicillatis. Antherae oblongae-lanceolatae, 2.5 mm longae, valde emarginatae et sagittatae; filamenta ca. 1 mm longa. Capsula ellipsoidea, acuminata, ca. 4 mm longa; placentatio axillaris. Semina numerosa, cylindrico-ellipsoidea, ca. 1 mm longa, translucida, pallide succinea, longitudinaliter spiraliter multicostata, ad apicem pallide et obtuse apiculata.

Densely cespitose perennial herb. Roots slender. Stems short. Leaves stiff, erect to slightly spreading, narrowly linear, 30–55 cm long, strongly flexuous and twisted; blades slightly compressed, in cross section elliptic, 1–2 times longer than the sheaths, 2–2.5 mm wide, distinctly few-nerved; apices gradually narrowed, narrowly incurved-acute, thickened, ventrally sulcate; margins somewhat thickened, densely white-tomentose, the inner edge sulcate from base to tip; sheaths much elongated, convex, dull brown, papillose-rugulose, very open, gradually narrowing from base to tip, eligulate, the edges long-ciliate with pale, villous hairs. Scape sheaths with blades as in foliage leaves. Scapes linear, somewhat compressed, twisted, 4–7 dm high, densely white tomentose, in cross section elliptic, apically subterete, prominently several-costate. Spikes broadly obovoid to turbinate, obtuse, several-flowered, the bracts convex, firm, red-brown, spirally imbricate, entire; sterile bracts several, triangular to ovate, 3–6 mm long, subacute, shorter than the fertile bracts and grading gradually into them, the lowest bracts retrorsely white-hirsute at the acute apex; fertile bracts oblong-ovate, 7–9 mm long, narrowly rounded apically; dorsal area distinct, triangular, 4–5 mm long, low-costate. Lateral sepals free, subequilateral, lanceolate, ca. 6 mm long, curved, acute; keel fimbriociliate, broad, firm. Petal blades obovate, ca. 5 mm long, yellow, nearly entire. Staminodia 2-branched, the branches long-penicillate. Anthers oblong-lanceoloid, 2.5 mm long, strongly emarginate and sagittate; filaments ca. 1 mm long. Capsule ellipsoid, acuminate, ca. 4 mm long; placentation axile. Seeds numerous, cylindric-ellipsoid, ca. 1 mm long, translucid, pale amber, longitudinally spirally multiribbed, at apex with a pale and obtuse apiculus.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Cerro Aracamuni, summit, Popa Camp, in low savanna, 01°26′N, 65°47′W, 1,550 m, 18 Oct. 1987, *R. Liesner & F. Delascio 22100* (MO, VDB, VEN).

Xyris liesneri Kral, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, Cerro Aracamuni, summit, Proa Camp, savanna with small to large patches of forest especially along streams, in ravines and near edge of tepui, 01°32′N, 65°49′W, 1,400 m, 25 Oct. 1987, *R. Liesner & G. Carnevali 22086* (holotype, VEN; isotypes, MO, VDB). Figure 22.

Herba perennis dense caespitosa, caulibus multis, ramificantibus, ramificationibus usque ad 3 cm longis, praeter margines scaporum et apices foliorum glabra. Radices graciles. Folia principalia anguste lineari-gladiata, 10 20 cm longa, flabellate expansa, vaginis scaporum longiora; laminae planae, 1 2 mm latae, compressae, flavo-virentes vel ferrugineae, inconspicue multinervosae, praeter apices integrae; apices gradatim contracti, anguste curvato-acuti, longe ciliati, pilis ferrugineis; margines aciebus incrassatis, atroferrugineis, nitidis; vaginae carinatae, carinibus atroferrugineis, ciliolatis, lateribus multicostatis, ferrugineis, basin versus fuscatis vel atro-ferrugineis, marginibus in laminas gradatim convergentibus, infimis gradatim expansis, aciebus integris. Vaginae scaporum multicostatae, a medio ad apicem valde rufo-carinatae, laminis brevibus, rufo-ciliatis. Scapi graciles, flexuosi, 20 30 cm longi, leviter torti, leviter compressi, ad apicem in sectione transversali anguste elliptici, ancipites, bicostati, costis piloso-ciliatis, pilis brunneolis. Spicae ellipsoideae, 7 8 mm longae, obtusae, pauciflorae; bracteis integris, fere uniformibus, ferrugineis, spiraliter imbricatis, convexis; bracteae steriles 4, decussatae, ovatae, carinatae, ca. 3.5 mm longae; bracteae fertiles paucae, obovatae, ca. 4 mm longae;

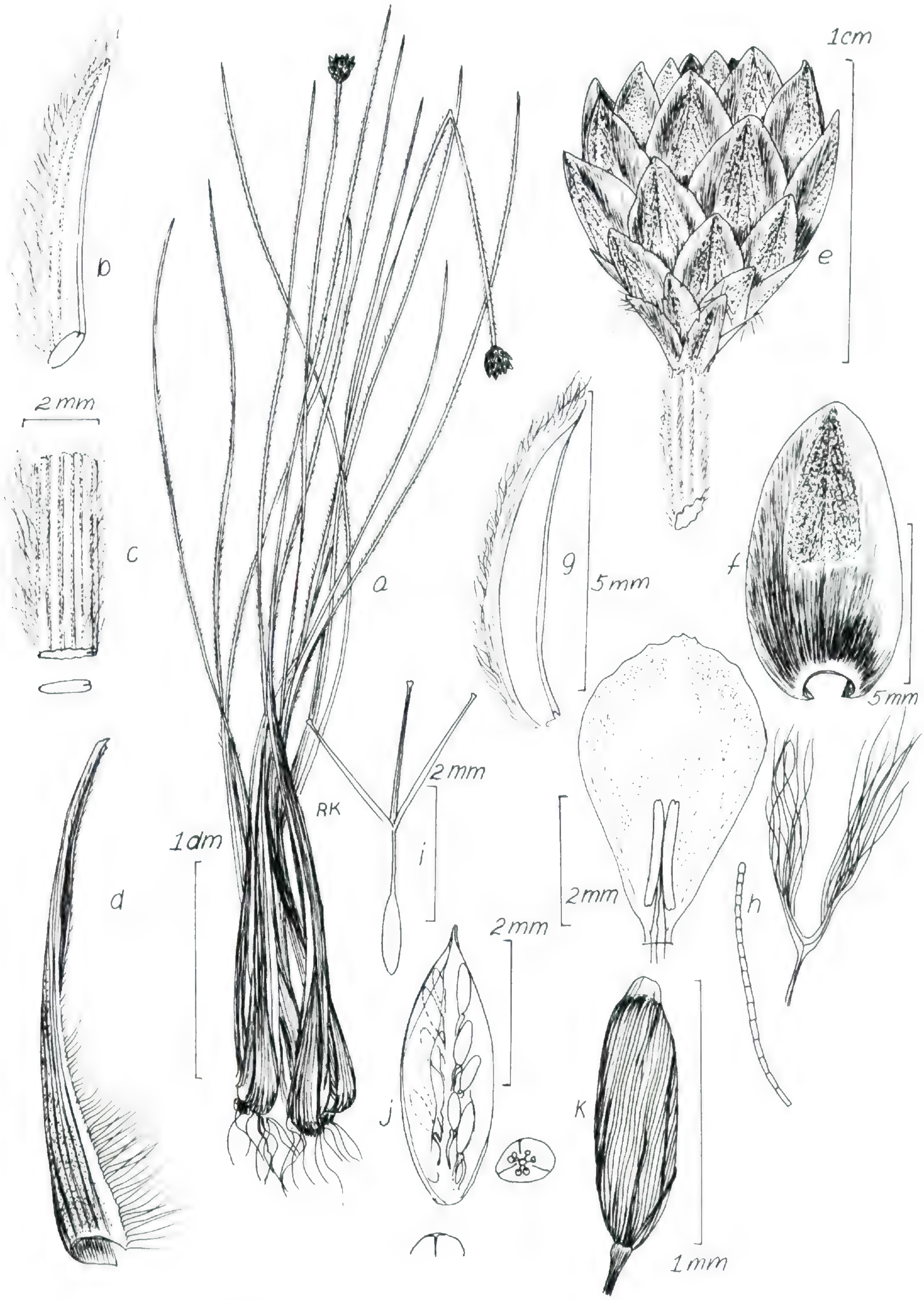

FIGURE 21. *Xyris aracamunae*.—a. Habit.—b. Leaf tip.—c. Sector of leafblade, midblade.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade, stamen, staminode, and enlarged beard hair.—i. Ovary and stylar apparatus.—j. Median sector of capsule, offsets showing placentation, septation.—k. Seed. (From *Liesner & Carnevali 22452.*)

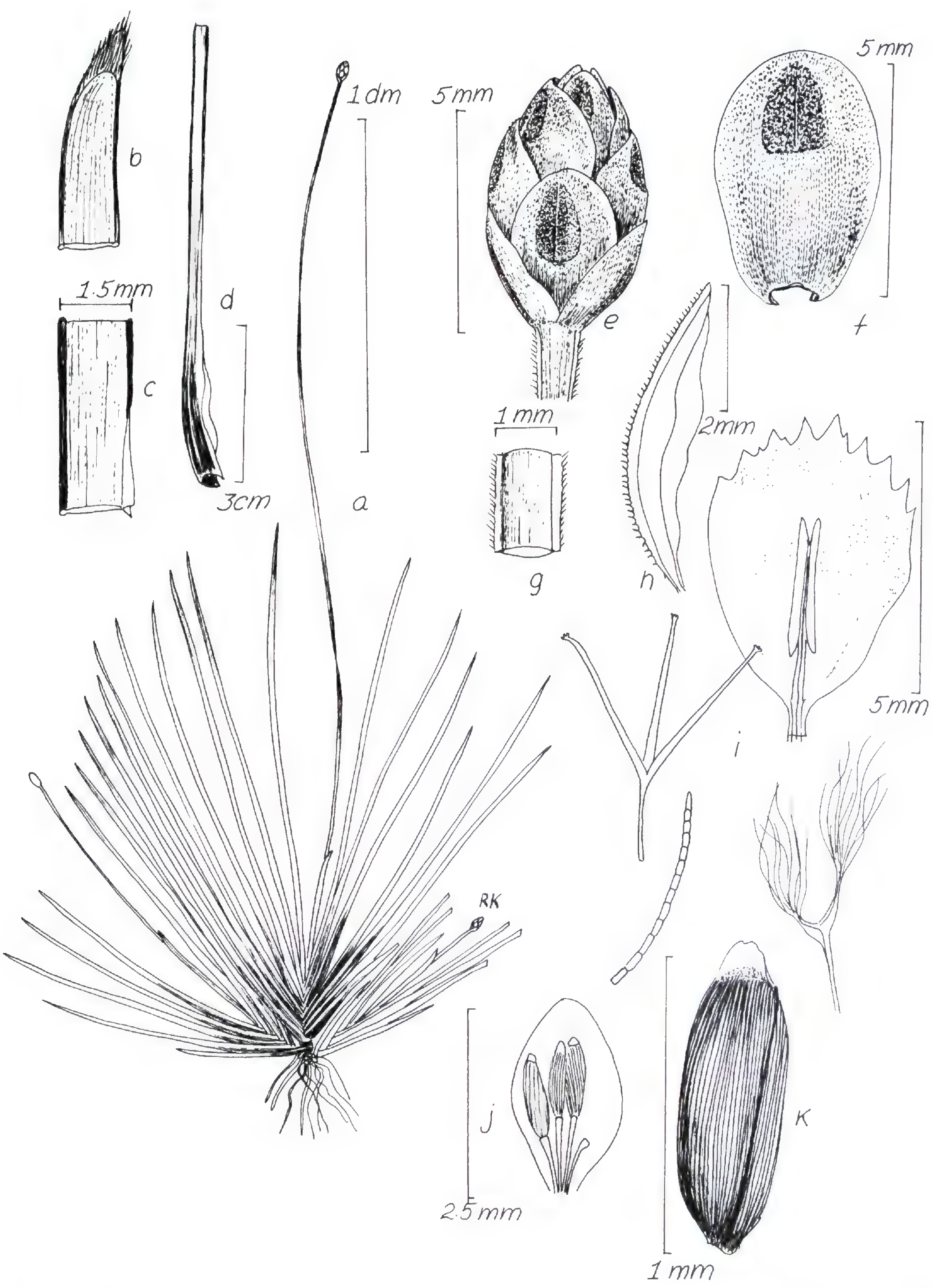

FIGURE 22. *Xyris liesneri*.—a. Habit. b. Leaf tip.—c. Sector of leaf at blade–sheath junction.—d. Leaf base.—e. Spike.—f. Fertile bract.—g. Sector of upper scape. h. Lateral sepal.—i. Petal blade and stamen (top); stylar apex (left); staminode and beard hair (below).—j. Capsule valve outline, also showing placenta and funiculi. k. Seed. (From *Liesner & Carnevali 22086*.)

apicem versus papillosae; area dorsalis inconspicue elliptica, atrobrunnea, leviter depressa, a medio indistincte 1-nervata. Sepala lateralia libera, valde inequilatera, lanceolata, 5 mm longa, acuta; ala carinali valida, usque ad apicum manifeste ciliata. Laminae petalorum late obovatae, ca. 5 mm longae, luteolae, prominenter laceratae. Antherae lanceolato-oblongae, 2 mm longae, emarginatae et sagittatae, filamentis longiores. Staminodia bibrachiata, brachiis longe penicillatis. Capsula ellipsoidea, ca. 2.5 mm longa, eseptata, placenta basali; semina cylindraceo-ellipsoidea, 1–1.3 mm longa, pallide et obtuse apiculata, atrobrunnea, longitudine obscurespiraliter multinervosae.

Dense cespitose perennial herb, the stems many, branching, the branches to 3 cm long, smooth except for leaf tips and scape edges. Roots slender. Principal foliage leaves narrowly linear-gladiate, 10–20 cm long, spreading flabellately, longer than the scape sheaths; blades flat, 1–2 mm wide, compressed, yellow-green to reddish brown, inconspicuously multinerved, entire except at tips; tips gradually narrowed, narrowly curved-acute, long-ciliate, the hairs reddish brown; margins with thickened, dark red-brown, shining edges; sheaths carinate, the carinas dark red-brown, ciliolate, the sides multicostate, red-brown, dull brown to dark red-brown toward base, the margins gradually narrowed into the blades, below gradually dilating, entire. Scape sheaths multicostate, strongly red-carinate from middle to tip, with short, red-ciliate blades. Scapes slender, flexuous, 20–30 cm long, slightly twisted, somewhat compressed, at tip in cross section narrowly elliptic, ancipital, bicostate, the costas pilose-ciliate, the hairs brownish. Spikes ellipsoid, 7–8 mm long, obtuse, few-flowered, the bracts entire, nearly uniform, red-brown, spirally imbricate, convex; sterile bracts 4, decussate, ovate, carinate, ca. 3.5 mm long; fertile bracts few, obovate, ca. 4 mm long, papillose toward tip; dorsal area inconspicuous, elliptic, dark brown, slightly depressed, medially indistinctly 1-nerved. Lateral sepals free, strongly inequilateral, lanceolate, 5 mm long, acute; keel strong to strongly ciliate up to the tip. Petal blades broadly obovate, ca. 5 mm long, yellow, strongly lacerate. Anthers lance-oblong, 2 mm long, emarginate and sagittate, longer than the filaments. Staminodia with 2 long-penicillate branches. Capsule ellipsoid, ca. 2.5 mm long, eseptate, the placenta basal; seeds cylindric-ellipsoid, 1–1.3 mm long, with a pale and obtuse apiculus, dark brown, longitudinally spirally multiribbed.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Cerro Aracamuni, summit, Proa Camp, savanna with small to large patches of forest, especially along streams, in savanna, 01°32′N, 65°49′W, 1,400 m, 25 Oct. 1987, *R. Liesner & G. Carnevali 22454* (MO, VDB, VEN).

This is a near relative of *Xyris frondosa* Maguire & Smith, a common high-altitude species of the tepuis of Estado Bolívar, particularly in habit and general leaf and spike dimensions. However, it is somewhat shorter-stemmed, its leaves are entire except at the very tips, and their margins more wirelike and thickened. The scapes, rather than being thick-edged and entire, are ancipital, the two costas thin, broad, and distinctly pilose-ciliate.

Xyris prolificans Kral, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Río Negro, slope of Cerro Aracamuni, Quebrada Camp, in area of rapids flowing over laja, 01°24′N, 65°38′W, 600 m, 20 Oct. 1987, *R. Liesner & F. Delascio 22200* (holotype, VEN; isotypes, MO, VDB). Figure 23.

Herba perennis caespitosa, tenella, glabra, laxa, rosulata, rhizomatosa. Rhizomata numerosa, gracilia, valde flexuosa, saepe ramificantia, breviter foliosa, ex axillis veternarum rosularum foliorum prodeuntia internodiis expositis. Radices graciles. Folia principalia rosularum leviter vel valde flabellate expansa, lineari-lanceolata, 3–7 cm longa, vaginis scaporum longiora; laminae planae, valde compressae, 0.8–1.5 mm latae, vaginis 1–3-plo longiores, longitudinaliter indistincte nervosae, olivaceae, a medio ad apicem gradatim contractae; apices anguste et acute incurvati; margines integri, tenues; vaginae carinatae, tenues, lateribus longitudinaliter multicostatis, marginibus in laminas gradatim convergentibus, apicibus ligula anguste acuta 1.5–2 mm longa ornatis, infimae gradatim dilatatae, a basi longe ciliatae. Vaginae scaporum laxae, apertae, tenues, ad apicem cuspidatae. Scapi subteretes, filiformes, spiraliter torti, 10–25 cm alti, ca. 0.4 0.5 mm crassi, olivacei, striati. Spicae lanceoloideae, in sicco turbinatae, 7 9 mm longae, pauciflorae, bracteis integris margine late scariosis, pallide brunneolis; bracteae steriles subdecussatae, ovatae, pari infimo carinatae, interiores breviores, 2.5 3 mm longae; bracteae fertiles oblongo-ovatae, 5–6 mm longae, convexae, rotundatae; area dorsalis viridis, ca. 2 mm longa, lanceolato-elliptica, medioindistincte costatis. Sepala lateralia libera, inequilateralia, curvata, 3–3.5 mm longa, acuta, ala carinali lata, a basi ad medium usque integra, a medio ad apicem usque indistincte lacerata. Laminae petalorum obovatae, 3 3.5 mm longae, luteolae, late rotundatae, valde erosae. Staminodia bibrachiata, brachiis dense longe penicillatis. Antherae oblongo-lanceolatae, ca. 1 mm longae, emarginatae et sagittatae; filamenta ca. 0.5 mm longa. Capsula matura non visa sed ovario placentationibus marginalibus et funiculis elongatis, praedito.

Cespitose, slender, smooth, lax, rosulate, rhizomatous herb. Rhizomes numerous, slender, strongly zig-zag, usually branching, short-leaved, from the axils of older rosette leaves and with the internodes exposed. Roots slender. Principal rosette leaves slightly to very flabellately spreading, lance-linear, 3–7 cm long, longer than the scape sheaths; blades flat, strongly compressed, 0.8–1.5 mm wide, 1–3 times longer than the sheaths, lon-

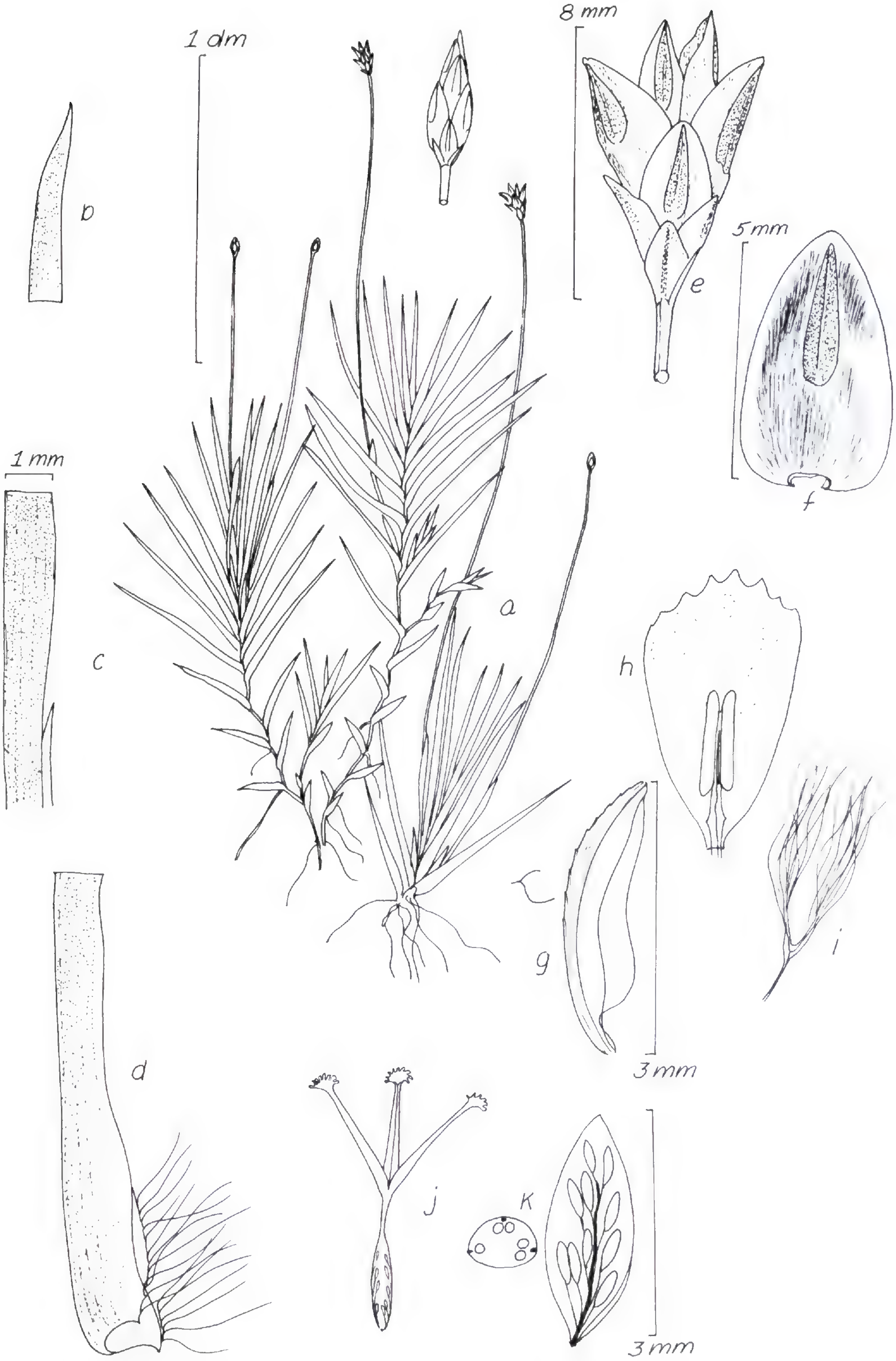

FIGURE 23. *Xyris prolificans.*—a. Habit with inset showing outline of mature spike.—b. Leaf tip.—c. Leaf blade sheath junction.—d. Leaf base. e. Dry spike.—f. Fertile bract.—g. Lateral sepal.—h. Petal blade and stamen.—i. Staminode.—j. Ovary and style.—k. Capsule valve (construction) showing placentation. (From *Liesner & Delascio 22200.*)

gitudinally indistinctly nerved, olivaceous, gradually narrowed from middle to tip; tips narrowly incurved-acute; margins entire, thin; sheaths carinate, thin, the sides longitudinally multicostate, the margins gradually narrowed, at apex producing a narrowly acute ligule 1.5–2 mm long, gradually dilating below, long-ciliate at base. Scape sheaths lax, open, slender and thin, cuspidate. Scapes subterete, filiform, spirally twisted, 10–25 cm high, ca. 0.4–0.5 mm thick, olivaceous, striate. Spikes lanceoloid, drying turbinate, 7–9 mm long, few-flowered, the entire bracts with broad, scarious pale brown borders; sterile bracts ca. 6, subdecussate, ovate, the lower pair carinate, shorter than the inner pairs, 2.5–3 mm long; fertile bracts oblong-ovate, 5–6 mm long, convex, rounded; dorsal areas green, ca. 2 mm long, lanceolate-elliptic, medially with an indistinct rib. Lateral sepals free, inequilateral, curvate, 3–3.5 mm long, acute, the keel broad, entire from base to middle, from middle to apex low-lacerate. Petal blades obovate, 3–3.5 mm long, yellow, broadly rounded, strongly erose. Staminodia bibrachiate, the branches densely long-penicillate. Anthers oblong-lanceolate, ca. 1 mm long, emarginate and sagittate; filaments ca. 0.5 mm long. Mature capsule not seen, but the ovary with marginal placentation and elongate funicles.

The growth habit of this species is somewhat unusual. From the limited material available one concludes that rosettes produce either scapes or rhizomal buds from older axillae. The rhizomes are elongate, zig-zag, and with short, evenly separated leaves. The offshoots frequently branch and ultimately produce new rosettes at the tips, the whole proliferating product presumably forming extensive clones. Mature seeds would be necessary to establish the relationship of this to others of the section *Xyris*.

Preliminary Checklist of the Vascular Plant Flora of Cerro Aracamuni

The checklist has been arranged into two groups: pteridophytes and seed plants. Within each group, families are arranged alphabetically and are divided up into the four main areas of collection in the following order: Summit, East Escarpment, Quebrada Camp, and Granitic Dome. Within each of the collecting areas, genus and species are listed alphabetically. Each species is followed by the name of the principal collector and number.

Details of the camp and collecting locations, along with a list of the co-collectors with their number ranges and dates of collection, are given below.

SUMMIT

The Dunsterville collections give the coordinates: 01°30′N Lat., 65°51′W Long., 1,510 m.

G.C.K. & E. Dunsterville s.n., Dec. 1972

Brewer Carias gives only elevation, 1,500 m.

Charles Brewer Carias s.n., 13 Dec. 1983

The 1987 expedition had two summit camps located at extreme ends of the massif: Popa Camp, situated at 01°26′N Lat., 65°47′W Long., 1,550 m, and Proa Camp, situated at 01°32′N Lat., 65°49′W Long., 1,400 m.

Carnevali & Santana 2362–2457, Popa Camp, 27–30 Oct. 1987
Carnevali & Liesner 2458–2584, Proa Camp, 30 Oct.–3 Nov. 1987
Liesner & Delascio 21934–22182, Popa Camp, 15–19 Oct. 1987
Liesner & Carnevali 22407–22730, Proa Camp, 25 Oct.–3 Nov. 1987

EAST ESCARPMENT

01°32′N Lat., 65°48′W Long., 750 m. Habitats here consisted of shrub thickets, exposed rock, and low dense forest.

Huber & Medina 5892–5942, 10 Feb. 1981

QUEBRADA CAMP

01°24′N Lat., 65°38′W Long., 500–600 m. Located along a stream slightly south and east of the summit in low open forest on a smooth, rocky outcrop near rapids.

Liesner & Delascio 22183–22270, 20–21 Oct. 1987
Liesner & Carnevali 22271–22406, 21–24 Oct. 1987

GRANITIC DOME

Collections from this site were made by Wurdack and Adderley from a 900-m granitic dome with low herbaceous vegetation on open rock and scrub forest. The dome is on the right side of Río Siapa, just below the rapids, Raudal Gallineta.

Wurdack & Adderley 43538-43572, 21 July 1959

PTERIDOPHYTA

Adiantaceae—Alan R. Smith (UC)

Summit:
Pterozonium scopulinum Lellinger—Liesner 22569

Aspleniaceae—John Mickel (UC), *Elaphoglossum*; Alan R. Smith (UC), *Asplenium*

Summit:
Asplenium serra Langsd. & Fischer—Liesner 22727
Elaphoglossum plumosum (Fée) T. Moore—Liesner 22507, 22690
Elaphoglossum productum Rosenstock—Liesner 22009, 22555, 22615, 22616, 22661

Quebrada camp:
Elaphoglossum glabellum J. Smith—Liesner 22277
Elaphoglossum obovatum Mickel—Liesner 22343

Cyatheaceae—Alan R. Smith (UC)

Summit:
Cyathea demissa (C. Morton) Lellinger—Liesner 21997, 22601
Cyathea platylepis (Hook.) Domin—Liesner 22482
Cyathea vel aff. *williamsii* (Maxon) Domin—Liesner 21966, 22014, 22660

Quebrada camp:
Cyathea macrosora (Baker) Domin var. *reginae* (Windisch) A. R. Smith—Liesner 22247

Davalliaceae—Alan R. Smith (UC)

Summit:
Oleandra articulata (Sw.) C. Presl—Liesner 22689
Oleandra duidae A. C. Smith—Liesner 22723

Dennstaedtiaceae—Alan R. Smith (UC)

Summit:
Lindsaea sp.—Liesner 21978
Lindsaea stenomeris Kramer Liesner 22550
Lindsaea stricta (Sw.) Dryander var. *jamesoniiformis* Kramer—Liesner 22539, 22591
Lindsaea stricta (Sw.) Dryander var. *stricta*—Liesner 22112, 22539

Quebrada camp:
Lindsaea cyclophylla Kramer—Liesner 22264

Gleicheniaceae—Alan R. Smith (UC)

Summit:
Dicranopteris flexuosa (Schrader) L. Underw.—Liesner 21962
Dicranopteris pectinata (Willd.) L. Underw.—Liesner 22567

Quebrada camp:
Dicranopteris pectinata (Willd.) L. Underw.—Liesner 22307

Grammitidaceae—L. E. Bishop (UC); Alan R. Smith (UC)

Summit:
Ceradenia capillaris (Desv.) L. Bishop—Liesner 22620
Ceradenia kalbreyeri (Baker) L. Bishop—Liesner 22493, 22709
Ceradenia spixiana (Mett.) L. Bishop—Liesner 22724
Cochlidium connellii (C. H. Wright) A. C. Smith—Liesner 22576, 22635
Cochlidium serrulatum (Sw.) L. Bishop—Liesner 21994, 22092, 22574
Cochlidium tepuiense (A. C. Smith) L. Bishop—Liesner 22547
Glyphotaenium campbellii (Baker) Copel.—Liesner 22504, 22685
Grammitis bryophila (Maxon) F. Seymour—Liesner 22547A, 22619
Grammitis melanosticta (Kunze) F. Seymour—Liesner 22671
Grammitis taenifolia (Jenman) Proctor—Liesner 22509
Grammitis aff. *williamsii* (Maxon) Lellinger—Liesner 22662

Quebrada camp:
Cochlidium serrulatum (Sw.) L. Bishop—Liesner 22299, 22301

Hymenophyllaceae—Alan R. Smith (UC)

Summit:
Hymenophyllum elegans Sprengel—Liesner 22552
Hymenophyllum fendlerianum Sturm in C. Martius—Liesner 22668
Hymenophyllum ferax Bosch—Liesner 22524, 22526
Hymenophyllum karstenianum Sturm—Liesner 22528
Trichomanes crinitum Sw.—Liesner 21972, 22566, 22586
Trichomanes cf. *pellucens* Kunze—Liesner 22548
Trichomanes sprucei Baker—Liesner 22434, 22435, 22551

Quebrada camp:
Trichomanes ankersii Parker ex Hook. & Grev.—Liesner 22398

Hymenophyllopsidaceae—Alan R. Smith (UC)

Summit:
Hymenophyllopsis hymenophylloides L. D. Gómez—Liesner 22568
Hymenophyllopsis superba Lellinger—Liesner 22432

Lycopodiaceae—Alan R. Smith (UC)

Summit:
Lycopodium funiforme Cham. ex Spring—Liesner 22721
Lycopodium iuliforme L. Underw. & Lloyd—Liesner 22175, 22491

Quebrada camp:
Lycopodium sp.—Liesner 22201
Lycopodium linifolium L. –Liesner 22351A

Metaxyaceae—Alan R. Smith (UC)

Quebrada camp:
Metaxya rostrata (H.B.K.) C. Presl—Liesner 22361

Polypodiaceae—Alan R. Smith (UC)

Summit:
Polypodium laevigatum Cav. Liesner 22691
Polypodium triseriale Sw.—Liesner 22083

Quebrada camp:
Microgramma baldwinii Brade—Liesner 22297

Schizaeaceae—Alan R. Smith (UC)

Summit:
Schizaea elegans (M. Vahl) Sw. Liesner 22658
Schizaea poeppigiana Sturm in C. Martius—Liesner 22171

Quebrada camp:
Actinostachys pennula (Sw.) Hook.—Liesner 22184A
Schizaea elegans (M. Vahl) Sw.—Liesner 22259, 22290
Schizaea stricta Lellinger (mixed collection with *Actinostachys pennula*) –Liesner 22184

Selaginellaceae—Alan R. Smith (UC)

Summit:
Selaginella rhodostachya Baker—Liesner 22553

Tectariaceae—Alan R. Smith (UC)

Quebrada camp:
Triplophyllum dicksonioides (Fée) Holttum—Liesner 22260, 22359

SEED PLANTS

Annonaceae—Paul J. M. Maas (U), *Anaxagorea*

Quebrada camp:
Anaxagorea brevipes Benth.—Liesner 22398A
Duguetia sp.—Liesner 22804

Apocynaceae—Bruce Hansen (USF), *Odontadenia*; A. J. M. Leeuwenberg (WAG), *Tabernaemontana*; Friedrich Markgraf (Z), *Parahancornia*; James Zarucchi (MO), misc.; G. Morillo (VEN), *Mandevilla*.

Summit:
Aspidosperma sp. Liesner 22042, 22167
Couma rigida Muell. Arg.—Liesner 22696
Galactophora schomburgkiana Woodson—Liesner 22411
Mandevilla aracamunensis Morillo Brewer Carias s.n. (type)

East escarpment:
Mandevilla annulariifolia Woodson.—Huber 5895
Parahancornia krukovii Monach. Huber 5928
Parahancornia negroensis Monach. Huber 5911

Quebrada camp:
Couma rigida Muell. Arg. Liesner 22400
Galactophora sp.—Liesner 22403
Lacmellea sp. Liesner 22206
Mandevilla spp. Liesner 22216, 22321
Odontadenia neglecta Woodson—Liesner 22296
Prestonia sp.—Liesner 22279
Tabernaemontana muelleriana C. Martius ex Muell. Arg. (?)—Liesner 22355

Aquifoliaceae—Julian Steyermark (MO)

Summit:
Ilex aracamuniana Steyerm. —Liesner 22060 (paratype), 22181 (paratype), 22473 (type)
Ilex retusa Klotzsch—Liesner 22109, 22043
Ilex tateana Steyerm. Liesner 22533

East escarpment:
Ilex divaricata C. Martius ex Reisseck—Huber 5896

Araceae—George S. Bunting

Summit:
Anthurium ptarianum Steyerm.—Liesner 22024, 22039, 22684
Philodendron callosum K. Krause subsp. *ptarianum* (Steyerm.) Bunting—Liesner 22672, 22720. Sterile and fertile specimens have slender, scandent stems and very small leaves.
Philodendron roraimae K. Krause subsp. *aracamuniense* Bunting—Liesner 22502, 22510, 21956
Philodendron tatei K. Krause subsp. *melanochlorum* (Bunting) Bunting Liesner 22178A, 22487, 22704. Described originally from collections from the Gran Sabana, similar material has subsequently been collected in Territorio Federal Amazonas, as well as some plants nearly intermediate between this and subsp. *tatei* that demonstrate the close relationship of these taxa. Four collections from Cerro Aracamuni appear to represent subsp. *melanochlorum*, which has a much narrower leaf blade than subsp. *tatei*. Of these, *Liesner & Delascio 22178A*, taken from an immature plant, has ovate leaf blades subcordate at base in contrast to the usually elliptic blades with obtuse or acute bases. The relevance of this variation is unknown.
Stenospermation cf. *nebulense* Bunting Liesner 22437. The type collection is from Cerro de la Neblina at 1,500 m.
Stenospermation ulei K. Krause—Liesner 22676

Quebrada camp:
Anthurium bonplandii Bunting subsp. *rionegrense* Bunting Liesner 22311
Heteropsis spruceana var. *robusta* Bunting Liesner 21926
Heteropsis spruceana Schott. var. *spruceana* Liesner 22832
Philodendron englerianum Steyerm. subsp. *duidae* (Steyerm.) Bunting—Liesner 22406
Philodendron maguirei Bunting—Liesner 22243. Known also from Cerro Arauicaua and Cerro de la Neblina.
Philodendron cf. *maroae* Bunting—Liesner 22332. The determination is in question because of the paucity of material and the lack of data concerning the petiole shape; until now *P. maroae* has been known only from lowland savanna near Maroa.
Schismatoglottis bolivariana Bunting & Steyerm. Liesner 22192. A rather rare species, this is apparently the first record outside of Estado Bolívar. The specimen is identical to other material except for the greater size of the leaf blade (45 cm long, 32.5 cm wide).
Stenospermation cf. *ulei* K. Krause—Liesner 22320. Specimen sterile but apparently pertaining to this widespread species with nodding inflorescence.

Arecaceae—Andrew Henderson (NY)

Summit:
Euterpe montis-duidae Burret ex Gleason Liesner 22120

Quebrada camp:
Bactris sp. (sterile)—Liesner 22256
Bactris simplicifrons C. Martius—Liesner 22283
Bactris cf. *simplicifrons* C. Martius Liesner 22258
Iriartella setigera (C. Martius) H. A. Wendl.—Liesner 22261

Asclepiadaceae—Gilberto Morillo (VEN)

Summit:
Blepharodon sp. Liesner 22420, 22752
Matelea neblinae Morillo—Liesner 22164, 22503, 22725

Asteraceae John Pruski (NY); Victor Badillo (MY)

Summit:
Gongylolepis huachamacari Maguire & Wurd.—Liesner 21960
Imeria memorabilis (Maguire & Wurd.) King & H. Robinson Liesner 21983
Mikania lucida H. L. Blake f. *lucida* Liesner 22449, 22693
Stomatochaeta crassifolia (H. L. Blake) Maguire & Wurd. Liesner 22081

East escarpment:
Gongylolepis martiana (Baker) Steyerm. & Cuatrecasas —Huber & Medina 5927
Imeria serratifolia V. Badillo Huber 5898 (type)
Stenopadus campestris Maguire & Wurd.—Huber 5941

Quebrada camp:
Eupatorium (*Praxelis*) *asperulaceum* Baker Liesner 22190

Bignoniaceae—Alwyn Gentry (MO)

Summit:
Digomphia densicoma (C. Martius ex DC.) Pilger—Liesner 22106, 22177, 22621
Distictella monophylla Sandw.—Liesner 21954

East escarpment:
Distictella monophylla Sandw.—Huber 5892

Quebrada camp:
Pleonotoma jasminifolium (H.B.K.) Miers—Liesner 22246
Schlegelia spruceana Schumann—Liesner 22399

Bombacaceae—Julian Steyermark (MO)

Summit:
Pochota aracamuniana Steyerm.—Liesner 22174 (paratype), 22559 (type), 22577 (paratype)
Pochota cf. *ewelii* Steyerm.—Liesner 22444, 22664

Quebrada camp:
Pochota sp.—Liesner 22390

Bromeliaceae—Lyman B. Smith (US), with Julian Steyermark (MO)

Summit:
Brocchinia acuminata Lyman B. Smith –Liesner 22027
Brocchinia hitchcockii Lyman B. Smith—Liesner 22590
Brocchinia micrantha (Baker) Mez (ovaries variable in form)—Liesner 22000
Brocchinia vestita Lyman B. Smith –Liesner 22028
Lindmania sp.—Liesner 22706
Lindmania argentea Lyman B. Smith—Liesner 22057, 22703
Lindmania aff. *gracillima* Lyman B. Smith, (leaf spines large)—Liesner 22440
Navia sp.—Liesner 22093
Navia patria Lyman B. Smith & Steyerm.—Liesner 22041 (type)
Navia platyphylla Lyman B. Smith & Steyerm.—Liesner 22062 (type)
Navia terramarae Lyman B. Smith & Steyerm.—Liesner 21998 (type), 22599 (paratype)
Tillandsia confinis Lyman B. Smith var. *caudata* Lyman B. Smith—Liesner 22446
Tillandsia confinis Lyman B. Smith var. *confinis*—Liesner 22019, 22715
Tillandsia spiculosa Griseb. var. *spiculosa*—Liesner 22056, 22442
Vriesea capituligera (Griseb.) Lyman B. Smith & Pittendr.—Liesner 22678
Vriesea duidae (Lyman B. Smith) Gouda (det. G. Carnevali)—Carnevali 2460, 2501
Vriesea incurva (Griseb.) Read –Liesner 22085

Quebrada camp:
Aechmea brevicollis Lyman B. Smith—Liesner 22345
Aechmea politii Lyman B. Smith (leaf blades attenuate)—Liesner 22363
Ananas parguazensis Camargo & Lyman B. Smith—Liesner 22394
Brocchinia paniculata Schult. f. (?)—Liesner 22319
Navia carnevalii Lyman B. Smith & Steyerm.—Liesner 22322 (type)
Navia iosothrix Lyman B. Smith & Steyerm.—Liesner 22203 (type)
Pitcairnia patentiflora Lyman B. Smith—Liesner 22198
Tillandsia paraensis Mez—Liesner 22303
Vriesea socialis Lyman B. Smith—Liesner 22294

Granitic dome:
Brocchinia acuminata Lyman B. Smith—Wurdack 43566
Brocchinia tatei Lyman B. Smith—Wurdack 43563, 43567
Pitcairnia patentiflora var. *armata* Lyman B. Smith—Wurdack 43565
Tillandsia confinis Lyman B. Smith—Wurdack 43561, 43562
Vriesea fibrosa Lyman B. Smith—Wurdack 43569
Vriesea platynema Gaudich. var. *platynema*—Wurdack 43568

Burmanniaceae—Paul J. M. & H. Maas (U)

Summit:
Dictyostega orobanchoides (Hook.) Miers subsp. *orobanchoides* –Liesner 22004, 22427
Hexapterella steyermarkii P. Maas & H. Maas—Liesner 22622 (type)

Quebrada camp:
Apteria aphylla (Nutt.) Barnhart ex Small Liesner 22281
Dictyostega orobanchoides (Hook.) Miers subsp. *parviflora* (Benth.) Snelders & P. Maas—Liesner 22253, 22402

Burseraceae—Douglas Daly (NY)

Summit:
Not determined to genus—Liesner 22072, 22465, 22626

Quebrada camp:
Dacryodes glabra (Steyerm.) Cuatrec.—Liesner 22187

Caesalpiniaceae—Richard S. Cowan (PERTH); Rupert Barneby (NY)

East escarpment:
Dimorphandra cuprea Sprague ex Sandw.—Huber 5926
Jacqueshuberia sp.—Huber 5929
Macrolobium discolor Benth.—Huber 5917

Quebrada camp:
Macrolobium sp. –Liesner 22196, 22357

Chloranthaceae—Carol Todzia (TEX)

Summit:
Hedyosmum vel aff. *gentryi* D'Arcy & Liesner—Liesner 22438, 22472, 22517, 22535

Chrysobalanaceae—Ghillean Prance (K)

Quebrada camp:
Hirtella punctillata Ducke Liesner 22295
Hirtella schultesii Prance Liesner 22360

Clusiaceae—Bassett Maguire (NY); Barry Hammel (MO)

Summit:
Clusia aff. *lopezii* Maguire—Liesner 22489, 22575
Clusia melchiorii Gleason—Liesner 22156, 22717
Clusia pusilla Steyerm. Liesner 22496, 22708
Clusia sessilis Klotzsch ex Engler—Liesner 22021, 22485
Oedematopus obovatus Spruce ex Planchon & Triana—Liesner 22111, 22543, 22632

East escarpment:
Clusia sp.—Huber 5922

Granitic dome:
Clusia pusilla Steyerm. subsp. *orinocensis* Maguire — Wurdack 43555, 43556, 43557

Quebrada camp:
Clusia columnaris Engler — Liesner 22225, 22233
Clusia aff. *gratula* Maguire — Liesner 22344
Clusia aff. *penduliflora* Engler — Liesner 22298

Cunoniaceae

Summit:
Weinmannia spp. — Liesner 21935, 22098, 22429, 22641

Cycadaceae

Quebrada camp:
Zamia sp. — Liesner 22367

Cyclanthaceae — Barry Hammel (MO)

Summit:
Sphaeradenia rubescens Harling Liesner 22447, 22587

Quebrada camp:
Dicranopygium imeriense Harling — Liesner 22309

Cyperaceae — Gerrit Davidse (MO)

Summit:
Didymiandrum stellatum (Boeckeler) Gilly — Liesner 22015
Rhynchocladium steyermarkii (T. Koyama) T. Koyama — Liesner 21941

Quebrada camp:
Calyptrocarya glomerulata (Brongn.) Urban — Liesner 22364
Cephalocarpus confertus Gilly — Liesner 22333
Hypolytrum pulchrum (Rudge) Pfeiffer — Liesner 22288
Mapania maguireana T. Koyama & Steyerm. ex T. Koyama — Liesner 22241
Mapaniopsis micrococca T. Koyama — Liesner 22193
Rhynchospora rigidifolia (Gilly) T. Koyama subsp. *planifolia* T. Koyama — Liesner 22224, 22227

Cyrillaceae — Julian Steyermark (MO)

Summit:
Cyrilla racemiflora L. — Carnevali 2365; Liesner 22073
Purdiaea nutans Planchon — Carnevali 2548; Liesner 22711

Dilleniaceae — Klaus Kubitzki (HBG); Ronald Liesner (MO)

East escarpment:
Doliocarpus savannarum Sandw. — Huber 5902

Quebrada camp:
Doliocarpus savannarum Sandw. — Liesner 22185, 22276

Dioscoreaceae

Summit:
Dioscorea spp. — Liesner 22415, 22436, 22484, 22541, 22710

Droseraceae — Bruce Holst (MO)

Summit:
Drosera roraimae (Klotzsch ex Diels) Maguire & Laundon — Liesner 22687, 22126

Quebrada camp:
Drosera roraimae (Klotzsch ex Diels) Maguire & Laundon — Liesner 22223

Elaeocarpaceae — Julian Steyermark (MO)

Summit:
Sloanea steyermarkii C. E. Smith subsp. *jauaensis* (Steyerm.) Steyerm. Sterile, but probably to be referred here. — Liesner & Carnevali 22722

Ericaceae — James Luteyn (NY)

Summit:
Cavendishia callista J. D. Smith, s.l. — Liesner 22536
Orthaea wurdackii Maguire, Steyerm. & Luteyn Liesner 22102, 22545. The two collections cited show an interesting transition from the type collection at Neblina with a short racemose inflorescence, to recent Neblina collections where the inflorescence is a very short raceme, to these Liesner (Aracamuni) collections where the flowers are essentially sessile to fasciculate, 1 4-flowered inflorescences. Otherwise they seem to be equal. The species is known previously from Cerro de la Neblina.
Satyria carnosiflora Lanj. — Liesner 22521
Sphyrospermum cordifolium Benth. — Liesner 21979, 22563, 22686
Thibaudia cupatensis H. E. Huber - Liesner 21946, 21946A, 22579

Quebrada camp:
Cavendishia callista Donn. Sm., s.l. — Liesner 22272
Satyria panurensis (Benth.) Benth. & Hook. — Liesner 22323
Thibaudia cupatensis H. E. Huber — Liesner 22189

Eriocaulaceae — Nancy Hensold (MO)

Summit:
Paepalanthus sulcatus Hensold Liesner 21940
Syngonanthus phelpsae Moldenke — Liesner 22443

East escarpment:
Syngonanthus anomalus (Koern.) Ruhl — Huber 5934

Quebrada camp:
Paepalanthus capillaceus Klotzsch ex Koern. — Liesner 22308
Syngonanthus biformis (N.E. Br.) Gleason — Liesner 22199

Euphorbiaceae — Michael Huft (MO); Grady Webster (DAV)

Summit:
Hyeronima oblonga (Tul.) Muell. Arg. var. *oblonga* — Liesner 22677
Phyllanthus cf. *anadenus* Jabl. — Liesner 21947, 22032
Phyllanthus vacciniifolius (Muell. Arg.) Muell. Arg. — Liesner 21984
Senefeldera yutajensis (Jabl.) Webster — Liesner 22625
Senefelderopsis sipapoensis Jabl. — Liesner 22466, 22475

Quebrada camp:
Pera bicolor (Klotzsch) Muell. Arg. — Liesner 22238

Granitic dome:
Phyllanthus gallinetae Jabl. — Wurdack 43550
Phyllanthus subapicaulis Jabl. — Wurdack 43549

Fabaceae — James Zarucchi (MO)

Quebrada camp:
Clitoria sp.—Liesner 22404
Ormosia sp.—Liesner 22234
Swartzia sp.—Liesner 22271

Flacourtiaceae—Julian Steyermark (MO)

East escarpment:
Laetia coriacea Spruce ex Benth.—Huber 5920

Quebrada camp:
Euceraea nitida C. Martius—Liesner 22300
Laetia coriacea Spruce ex Benth.—Liesner 22284, 22348
Ryania speciosa var. *subulifera* (Sandw.) Monach.—Liesner 22380

Gentianaceae—Paul J. M. Maas (U), in part

Summit:
Celiantha bella Maguire & Steyerm.—Liesner 22126
Symbolanthus aracamuniensis Steyerm.—Liesner 22079 (type)
Tapeinostemon spenneroides Benth.—Liesner 22082, 22585, 22666

East escarpment:
Irlbachia alata (Aubl.) P. Maas subsp. *alata* Huber 5940

Quebrada camp:
Irlbachia alata (Aubl.) P. Maas subsp. *alata*—Liesner 22305
Tachia grandifolia Mag. & Weaver var. *orientalis* Maguire & Weaver—Liesner 22254, 22382
Tapeinostemon spenneroides Benth.—Liesner 22082
Voyria aphylla (Jacq.) Pers.—Liesner 22337
Voyria (?) sp.—Liesner 22252

Granitic dome:
Chelonanthus angustifolius (H.B.K.) Gilg—Wurdack 43552
Chelonanthus uliginosus Griseb. Wurdack 43554

Gesneriaceae

Summit:
Not determined to genus Liesner 22525, 22530, 22679

Quebrada camp:
Not determined to genus—Liesner 22324, 22346
Codonanthe sp.—Liesner 22389

Humiriaceae—Ronald Liesner (MO)

Summit:
Humiria balsamifera (Aublet) Standley—Liesner 22410, 22589, 22633

Icacinaceae—Richard A. Howard (A)

Summit:
Emmotum glabrum Benth. ex Miers—Carnevali 2583; Liesner 21953, 22670

Lauraceae—Henk van der Werff (MO)

Summit:
Aniba cinnamomiflora Allen—Liesner 21967, 22065. The type of this species is from Cerro Sipapo, Territorio Federal Amazonas. *Aniba cinnamomiflora* has also been reported from lowlands in Estados Apure, Aragua, and Táchira. Distribution and habit (a shrub or small tree from Cerro Sipapo and Aracamuni, large timber tree from the other localities) suggest that the collections outside Territorio Federal Amazonas do not belong in *Aniba cinnamomiflora*; additional collections are needed to solve this problem.
Endlicheria vinotincta Allen Liesner 22008 (♀), 22414 (♂), 22292 (♂). On the summit and slopes of Cerro Aracamuni, 600 1,500 m. Previously known from two collections from Cerro Neblina. *Liesner & Carnevali 22414* and *22292* are the first staminate collections of this species.
Licaria trinervis van der Werff Liesner 22161 (type), 22451 (paratype), 22714 (paratype)
Persea perseiphylla (Allen) van der Werff—Liesner 22099, 22169

Quebrada camp:
Aniba sp.—Liesner 22374

Lentibulariaceae—Peter Taylor (K)

Summit:
Genlisea guianensis N.E. Br. Liesner 22488
Genlisea repens Beuj.— Liesner 22573
Utricularia alpina Jacq. Liesner 21971
Utricularia amethystina A. St. Hil. Liesner 22051, 22490
Utricularia humboldtii Schomb.— Liesner 21950
Utricularia jamesoniana Oliver—Liesner 21992, 22078
Utricularia neottioides A. St. Hil.—Liesner 21995
Utricularia pubescens Sm. Liesner 22565
Utricularia steyermarkii P. Taylor Liesner 21989
Utricularia subulata L.—Liesner 22121
Utricularia triloba Benj.—Liesner 22617

East escarpment:
Genlisea pygmaea A. St. Hil.—Huber 5935
Genlisea repens Benj.—Huber 5936

Quebrada camp:
Genlisea pygmaea A. St. Hil. Liesner 22195
Utricularia jamesoniana Oliver Liesner 22376

Granitic dome:
Utricularia humboldtii Schomb. Wurdack 43560

Liliaceae—Robert Cruden (IA)

Summit:
Tofieldia schomburgkiana Oliver Liesner 22469

Loganiaceae—Rupert Barneby (NY)

Quebrada camp:
Strychnos guianensis (Aublet) C. Martius Liesner 22405

Loranthaceae

Summit:
Not determined to genus Liesner 22155, 22170, 22630, 22455, 22544, 22561, 22628, 22729

Quebrada camp:
Not determined to genus—Liesner 22084, 22191, 22293, 22393

Lythraceae—Alicia Lourteig (P)

Summit:
Cuphea annulata Koehne Liesner 21948

East escarpment:
Cuphea annulata Koehne Huber 5906

Quebrada camp:
Cuphea annulata Koehne—Liesner 22207

Malpighiaceae—William R. Anderson (MICH)

Summit:
Banisteriopsis maguirei Gates—Liesner 22162
Byrsonima amoena Cuatrec.—Liesner 22422, 22578
Diacidia glaucifolia (Maguire) W. R. Anderson Liesner 21963, 22542

East escarpment:
Blepharandra hypoleuca (Benth.) Griseb.—Huber 5904
Heteropterys huberi W. R. Anderson—Huber 5893

Marantaceae—Lennart Andersson (GB), *Ischnosiphon*

Quebrada camp:
Ischnosiphon surumuensis Loesn. Liesner 22255
Ischnosiphon puberulus Loesn.—Liesner 22377
Monotagma sp.—Liesner 22249, 22327 [Note: this new species will be described soon in the *Annals*.]

Melastomataceae—John J. Wurdack (US)

Summit:
Clidemia tepuiensis Wurd.—Liesner 22070
Graffenrieda cf. *polymera* Gleason subsp. *neblinensis* Wurd.—Liesner 22423, 22699, 22730. The Aracamuni collections, mostly in young bud, differ from the Cerro Neblina subspecies by having lower leaf surfaces with very attenuated pubescence and very faint secondary nerves, obscure pedicels only 0.5–1 mm long, and smaller flowers (petals ca. 8 × 5.5 mm, anthers 3.5–4.5 mm long with basal spur 1–1.3 mm long). I am reluctant to describe a new subspecies until more material is available.
Macairea theresiae Cogn.—Liesner 21949. Otherwise known from lowland white sand savannas of the middle and lower Amazon and Rio Negro basins in Brazil, the closest locality being the Rio Araca (fide Renner Mss.).
Maieta neblinensis Wurd.—Liesner 22068, 22583. Otherwise known only from the upper slope forests of Cerro Neblina in Venezuela and Brazil, 650–1,300 m.
Miconia curta (Gleason) Wurd.—Liesner 22688
Miconia dodecandra (Desr.) Cogn.—Liesner 22166
Miconia roraimensis Ule—Liesner 22150, 22523, 22663
Neblinanthera cumbrensis Wurd.—Liesner 21937, 22657. Otherwise known from the upper slopes of Cerro Neblina in Venezuela and Brazil, 1,300–1,800 m.
Salpinga pusilla (Gleason) Wurd. Liesner 21986, 21987, 22063. Otherwise restricted to the summit and upper slopes of Duida and Neblina, often a quasi-rheophyte.
Tateanthus duidae Gleason—Liesner 22627
Tibouchina dissitiflora Wurd.—Liesner 22080
Tococa liesneri Wurd.—Liesner 22007 (paratype), 22700 (type)
Tococa pachystachya Wurd.—Liesner 21938. Otherwise known only from cloud forest of the upper slopes of Cerro Neblina, 1,450–2,000 m.

East escarpment:
Macairea lanata Gleason subsp. *lanata*—Huber 5897
Macairea thyrsiflora DC.—Huber 5931
Meriania urceolata Triana—Huber 5901
Pachyloma huberioides (Naudin) Triana—Huber 5903

Quebrada camp:
Adelobotrys rotundifolia Triana—Liesner 22378
Adelobotrys saxosa Wurd.—Liesner 22285
Clidemia heteroneura (DC.) Cogn.—Liesner 22395
Clidemia novemnervia (DC.) Triana—Liesner 22306
Macairea thyrsiflora DC. Liesner 22188
Maieta poeppigii C. Martius ex Cogn.—Liesner 22831
Miconia sp.—Liesner 22379
Miconia cautis Wurd.—Liesner 22242, 22795
Miconia marginata Triana—Liesner 22213
Miconia rugosa Triana—Liesner 22371
Miconia splendens (Sw.) Griseb.—Liesner 22758
Miconia cf. *traillii* Cogn. Liesner 22830
Myrmidone macrosperma (C. Martius) C. Martius—Liesner 22326
Pachyloma huberioides (Naudin) Triana—Liesner 22215
Tococa macrophysca Spruce ex Triana Liesner 22286

Granitic dome:
Adelobotrys saxosa Wurd.—Wurdack 43543
Miconia ciliata (Rich.) DC.—Wurdack 43544

Mimosaceae Rupert Barneby (NY)

Summit:
Abarema arenaria (Ducke)—Liesner 22113

Quebrada camp:
Calliandra sp.—Liesner 22304
Inga sp.—Liesner 22211
Zygia basijuga (Ducke) Barneby & Grimes—Liesner 22269

Monimiaceae

Quebrada camp:
Mollinedia sp.—Liesner 22270

Moraceae—C. C. Berg (BG)

Summit:
Coussapoa sp.—Liesner 22180
Ficus sp.—Liesner 22160

Myrsinaceae–John Pipoly

Summit:
Not determined to genus—Liesner 21936, 22416, 22479, 22486, 22726

East escarpment:
Cybianthus deltatus Pipoly—Huber 5910

Quebrada camp:
Not determined to genus Liesner 22273

Myrtaceae Bruce Holst (MO)

Summit:
Blepharocalyx eggersii (Kiaerskov) Landrum—Liesner 22061, 22588. Known previously in Venezuela only from Isla Margarita in Estado Nueva Esparta, and northeast Estado Bolívar.
Eugenia sp. Liesner 22680
Marlierea summa McVaugh var. *summa*—Liesner 22002, 22419
Myrcia bolivarensis (Steyerm.) McVaugh—Liesner 22581
Myrcia revolutifolia McVaugh—Liesner 22097, 22702

Quebrada camp:
Marlierea sp.—Liesner 22330
Myrcia revolutifolia McVaugh—Liesner 22274

Granitic dome:
Myrcia deflexa (Poiret) DC.—Wurdack 43559

Nyctaginaceae—Julian Steyermark (MO)

East escarpment:
Neea obovata Spruce ex Heimerl—Huber 5900

Ochnaceae—Julian Steyermark (MO)

Summit:
Philacra auriculata Dwyer—Liesner 22168. Known previously only from Cerro de la Neblina.
Poecilandra retusa Tul.—Liesner 21942, 22631
Sauvagesia guianensis (Eichler) Sastre subsp. *aracamuniensis* Steyerm.—Liesner 22075 (type)
Tyleria silvana Maguire—Liesner 22006. This species was originally described from the upper slopes of Serra Pirapucú, a sandstone table mountain in northern Brazil just south of and adjacent to the Brazilian side of Serra da Neblina. The collection of *Liesner & Delascio 22006* from the summit of Cerro Aracamuni at an altitude of 1,550 m marks the first report of this taxon from Venezuela. The Cerro Aracamuni specimens differ from typical *Tyleria silvana* by having fimbriate intermediate appendages between the staminodes 5.5 mm vs. 2.5 mm and primary bracts of the inflorescence 20–30 mm vs. 18–22 mm. The Venezuelan collection has the glandular-scarious apices of the sepals and bracts typical of *T. silvana* and agrees in all other characters.

East escarpment:
Sauvagesia falcisepala Sastre—Huber 5918 (type)

Quebrada camp:
Ouratea ramosissima Maguire & Steyerm.—Liesner 22217

Granitic dome:
Sauvagesia longifolia Eichler—Wurdack 43545

Olacaceae

Quebrada camp:
Not determined to genus—Liesner 22358

Orchidaceae—Germán Carnevali & Ivón Ramírez (MO)

Summit:
Aracamunia liesneri Carnevali & I. Ramírez—Liesner 21988 (type)
Bifrenaria maguirei C. Schweinf.—Carnevali 2401; Dunsterville s.n.; Liesner 22176, 22108
Cleistes stricta C. Schweinf. Carnevali 2363, 2388, 2471; Liesner 22052, 22421, 22540
Dichaea hystricina Reichb. f.—Carnevali 2515; Liesner 22439, 22508
Elleanthus sp.—Carnevali 2525; Liesner 22431
Epidendrum dendrobioides Thunb.—Liesner 22054
Epidendrum elongatum Jacq.—Carnevali 2496
Epidendrum nocturnum Jacq.—Carnevali 2571; Liesner 22017, 22572
Epidendrum pachyphyton Garay Carnevali 2551
Epidendrum ramosum Jacq.—Carnevali 2568
Epistephium hernandii Garay –Carnevali 2480; Liesner 22172, 22483
Epistephium subrepens Hoehne—Carnevali 2459; Liesner 22096
Eriopsis biloba Lindley—Liesner 22049
Helonoma americana (C. Schweinf. & Garay) Garay—Liesner 22023
Jacquiniella globosa (Jacq.) Schltr.—Carnevali 2452; Liesner 22131
Lepanthes duidensis Ames & C. Schweinf.—Carnevali 2481
Maxillaria amazonica Schltr.—Carnevali 2482; Liesner 22163
Maxillaria aff. *arachnites* Reichb. f.—Liesner 22036
Maxillaria mapiriensis (Kranzl.) L. O. Williams—Carnevali 2422
Maxillaria meridensis Lindley –Liesner 21970, 22495
Octomeria sp. –Carnevali 2550; Liesner 22597, 22602
Octomeria cordilabia C. Schweinf.—Carnevali 2439, 2569; Liesner 21965, 22089
Octomeria erosilabia C. Schweinf.—Liesner 22600
Ornithidium aureum Poeppig ex Endl.—Carnevali 2423, 2504; Liesner 22445
Pleurothallis callifera C. Schweinf.—Carnevali 2533; Liesner 22462, 22538
Pleurothallis pluriracemosa Garay—Carnevali 2402, 2486; Liesner 22522
Prescottia stachyoides (Sw.) Lindley—Liesner 22460
Psilochilus dusenianus Kranzl. ex Garay & Dunsterv.—Carnevali 2410, 2495; Liesner 22537
Sobralia speciosa C. Schweinf. Carnevali 2366; Dunsterville s.n.; Liesner 21945
Sobralia yauaperyensis Barb. Rodr.—Carnevali 2420, 2474; Liesner 22152, 22467
Stelis tristyla Lindley—Carnevali 2526; Liesner 22692
Trichosalpinx foliata (Griseb.) Luer—Carnevali 2437, 2547, 2554; Liesner 22128
Trichosalpinx obliquipetalus (Ames & C. Schweinf.) Luer—Carnevali 2549
Vanilla wrightii Reichb. f.—Carnevali 2403; Liesner 22456

Quebrada camp:
Catasetum ochraceum Lindley, vel sp. aff.—Liesner 22349
Dichaea hystricina Reichb. f.—Liesner 22396
Epidendrum nocturnum Jacq. Liesner 22232
Epistephium subrepens Hoehne Liesner 22275
Maxillaria grobyoides Garay & Dunsterv.—Liesner 22342
Maxillaria nasuta Reichb. f.—Liesner 22289
Octomeria sp. Liesner 22282
Palmorchis sp. Liesner 22385
Sobralia liliastrum Lindley Liesner 22240

Granitic dome:
Epidendrum ramosum Jacq.—Wurdack 43570, 43571

Passifloraceae—Julian Steyermark (MO)

Summit:
Passiflora sclerophylla Harms—Liesner 22053, 22474, 22564, 22705

Piperaceae—Julian Steyermark (MO)

Summit:
Peperomia duidana Trel.—Liesner 22707. This collection from the summit at the Proa Camp has some

leaves as much as 4 × 4 cm and suborbicular and rounded at summit, but most of same collection number has smaller leaves with narrowed apex (obtuse) from a broadly ovate shape.
Peperomia hernandiifolia (M. Vahl) A. Dietr.—Liesner 22518, 22695
Peperomia tenella (Sw.) A. Dietr.—Liesner 22527, 22718
Piper lemaense Yuncker—Liesner 22580. Previously known from the eastern Venezuelan Guayana of Estado Bolívar.
Piper mosaicum Steyerm.—Liesner 21968 (type)
Piper poiteanum Kunth—Liesner 22425

Quebrada camp:
Piper alatabaccum Trel. & Yuncker—Liesner 22368. Previously known from the eastern Venezuelan Guayana.
Piper francovilleanum C. DC.—Liesner 22266
Piper cf. *pubivaginatum* Steyerm.—Liesner 22353
Piper cf. *jauaense* Steyerm.—Liesner 22214

Poaceae—Gerrit Davidse (MO)

Summit:
Ichnanthus ephemeroblepharis Black & Fróes ex Black & Pires—Liesner 22034, 22637
Ichnanthus panicoides Beauv.—Liesner 21918
Myriocladus grandifolius Swallen—Liesner 22040, 22005, 22675
Myriocladus neblinaensis Swallen—Liesner 22634
Myriocladus simplex Swallen—Liesner 22634A
Myriocladus virgatus Swallen—Liesner 22118, 22182, 22497, 22501
Panicum chnoodes Trin.—Liesner 22441
Panicum eligulatum N.E. Br.–Liesner 22107, 22642
Panicum tepuianum Davidse & Zuloaga—Liesner 22645

East escarpment:
Myriocladus aff. *grandifolius* Swallen—Huber 5942
Paspalum petilum Chase—Huber 5932

Quebrada camp:
Andropogon bicornis L.—Liesner 22235
Andropogon leucostachyus H.B.K.—Liesner 22237
Ichnanthus ephemeroblepharis Black & Fróes ex Black & Pires—Liesner 22183
Ichnanthus panicoides Beauv.—Liesner 22375
Olyra micrantha H.B.K.—Liesner 22267
Panicum froesii Swallen—Liesner 22209
Raddiella esenbeckii (Steudel) Calder & Söderstrom—Liesner 22239
Thrasya petrosa (Trin.) Chase—Liesner 22230

Granitic dome:
Olyra micrantha (H.B.K.) Swallen—Wurdack 43558
Olyra wurdackii Swallen—Wurdack 43540
Panicum nervosum (Lam.) Swallen—Wurdack 43541, 43542

Polygalaceae—John J. Wurdack (US)

East escarpment:
Securidaca retusa Benth. Huber 5894

Rapateaceae—Julian Steyermark (MO)

Summit:
Saxofridericia compressa Maguire—Liesner 22055
Stegolepis celiae Maguire—Liesner 22030, 22546
Stegolepis grandis Maguire—Liesner 21944
Stegolepis linearis Gleason—Liesner 22058. 7th collection. Known previously from Cerro Duida, Avispa.

East escarpment:
Cephalostemon cyperaceoides (Ducke) Maguire—Huber 5905
Monotrema xyridoides Gleason—Huber 5939
Saxofridericia spongiosa Maguire—Huber 5924
Schoenocephalium teretifolium Maguire—Huber 5923

Quebrada camp:
Rapatea aracamuniana Steyerm.—Liesner 22197 (type)
Rapatea spruceana Koern.—Liesner 22226

Granitic dome:
Saxofridericia spongiosa Maguire—Wurdack 43538

Rubiaceae—Julian Steyermark (MO)

Summit:
Cephalodendron aracamuniensis Steyerm.—Liesner 22064 (type), 22682 (paratype)
Gleasonia duidana Standley var. *duidana*—Liesner 22418
Veblinathamnus aracamunianus Steyerm.—Liesner 22153 (type)
Pagamea montana Gleason & Standley—Liesner 22629
Pagameopsis maguirei Steyerm. subsp. *neblinensis* Steyerm. var. *neblinensis*—Liesner 21951. Previously known from Cerro de la Neblina.
Perama dichotoma var. *scaposa* (Gleason & Standley) Steyerm.—Liesner 22624
Psychotria campylopoda Standley—Liesner 22173, 22665
Psychotria ceratantha Standley—Liesner 22531
Psychotria coussarioides Standley—Liesner 22667
Psychotria duricoria Standley & Steyerm. var. *duricoria*—Liesner 21993, 22644
Psychotria tapajozensis Standley—Liesner 21996, 22623
Psychotria tepuiensis (Standley) Steyerm.—Liesner 22532
Remijia reducta Steyerm.—Liesner 22045 (paratype), 22407 (type)

East escarpment:
Pagamea vel aff. *capitata* Benth. subsp. *caudata* (H. E. Huber) Steyerm.—Huber 5916
Pagamea coriacea Spruce ex. Benth.—Huber 5915
Retiniphyllum truncatum Muell. Arg. Huber 5899

Quebrada camp:
Chomelia tenuiflora Benth.—Liesner 22369
Coussarea liesneri Steyerm.—Liesner 22262 (type)
Faramea boomii Steyerm.—Liesner 22350. Previously known from Cerro de la Neblina
Ferdinandusa neblinensis Steyerm. Liesner 22338. Previously known from Cerro de la Neblina.
Pagamea coriacea Spruce ex Benth. var. *coriacea*—Liesner 22352
Palicourea nitidella (Muell. Arg.) Standley—Liesner 22329
Perama dichotoma Poeppig & Endl. var. *dichotoma*—Liesner 22205, 22231
Psychotria barbiflora Muell. Arg.—Liesner 22383
Psychotria deflexa DC. subsp. *venulosa* (Muell. Arg.) Steyerm.—Liesner 22354
Psychotria iodotricha Muell. Arg. subsp. *iodotricha*—Liesner 22248, 22366

Psychotria medusula Muell. Arg.—Liesner 22362
Psychotria cf. *paupertina* Standley & Steyerm. Liesner 22340
Psychotria podocephala (Muell. Arg.) Standley Liesner 22268, 22373
Psychotria spadicea (Pittier) Standley & Steyerm. Liesner 22208
Psychotria turbinella var. *sororiella* (Muell. Arg.) Steyerm.—Liesner 22257, 22370
Remijia roraimae (Benth.) Schumann var. *adpressa* Steyerm.—Liesner 22251, 22291, 22335
Retiniphyllum truncatum Muell. Arg.—Liesner 22229
Rudgea stipulacea (DC.) Steyerm. —Liesner 22244

Granitic dome:
Isertia rosea Spruce ex Schumann—Wurdack 43553
Retiniphyllum laxiflorum (Benth.) N.E. Br. var. *laxiflorum*—Wurdack 43551

Rutaceae—Julian Steyermark (MO)

Summit:
Spathelia neblinaensis R. Cowan & Briz. Liesner 22554. Known previously only from Neblina.

Sapindaceae

Summit:
Toulicia sp.—Liesner 22477, 22683

Quebrada camp:
Not determined to genus—Liesner 22334

Sapotaceae—Terence D. Pennington (K)

Summit:
Micropholis suborbicularis Aubrév.—Liesner 21939, 22179, 22413

East escarpment:
Pradosia schomburgkiana (A.DC.) Cronq.—Huber 5927

Quebrada camp:
Pradosia schomburgkiana (A.DC.) Cronq. subsp. *schomburgkiana*—Liesner 22218

Sarraceniaceae—Julian Steyermark (MO)

Summit:
Heliamphora tatei Gleason var. *neblinae* (Maguire) Steyerm. f. *parva* (Maguire) Steyerm.—Liesner 22119, 22643, 22669

Simaroubaceae

Quebrada camp:
Picramnia sp.—Liesner 22384

Smilacaceae

Summit:
Smilax sp.—Liesner 22022, 22560

Quebrada camp:
Smilax sp.—Liesner 22250, 22287

Solanaceae

Summit:
Cestrum sp.—Liesner 22505

Styracaceae—Reinaldo Monteiro (HRCB)

Summit:
Styrax sp.—Liesner 22681
Styrax longipedicellatus Steyerm. —Liesner 22151, 22639

Theaceae—Brian Boom (NY), *Ternstroemia*; Anna Weitzman (US), *Frezierea*, Julian Steyermark (MO), *Bonnetia*, *Neotatea*

Summit:
Archytaea multiflora Benth. Liesner 22123
Bonnetia liesneri Steyerm.—Liesner 22105 (type)
Bonnetia tristyla Gleason subsp. *nervosa* Steyerm.—Liesner 21952, 22029
Freziera carinata Weitzman—Liesner 22154
Neotatea longifolia (Gleason) Maguire —Liesner 22110
Ternstroemia distyla Kobuski—Liesner 21957, 22044, 22157, 22165, 22450, 22481
Ternstroemia maguirei B. Boom—Liesner 21985, 22117, 22158, 22506 (all paratypes)
Ternstroemia pungens Gleason—Liesner 22618

East escarpment:
Archytaea angustifolia Maguire—Huber 5943

Quebrada camp:
Ternstroemia guanchezii B. Boom —Liesner 22236 (paratype)

Granitic dome:
Bonnetia paniculata Spruce —Wurdack 43548

Verbenaceae—Julian Steyermark (MO)

Summit:
Aegiphila roraimensis Moldenke—Liesner 21958, 22159

Quebrada camp:
Not determined to genus—Liesner 22265

Xyridaceae—Robert Kral (VDB)

Summit:
Abolboda grandis Griseb. var. *grandis*—Liesner 21955. This material is rather large for the variety, with forms becoming larger at higher elevations and grading into var. *guayanensis* in the highlands of the state of Bolívar and the Guianas, toward var. *rigida* in Territorio Federal Amazonas. Var. *grandis* is mostly in medium- to low-elevation savannas from northern Brazil north into the Guianas, westward through Venezuelan Guayana into southeastern Colombia.
Abolboda scabrida Kral—Liesner 22071 (paratype), 22598 (type)
Xyris aracamunae Kral—Liesner 22100 (paratype), 22452 (type)
Xyris involucrata Nees Liesner 21943, 22701
Xyris liesneri Kral Liesner 22086 (type), 22454 (paratype)
Xyris witsenioides Oliver Liesner 22025

East escarpment:
Abolboda grandis Griseb. var. *grandis* Huber 5912

Quebrada camp:
Abolboda grandis Griseb.—Liesner 22194
Xyris esmeraldae Steyerm. —Liesner 22339
Xyris fallax Malme—Liesner 22221
Xyris prolificans Kral—Liesner 22200 (type)
Xyris spruceana Malme Liesner 22219. Locally abundant in mostly low-elevation white sand savannas, northwestern Amazonian Brazil, contiguous Territorio Federal Amazonas of Venezuela and southwestern Colombia. This example from 600 m elevation is from one of the higher sites known, probably

migrating upward along edges of gallery forest in the lajas.

Granitic dome:
Abolboda grandis Griseb. var. *guayanensis* Maguire—Wurdack 43539
Aratitiyopea lopezii (Lyman B. Smith) Steyerm. & P. Berry subsp. *lopezii*—Wurdack 43564

The first set of the Wurdack & Adderley collections is deposited at NY, with a second set at VEN. The first set of the Huber & Medina collections is deposited at VEN with duplicates at NY. The collections of Liesner have the first set at VEN, the second at MO, and the third at the institutions of the specialists that provided identifications. The Carnevali, Dunsterville, and Brewer Carias collections are deposited at VEN.

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COMPOSITAE OF THE GUAYANA HIGHLAND—II. NOVELTIES IN *GONGYLOLEPIS* AND *STENOPADUS* (MUTISIEAE)[1]

John F. Pruski[2]

ABSTRACT

Described from the Guayana Highland are: *Gongylolepis oblanceolata* from Serra Aracá, Brazil, and from Sierra de Unturán and Cerro de la Neblina, Venezuela; *Stenopadus aracaënsis* from Serra Aracá, Brazil; and *Stenopadus megacephalus* from Mount Ayanganna, Guyana. The relationships of each new taxon are discussed and a key to species of both genera is given. *Stomatochaeta colveei* is transferred to *Stenopadus* and the combination *Stenopadus colveei* is proposed. Additionally, five species from the Guayana Highland are newly documented for the flora of Brazil.

The shrubby, homogamous, generally large-headed Mutisieae are a striking element of the Guayana Highland flora and are typically found on tepui summits. Among Guayanan taxa of its size—57 of the 61 currently recognized species (93%) are endemic to Guayana—the Mutisieae are unparalleled in their endemism level (Maguire, 1956; Pruski, 1989). The woody, hermaphroditic members of the tribe Mutisieae from Guayana fall into two main generic groups. The first group (subtribe Mutisiinae sensu Cabrera, 1977) consists of six genera having homogamous capitula composed of zygomorphic flowers and includes *Gongylolepis* Schomb., with one species described herein. The second group (subtribe Gochnatiinae sensu Cabrera, 1977) contains four genera, which have only actinomorphic flowers within their capitula. The second group was previously represented in Guayana only by *Quelchia* N. E. Brown and *Stenopadus* S. F. Blake, but has been redefined to admit two new genera, equivalent in part to species formerly placed in *Stenopadus* s.l. The newer genera are *Stomatochaeta* (S. F. Blake) Maguire & Wurdack (1957), which was raised from subgeneric level within *Stenopadus*, and *Chimantaea* Maguire et al. (1957), which was described as new. All subsequent authors (Aristeguieta, 1964, 1968; Steyermark, 1980, 1984; Pruski, 1989) have recognized *Stomatochaeta* and *Chimantaea*, the generic status of which is justified by floral morphology.

In this paper new species of *Gongylolepis* and *Stenopadus* are described preliminary to my treatment of the Compositae for the *Flora of the Venezuelan Guayana* by Julian Steyermark and collaborators, where the localities and complete synonymies of all our Mutisieae will be given. Also, fertile material of *Stomatochaeta colveei*, recently made available to me for study, shows that this species has the flower color and morphology typical of *Stenopadus*, to which it is herein transferred.

GONGYLOLEPIS

Gongylolepis is a genus of 15 species with bilabiate flowers and glabrous, reticulate, lanceolate to obovate leaves. Fourteen of these occur in the Guayana Highland and 11 are endemic to the Venezuelan Guayana. The nearest generic relative of *Gongylolepis* is the monotypic *Eurydochus* Maguire & Wurdack. The two genera have similar leaves and capitulescences, but *Eurydochus* differs

[1] I thank Rupert Barneby for help with the Latin diagnoses and for many helpful comments; Victor Badillo, Harold Robinson, and an anonymous reviewer for their suggestions; Bruno Manara for drawing Figure 2; Hans Beck, Otto Huber, and Iain Prance for permission to publish their photographs; and Don Black, María Lebrón-Luteyn, Marcia Stevens, and Muriel Weinerman for helping me prepare the figures. My herbarium studies in Venezuela have been financially supported by the Missouri Botanical Garden, *Flora of the Venezuelan Guayana* project.

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FIGURE 1. *Gongylolepis oblanceolata*. —A. Note the nearly glabrous, minutely bracteolate peduncle and the occurrence of two capitula at the stem apex (*Prance et al. 29014*). Photo by G. T. Prance.—B. Note the larger, solitary capitulum, zygomorphic flowers, and the pubescent peduncle (*Henderson et al.* 961). Photo by H. Beck.

from *Gongylolepis* by deciduous (vs. persistent) pappus setae, by pubescent (vs. glabrous) phyllaries, and by pubescent (vs. glabrous) achenes. Less closely related to *Gongylolepis* are *Glossarion* Maguire & Wurdack and *Duidaea* S. F. Blake, which differ, respectively, in abaxially tomentose and one-nerved leaves. Described and keyed below is a new, predominantly monocephalous *Gongylolepis*. It is most closely related to the other pedunculate, monocephalous species of the genus, these mostly confined to T. F. Amazonas, Venezuela.

Gongylolepis oblanceolata Pruski, sp. nov. TYPE: Brazil. Amazonas: Platô da Serra Aracá, 200 km N de Barcelos, Mar. 1984, *M. G. Silva et al.* [co-collector names not given on type labels] *7169* (holotype, INPA; isotypes, K, MO, NY, US). Figures 1, 4.

Gongylolepidi bracteatae et *G. pedunculatae* affinis, quibuscum capitulis pedunculatis foliisque aut petiolatis aut basin versus angustatis congruit, sed a priori pedunculis ebracteatis et a secunda phyllariis magis numerosis et minoribus differt.

Branched shrubs 1–3 m tall; *stems* terete, striate, leafy and often lanate (especially in upper leaf axis) distally, glabrous and leafless proximally, internodes to ca. 1 cm long, thereby much shorter than the leaves. *Leaves* simple, alternate, often apically clustered, subsessile or petiolate; *blade* coriaceous, oblanceolate, ca. 5–21 × 1.5–4.5 cm, narrowly cuneate or attenuate basally, often narrowed into a subpetiolar base, apically acute, obtuse or rounded, margins entire, these not thickened, rarely revolute, venation pinnate, reticulate, upper blade surface dark green, often puberulent when young, especially so along midrib, glabrous with age, lower blade surface light green, often pubescent when young, glabrous with age; *petiole* often represented only by a petioliform leaf base to 5 mm long, clasping and stout. *Capitula* generally solitary, terminal, pedunculate, homogamous, with ca. 14–31 flowers, these perfect and fertile; *peduncle* often bracteolate, nearly glabrous to densely pubescent, ca. 3–8 cm long; *involucre* narrowly hemispheric, ca. 2.5–3.8 × 1.8–2.5(3) cm, 5–6-seriate; *phyllaries* ca. 25–30, imbricate, graduated, erect or

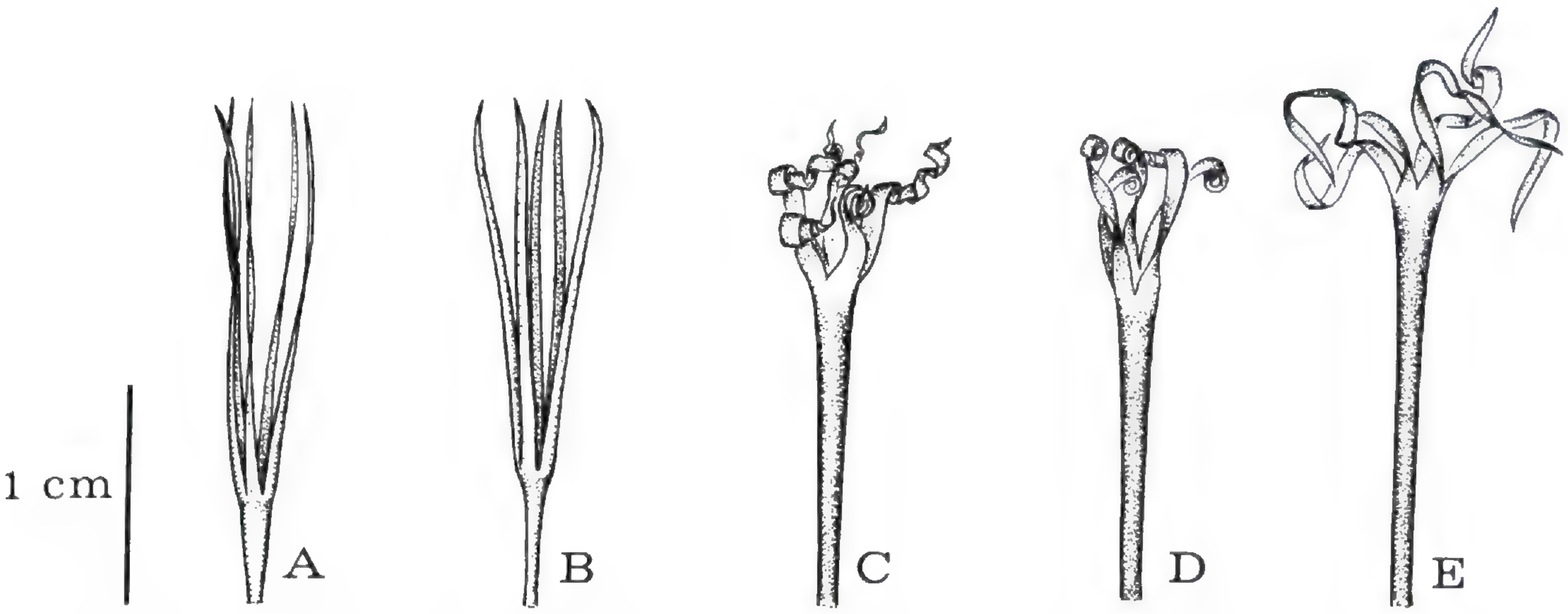

FIGURE 2. Corollas of representative species of *Stomatochaeta* and *Stenopadus*.—A. *Stomatochaeta condensata* (Baker) Maguire & Wurd. (Drawn from *Pruski & Steyermark 1454*, NY.)—B. *Stomatochaeta acuminata* Pruski. (Drawn from the holotype, *Huber 11374*, VEN.)—C. *Stenopadus chimantensis* Maguire, Steyerm. & Wurd. (Drawn from *Pruski & Huber 3616*, NY.)—D. *Stenopadus aracaënsis* Pruski. (Drawn from the holotype, *Prance et al. 29184*, INPA.)—E. *Stenopadus colveei* (Steyerm.) Pruski. (Drawn from *Huber 12405*, VEN.) Note in *Stomatochaeta* (A, B) the short corolla tube and the long, stiffly erect lobes. The corollas of *Stomatochaeta* are yellowish. Note in *Stenopadus* (C–E) the long corolla tube and the coiled or flexuous lobes as long as or shorter than the tube. The corollas of *Stenopadus* are magenta.

sometimes slightly spreading, thickly coriaceous, glabrous, entire, often somewhat purple; outer phyllaries triangular-ovate, ca. 2.5–6 × 2.5–5.5 mm, apex broadly acute to rounded, basally rounded or cordate, sometimes decurrent onto peduncle; inner phyllaries elliptic-lanceolate to lanceolate, to ca. 2.5 cm × 3.5 mm, apex commonly rounded; *receptacle* broadly dome-shaped, naked, aveolate, these pits 5- or 6-sided. *Corollas* bilabiate, 15–21(24) mm long, glabrous, reddish, or tube sometimes pale yellow; *tube* 9–14 mm long, narrow or with upper portion broadened near sinuses of the 2 lips, obscurely ca. 10-nerved; *lips* coiled; the outer, larger lip apically 3-dentate, to ca. 10–12 mm long when uncoiled, commonly coiled at apex or for more than half its length; the inner, lower lip 2-cleft, generally strongly coiled, thereby shorter than the outer lip; *anthers* exserted, linear, reddish, less commonly pale yellow, 10–12 mm long, apically acuminate, prominently sagittate basally; tails white, squamose, linear, 5–7 mm long, thereby more than half as long as the anthers, tails of adjacent anthers commonly completely connate or occasionally free basally; *filaments* yellowish or reddish, inserted well below bases of lobes; *styles* reddish above, yellowish below, branches spreading, ca. 1 mm long, apically obtuse. *Achenes* linear or slightly fusiform, ca. 10-costate, 10–11 mm long, brown, glabrous; *pappus setae* numerous, persistent, linear, brown, ca. 13–17 mm long, thereby longer than the achenes.

Distribution. Known from the plateau of Serra Aracá, Brazil, ridges of Sierra Unturán, Venezuela, and low elevation slopes and canyon walls of Cerro de la Neblina, Venezuela. This species has been collected from (400) 700–1,250 m and is known to flower and fruit from February to July.

Paratypes. BRAZIL. AMAZONAS: Município de Barcelos: platô da Serra Aracá, parte SE da Serra Norte, 0°51′N, 63°22′W, 1,150–1,250 m, 14 Feb. 1984, *I. L. Amaral 1557* (F, INPA, NY, US); plateau of northern massif of Serra Aracá, savanna, S side of north mountain, 0°51–57′N, 63°21–22′W, 1,200 m, 12 Feb. 1984, *G. T. Prance, I. L. Amaral, J. J. Pipoly, A. S. Tavares, M. G. Silva, C. D. A. Mota & A. Cress 29014* (INPA, K, NY, UC); platô da Serra Aracá, parte SE da Serra Norte, beira do rio mais próximo a pista, 0°51′N, 63°22′W, 1,150–1,250 m, 13 Feb. 1984, *A. S. Tavares, L. A. Cisneros & M. G. Silva 22* (INPA, NY). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, Neblina massif, Cañón Grande, along the Río Mawarinuma between the mouth of the canyon and the first major fork of the river, ca. 7 airline km ENE of Puerto Chimo, 0°50-51′N, 66°02 06′W, 400–700 m, 9–14 July 1984, *G. Davidse & J. Miller 27363* (MY); Dept. Río Negro, Neblina massif, S-facing slope at the mouth of Cañón Grande, N of Puerto Chimo, 0°50′N, 66°06′W, 500–700 m, 15 July 1984, *G. Davidse & J. Miller 27399* (VEN); Sierra de Unturán, ridge opposite camp, 01°33′N, 65°12′W, 1,150 m, 4 Feb. 1989, *A. Henderson, H. Beck, H. Scott & L. Leigh 961* (NY, VEN); Cerro de la Neblina, slope N of Río Mawarinuma, above Puerto Chimo, 0°50′N, 66°05′W, 500–700 m, 25 Apr. 1984, *B. Stein & A. Gentry 1686* (VEN).

Gongylolepis oblanceolata, most readily recognized by its minutely bracteolate peduncles, is

FIGURE 3. *Stenopadus colveei* showing a few-flowered, narrowly cylindric capitulum (*Huber 12405*). Photo by O. Huber.

closely related to *G. bracteata* and *G. pedunculata*. These three species are linked by having pedunculate heads and large leaves that are either petiolate or narrowed into a petioliform base. *Gongylolepis oblanceolata* differs from *G. bracteata* in apically nonbracteate (vs. bracteate) peduncles and from *G. pedunculata* in smaller, more numerous (vs. larger and fewer) involucral bracts. Other seemingly less closely related monocephalous species of *Gongylolepis* generally have sessile heads and smaller, sessile leaves.

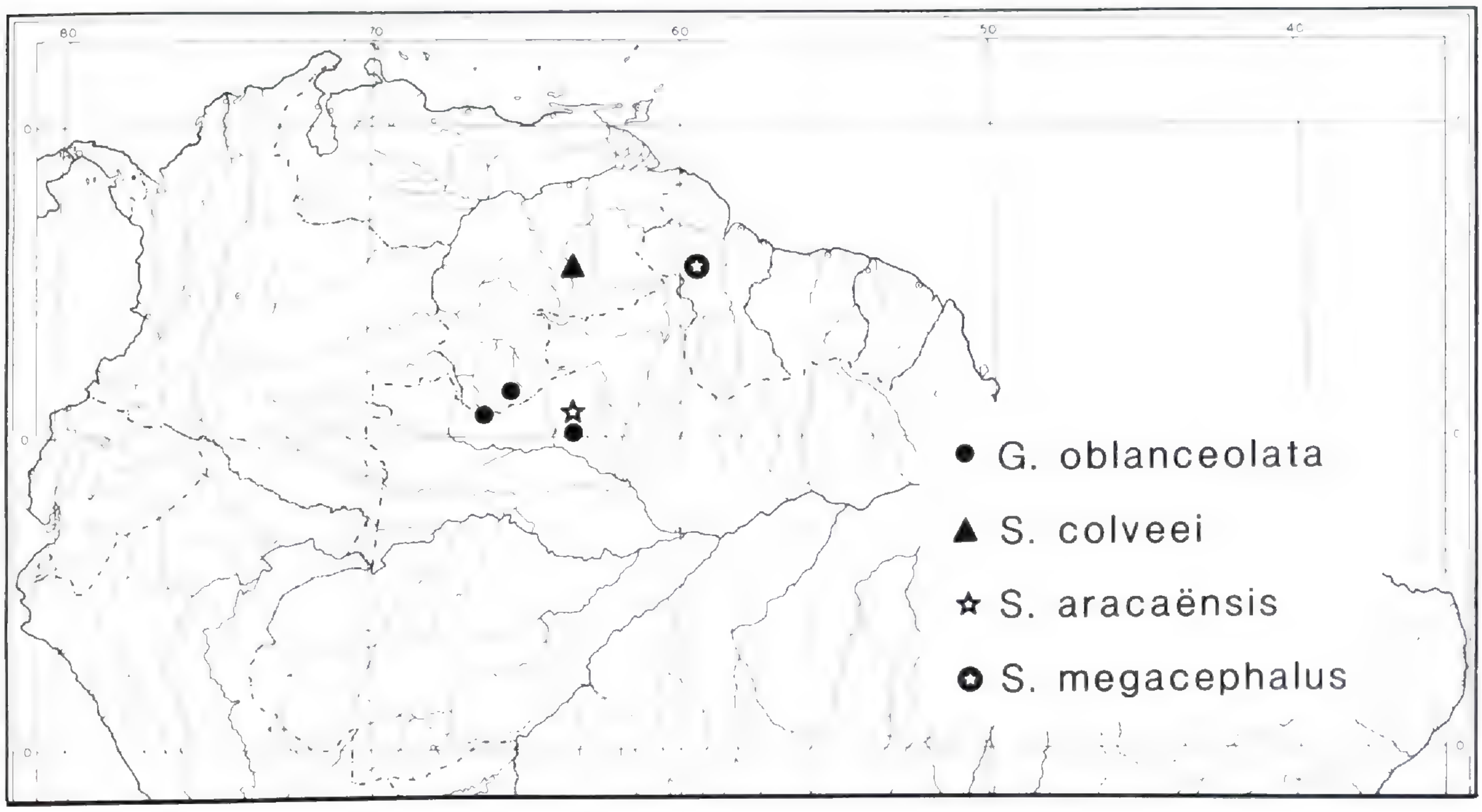

FIGURE 4. Distributions of *Gongylolepis oblanceolata*, *Stenopadus colveei*, *S. aracaënsis*, and *S. megacephalus*.

KEY TO THE SPECIES OF *GONGYLOLEPIS*

1a. Capitulescences monocephalous, rarely with two capitula per stem.
2a. Capitula stalked on a naked or leafy peduncle ca. 3 10 cm long.
3a. Leaves with subparallel venation, 8.5–15 × 3.3–6 cm, sessile; capitula ca. 60-flowered, ca. 5.5 cm tall ..... *G. jauaensis* (Aristeg., Maguire & Steyerm.) V. Badillo
3b. Leaves pinnately veined, 5–21(50) × (1.5)4–8.5 cm, sessile or petiolate; capitula 14–35-flowered.
4a. Capitula taller than 5 cm, outer and intermediate phyllaries ca. 1 cm or more wide; peduncles naked or leafy (bracteate); leaves (10)12–20(50) × 4–8.5 cm, basally cuneate, essentially sessile, wider than 5 mm at base.
5a. Peduncles leafy, capitula subtended by 1–3 large, leafy bracts; stem apex lightly pubescent ..... *G. bracteata* Maguire
5b. Peduncles naked, capitula not subtended by bracts; stem apex often densely pubescent to floccose ..... *G. pedunculata* Maguire
4b. Capitula shorter than 4.5 cm, phyllaries narrower than 8 mm; peduncles minutely bracteolate; leaves 5–21 × 1.5–4.5 cm, basally attenuate, subsessile or petiolate, narrower than 4 mm at base ..... *G. oblanceolata* Pruski
2b. Capitula sessile or on peduncles shorter than 2 cm, capitula ca. 8–15-flowered, shorter than 4 cm, outer and intermediate phyllaries narrower than 8 mm; leaves 3–10 cm long, sessile or petiolate.
6a. Subshrubs to 0.5 m tall, leaves often clustered at apex of naked spreading stems; leaves oblanceolate, sessile, ca. 3–7 × 0.7 2 cm wide and at least 3 times as long as wide ..... *G. fruticosa* Maguire, Steyerm. & Wurd.
6b. Shrubs or trees commonly 1.5 3(5) m tall, leaves not apically clustered; leaves elliptic to obovate, sessile to petiolate, ca. 2.5–10 × 1.2–5 cm, less than 2½ times long as wide.
7a. Leaves and branches glabrous; leaves obovate, sessile, to 10 × 4 cm ..... *G. glaberrima* S. F. Blake
7b. Young leaves and young branches pilose; leaves oblanceolate to broadly elliptic, subsessile to petiolate, less than 7 × 3 cm.
8a. Leaves with petioles ca. 5 mm long, secondary veins obviously pinnate; phyllaries obtuse to rounded at apex, wider than 5 mm ..... *G. paruana* Maguire
8b. Leaves subsessile or with petioles shorter than 3 mm, secondary veins subpalmate; phyllaries acute to acuminate, narrower than 5 mm ..... *G. erioclada* S. F. Blake
1b. Capitulescences branched, of few to many capitula, each of these pedunculate.
9a. Stems pubescent when young.
10a. Capitulescence leafy.
11a. Main stem leaves commonly (12)15 20 cm long; corollas glabrous ..... *G. yapacana* Maguire
11b. Leaves shorter than 13 cm; corollas hairy ..... *G. benthamiana* Schomb.

10b. Capitulescence naked, not leafy.
12a. Capitulescence umbelliform, peduncles 3–6 cm long; leaves thickly coriaceous, narrower than 3.5 cm, margins often thickened and revolute; stem apex often densely pubescent to floccose ..... *G. huachamacari* Maguire
12b. Capitulescence corymbiform, peduncles 1 3 cm long; leaves thinly coriaceous, 3–6 cm wide, margins slightly thickened, not revolute; stem apex generally lightly pubescent ..... *G. terramarae* Steyerm.
9b. Stems glabrous.
13a. Capitulescence naked, not leafy; leaves commonly petiolate, often prominently so.
14a. Leaves of flowering stems subsessile or with petioles to ca. 1 cm long; pappus straw-colored.
15a. Leaves subsessile; capitulescence corymbiform; plants of the Andes of Colombia and Venezuela ..... *G. colombiana* (Cuatrec.) Cuatrec.
15b. Leaves with petioles to ca. 1 cm long; capitulescence umbelliform or corymbiform; plants of Guayana, occurring 1,000–2,700 m ..... (return to couplets 12)
14b. Leaves of flowering stems with petioles 1–3 cm long; pappus straw-colored to rose-colored; plants generally occurring below 150(–750) m ..... *G. martiana* (Baker) Steyerm. & Cuatrec.
13b. Capitulescence leafy or sometimes naked when in fruit; leaves sessile or shortly petiolate.
16a. Capitulescence umbelliform ..... *G. huachamacari* Maguire
16b. Capitulescence corymbiform.
17a. Corollas hairy, tube broadened; leaves 7.5–16.5 × 2–5.5 cm, upper surface strongly reticulate; heads rounded at the base, involucre ca. 3 cm tall, ca. 6-seriate; achenes 6–13 mm long, mostly cylindric ..... *G. benthamiana* Schomb.
17b. Corollas glabrous, tube narrow; leaves 12–27 × (2.5) 5–8(9) cm, upper surface moderately reticulate; heads narrowed at the base, involucre ca. 3–3.5 cm tall, ca. 6 8-seriate; achenes 8–15 mm long, frequently fusiform ..... *G. paniculata* Maguire

Stenopadus

Described and keyed below are two new species of *Stenopadus* which, following the transfer of *Stomatochaeta colveei* to *Stenopadus*, raises to 14 the number of species recognized in this genus. All are endemic to the Guayana Highland and eight species are restricted to Venezuelan Guayana. *Stenopadus* is closely related to *Stomatochaeta*, which was originally described as a subgenus of *Stenopadus*. The yellowish corollas of *Stomatochaeta* (Fig. 2A, B) with stiffly erect lobes much longer than the tube distinguish it from *Stenopadus* (Fig. 2C–E), which has magenta corollas with (at maturity) coiled or flexuous lobes about as long as or shorter than the tube. By these features generic status for the two taxa is justified (Maguire & Wurdack, 1957; Pruski, 1989).

Stomatochaeta colveei resembles *Stenopadus* in a magenta corolla with tube longer than the lobes. It was originally (incorrectly) described and illustrated as having corolla lobes stiffly erect and was thus placed by Steyermark (1980) in *Stomatochaeta*. Pruski (1989) noted it as possibly intermediate between these two genera, but he retained it within *Stomatochaeta* until flowering material could be observed. Specimens examined by me during a recent visit to the Instituto Botánico in Caracas show that the corolla lobes of *Stomatochaeta colveei* are flexuous and shorter than the tube (Fig. 2E). Thus, this species fits well within *Stenopadus* as envisioned here, and the formal transfer of this species to *Stenopadus* is proposed below.

Stenopadus and *Stomatochaeta* now stand clearly apart from each other on the basis of flower morphology. Furthermore, *Stenopadus*, a genus of stately plants up to 25 m tall, is typically more robust than *Stomatochaeta*, plants of which are less than five m tall. Other genera from Guayana commonly with only actinomorphic flowers, and slightly less closely related to *Stenopadus* are *Chimantaea*, which has abaxially tomentose leaves and corolla lobes pilose when young, and *Quelchia*, which has small, uniflorous capitula.

Stenopadus colveei (Steyerm.) Pruski, comb. nov. *Stomatochaeta colveei* Steyerm., Brittonia 32: 21. 1980. TYPE: Venezuela. Bolívar: cumbre Cerro Guaiquinima, sector SE, cerca del borde, 5°40′N, 63°26′W, 1,250 m, 26 May 1978, *Steyermark, Berry, Dunsterville & Dunsterville 117407* (holotype, VEN). Figures 2E, 3, 4.

This species is a shrub 1.5–2.5 m tall characterized by basally attenuate, oblanceolate leaves and by narrowly cylindric, 5–6-flowered capitula. It is endemic to Cerro Guaiquinima, where it occurs in rocky or sparsely covered shrubby chaparral from 900–1,350 m and flowers in December and May.

Additional specimens examined. Venezuela. Bolívar: meseta del Guaiquinima, sector SE de la cumbre, 5°51′N, 63°25′W, 1,350 m, 26 Sep. 1985 (sterile), *Huber & Medina 10925* (VEN); cumbre de la meseta del Guaiquinima, sector S, a lo largo del Río Carapo, aprox. 8 km al N del Salto Carapo, 5°51′N, 63°33′W, 900 m, 6 Dec. 1987, *Huber 12405* (AAU n.v., HBG n.v., MY, NY, TFAV n.v., US n.v., VEN).

NY NEGATIVE
No. 12531

FIGURE 5. Holotype of *Stenopadus aracaënsis* (*Prance et al. 29184*, INPA).

Stenopadus aracaënsis Pruski, sp. nov. TYPE: Brazil. Amazonas: plateau of northern massif of Serra Aracá, N part of N slope, 0°51–57′N, 63°21–22′W, 1,400 m, 20 Feb. 1984, *G. T. Prance, I. L. Amaral et al. 29184* (holotype, INPA; isotypes, K, MO, NY, US). Figures 2D, 4, 5.

Stenopado kunhardtii affinis et cum illa corollae lobulis tubo multo brevioribus congruens, sed capitulis haud stipitatis ad maximum 25 (nec 35–70) flosculosis diversa.

Tress 10 m tall, 30 cm diam.; *stems* terete, striate, glabrous, leafy distally, leafless proximally, internodes to ca. 1.5 cm long, thereby shorter than the leaves. *Leaves* simple, alternate, often apically

FIGURE 6. Holotype of *Stenopadus megacephalus* (*Tillett et al. 45100*, NY).

clustered, petiolate; *blade* rigid-coriaceous, glabrous, broadly oblanceolate or obovate, ca. (4)6–13.5 × (1.5)2.5–4.7 cm, narrowly cuneate or attenuate basally, apically rounded, margins entire, thickened, somewhat revolute, venation pinnate, reticulate or third-order veins often obscure, upper blade surface dark green, lower blade surface pale green; *petiole* ca. 0.9–1.5 cm long, thin and nonclasping. *Capitula* solitary, terminal, sessile and thus nonstipitate, homogamous, with 21–25 flowers, these perfect and fertile; *involucre* cylindric, ca. 4.2–4.8 × 2–2.5 cm, 7–8-seriate; *phyllaries*

ca. 40–45, imbricate, graduated, tightly appressed and rigidly erect, coriaceous, glabrous, entire; outer phyllaries slightly carinulate, triangular-ovate, ca. 4–8 mm long and broad, apex broadly acute or obtuse, not decurrent onto stem; inner phyllaries elliptic-lanceolate to lanceolate, ca. 3 cm × 3.5–5 mm, apex commonly rounded; *receptacle* weakly paleaceous, paleae linear, ca. 2.5 cm long, cream-colored. *Corollas* actinomorphic, tubular, strongly 5-cleft, ca. 19–22 mm long, magenta, glabrous; *tube* 14–16.5 mm long, narrow and much longer than the lobes, weakly ca. 15-nerved; *lobes* either flexuous and only apically coiled or strongly coiled nearly to base, ca. 5–6 mm long, generally 3(–5)-nerved and with an obvious central nerve; *anthers* exserted, linear, cream-colored but prominently purple-spotted, 8.5–9 mm long, apically acuminate, basally sagittate; tails white, smooth, linear, 2.5–3 mm long, tails of adjacent anthers connate; *filaments* yellowish or reddish, inserted within the tube; *styles* obscurely branched, magenta, glabrous but asperulous apically, to 4 cm long. *Achenes* (immature) obconic, ca. 10-costate, ca. 6 mm long, olivaceous, glabrous; *pappus setae* numerous, linear, cream-colored, ca. 13–19 mm long, thereby longer than the achenes.

Distribution. Known only from the type collection made on the plateau of Serra Aracá, Brazil at 1,400 m. Flowers in February.

Stenopadus aracaënsis, collected on a recent Projeto Flora Amazônica expedition, is most closely related to *S. kunhardtii*. Both species have three-nerved corolla lobes that are much shorter than the corolla tube and thereby closely resemble one another. However, *S. aracaënsis* clearly differs from *S. kunhardtii* by nonstipitate (vs. stipitate) heads, smaller basally attenuate (vs. larger basally cuneate) leaves, and capitula that contain 25 or fewer (vs. 35–70) flowers. Also closely related is *S. huachamacari*, but this differs from the two former species by two-nerved (vs. three-nerved) corolla lobes that are about as long as (vs. much shorter than) the corolla tube.

Stenopadus megacephalus Pruski, sp. nov. TYPE: Guyana: upper Mazaruni River basin, Mount Ayanganna, shoulder of E flank, above Thompson Camp, 1,418–1,585 m, 11 Aug. 1960, *S. S. Tillett, C. L. Tillett & R. Boyan 45100* (holotype, NY). Figures 4, 6.

Affinis *S. sericeo*, etiam in monte Ayanganna obvio, sed foliis subsessilibus et glaberrimis (nec petiolatis et infra sericeis) abstans.

Shrubs 2 m tall; *stems* terete, nonstriate, thick, glabrous, leafy distally, leafless proximally, internodes to ca. 1.5 cm long, thereby shorter than the leaves. *Leaves* simple, alternate, clustered toward end of branches, subsessile; *blade* rigidly and thickly coriaceous, glabrous, oblanceolate or obovate, 8.5–19 × 3–8.5 cm, cuneate basally and mostly narrowed into a petiolariform base, apically rounded, margins entire, thickened, slightly revolute, venation pinnate, obscurely reticulate with third-order veins often immersed, upper blade surface dark green, lower blade surface lighter green; *petioliform base* stout, ca. 5 mm long and broad, not clasping the stem. *Capitula* (well past maturity with flower parts mostly fragmentary) solitary, terminal, sessile or very shortly pedunculate, homogamous, with many (ca. 40 or more) flowers, these perfect and fertile; *involucre* hemispheric, ca. 5 × 4.5 cm, ca. 5-seriate; *phyllaries* ca. 40, imbricate, graduated, erect, coriaceous, glabrous, entire; outer phyllaries broadly triangular-ovate, ca. 1.4–1.8 × 1.3–1.5 cm, apex broadly acute or obtuse; inner phyllaries lanceolate, ca. 4.5 cm × 5–7 mm, apex acuminate to rounded; *receptacle* seemingly naked. *Corollas* actinomorphic, tubular, strongly 5-cleft, ca. 13 mm long, magenta, glabrous or weakly puberulent internally near sinuses of lobes; *tube* ca. 8–10 mm long, broadened near sinuses of lobes, weakly ca. 10-nerved; *lobes* sometimes flexuous but more commonly strongly coiled nearly to base, ca. 2–6 mm long, seemingly 2-nerved; *anthers* partly exserted, linear, cream-colored, ca. 13 mm long, apically acuminate, basally sagittate; tails cream-colored, smooth, linear, ca. 3–4 mm long, those of adjacent anthers apparently appressed but not connate; *filaments* mostly disintegrated, seemingly inserted within the corolla tube; *styles* not seen. *Achenes* broadly obconic, with ca. 4 or 5 main angles, ca. 5.5 × 2.5 mm, light brown, glabrous; *pappus setae* numerous, linear, light brown, tips mostly broken off, but intact setae to 15 mm long, thereby much longer than the achenes.

Distribution. Known only from the holotype, collected on Mount Ayanganna, Guyana, where the new species is frequent in dense scrubland between 1,418 and 1,585 m. Known to be in fruit in August.

Stenopadus megacephalus is closely related to *S. sericeus*, the only other species of *Stenopadus* reported from Mount Ayanganna. However, the leaves of *S. sericeus* are clearly petiolate and are sericeous below, whereas those of *S. megacephalus* are subsessile and completely glabrous. Also closely

related are *S. chimantensis*, which has wider leaves and smaller heads, and the distantly disjunct *S. campestris*, which has flexuous three-nerved (vs. strongly coiled two-nerved) corolla lobes.

KEY TO THE SPECIES OF *STENOPADUS*

1a. Anther filaments attached to corolla tube 1–4(10) mm below base of lobes.
  2a. Leaves subsessile or brevipetiolate with petioles shorter than 7 mm.
    3a. Leaves shorter than 11 cm; capitula with up to 25 florets; involucres shorter than 3 cm; corolla lobes 3-nerved ..... *S. campestris* Maguire & Wurd.
    3b. Leaves to 19 cm long; capitula with more than 30 florets; involucres 4–5 cm tall; corolla lobes 2-nerved ..... *S. megacephalus* Pruski
  2b. Leaves with petioles 8–20(35) mm long.
    4a. Outer phyllaries acuminate, inner ones attenuate; capitula often 2–4 per branch ..... *S. obconicus* Maguire & Wurd.
    4b. Outer phyllaries obtuse to acute, inner ones usually acute or obtuse, never attenuate; capitula solitary.
      5a. Corolla lobes 2-nerved, about as long as the tube ..... *S. huachamacari* Maguire
      5b. Corolla lobes 3-nerved, about 2½ to 3 times shorter than the tube.
        6a. Phyllaries not decurrent, involucre cylindric; leaves 6–13.5 cm long, basally attenuate; capitula with up to 25 flowers; corollas ca. 19–22 mm long; anthers (including tails) ca. 11–12 mm long, tails of adjacent anthers connate ..... *S. aracaënsis* Pruski
        6b. Outer phyllaries decurrent onto peduncle, the heads thereby stipitate and the involucres campanulate; leaves 9–21 cm long, basally cuneate to narrowly so; capitula 35–70-flowered; corollas (20)28–35 mm long; anthers (including tails) (12)15–16 mm long, tails of adjacent anthers connate, but easily separable ..... *S. kunhardtii* Maguire
1b. Anther filaments attached to corolla tube at the sinuses of the lobes.
  7a. Mature leaves sericeous below ..... *S. sericeus* Maguire & Aristeg.
  7b. Mature leaves glabrous or puberulent below.
    8a. Capitula narrowly cylindric, 5–6-flowered; leaves narrower than 2.3 cm ..... *S. colveei* (Steyerm.) Pruski
    8b. Capitula cylindric to hemispheric, ca. 12–100-flowered; leaves wider than 3 cm.
      9a. Outer phyllaries keeled, shiny ..... *S. connellii* (N. E. Brown) S. F. Blake
      9b. Outer phyllaries not keeled, not shiny.
        10a. Leaves to 35 cm long ..... *S. colombianus* Cuatrec. & Steyerm.
        10b. Leaves shorter than 26 cm.
          11a. Outer phyllaries ca. 1–2 cm long, elliptic-lanceolate, apically obtuse to rounded ..... *S. cucullatus* Maguire & Wurd.
          11b. Outer phyllaries shorter than 1 cm, triangular, apically acute.
            12a. Leaves shorter than 6 cm, rotund with rounded bases and apices ..... *S. jauaensis* Aristeg.
            12b. Leaves commonly longer than 6 cm, elliptic to ovate with attenuate to obtuse bases and apices.
              13a. Leaves subsessile, basally cuneate to obtuse; petioles shorter than 7 mm; young leaves sometimes sericeous ..... *S. chimantensis* Maguire, Steyerm. & Wurd.
              13b. Leaves petiolate, basally attenuate to narrowly acute; petioles ca. 1–2.5 cm long; leaves glabrous or puberulent, never sericeous ..... *S. talaumifolius* S. F. Blake

Known previously only from the Guayana Highland of Guyana and/or Venezuela, the following species are here recorded for Brazil, mostly from Serra Aracá:

Calea abelioides S. F. Blake (*Prance et al. 9810, 9876, 21555*; *Tavares et al. 141*). The first three collections cited above were reported from Brazil by Huber et al. (1984) as *C. cardonae* var. [subsp. in protologue] *neblinensis* Maguire & Wurd., a taxon not known to occur in Brazil.

Calea lucidivenia Gleason & S. F. Blake (*Amaral 1628*; *Prance et al. 28975*; *Prance & Guedes 29600*; *Rosa & Lira 2250*; *Tavares & Silva 36*).

Eupatorium (*Guayania*) *bulbosum* Aristeg. (*Pipoly et al. 6664*; originally determined as *Guayania* by H. Robinson). King & Robinson (1987, p. 412) listed it as restricted to Venezuela.

Eupatorium (*Chromolaena*) *pharcidodes* B. L. Robinson (*Prance et al. 29185*; *Rosa & Lira 2341*). This species is not reported from Brazil on p. 387 of King & Robinson (1987).

Mikania lucida S. F. Blake (*Amaral 1578, 1619*; *Prance et al. 20058, 29021*; *Tavares & Silva 63*; *Tavares et al. 120*). The provisional determination of *M.* cf. *lucida* based on *Prance et al. 20058* from near Auaris, Brazil and reported on p. 123 of Huber et al. (1984) is herein confirmed. King & Robinson (1987, p. 425) listed it as restricted to Venezuela.

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CHROMOSOME NUMBERS IN COMPOSITAE, XVI: EUPATORIEAE II[1]

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ABSTRACT

An additional 159 chromosome reports are provided for the tribe Eupatorieae with 13 new generic and 60 new species reports. Numbers now known include 94 of the 180 genera and over 450 of the more than 2,000 species. A primary base of $x = 10$ is confirmed for most of the subtribes, including the Adenostemmatinae (with first report of *Sciadocephala*), Eupatoriinae, Gyptidinae, most of the Ageratinae and Alomiinae, Liatrinae (with first report of *Hartwrightia*), Fleischmanniinae, Critoniinae, and Praxelinae. The occurrence of $n = 9$ is consistent for four additional species in *Acritopappus* of the Ageratinae, independent of that base number in the *Brickellia* group of the Alomiinae. Numerous reports are added for the Central American polyploid complex in *Fleischmannia*. Consistent higher base numbers of $x = 16$ 25 are found in new reports for the subtribes Neomirandeinae, Mikaniinae, and Oxylobinae. Numbers of $n =$ ca. 20–26 are noted in two species of *Kaunea* of the Oxylobinae with correction of one previous lower count erroneously credited to *K. lasiophthalma*. Distribution of the two bases, $x = 10$ and 16, in the Hebecliniinae are cited and problems in *Bartlettina* and the Critoniine genus *Eupatoriastrum* are discussed.

This paper continues a series dealing with chromosome numbers of Compositae (Raven et al., 1960; Raven & Kyhos, 1961; Ornduff et al., 1963, 1967; Payne et al., 1964; Solbrig et al., 1964, 1969, 1972; Anderson et al., 1974; Powell et al., 1974, 1975; King et al., 1976; Tomb et al., 1978; Robinson et al., 1981, 1985) and is the second dealing with the tribe Eupatorieae (King et al., 1976). New reports are provided for 13 genera and 59 species (marked by ** and * respectively in Appendix).

The new reports in this paper are based primarily on material collected by R. M. King and counted by A. M. Powell and J. F. Weedin (not coded) and G. D. Carr (C). The chromosome counts have been made from aceto-carmine or aceto-orcein squashes of microsporocytes in meiosis. Voucher specimens of the King collections are in US and a second set is in MO.

The previous paper in the series dealing with the Eupatorieae summarized the numbers then known from 327 of the approximately 2,000 species and 70 of the 180 genera now known in the tribe. The chromosome data were summarized again with few additions in the survey of the tribe by King & Robinson (1987). Studies subsequent to that of King et al. (1976) have added reports of ten additional genera: *Urolepis* $n = 10$ (Turner et al., 1979; Waisman & Rozenblum, 1986); *Hatschbachiella* $n = 10$ (Waisman & Rozenblum, 1986); *Lorentzianthus* $n = 10$ (Bernardello, 1986); *Alomia* $n = 10$ (Mabry et al., 1981; Baker & Turner, 1986; Sundberg et al., 1986); *Amolinia* $n = 10$ (Strother, 1983); *Flyriella* $n = 10$ (Baker & Turner, 1986; Sundberg et al., 1986); *Erythradenia* $n = 16$, *Eupatoriastrum* $n = 16$; *Kyrsteniopsis* $n = 10$; and *Piptothrix* $n =$ ca. 17 (Sundberg et al., 1986).

The present paper adds chromosome counts for the 13 additional genera: *Bahianthus* $n = 10$; *Bejaranoa* $n = 10$; *Bishovia* $n =$ ca. 10; *Cronquistianthus* $n =$ ca. 10; *Fleischmanniopsis* $n = 10$; *Goyazianthus* $n = 20$; *Platypodanthera* $n = 10$; *Pseudokyrsteniopsis* $n = 10$; *Sciadocephala*

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$n = 10$; and *Trichogonia* $n = 10$. The new counts of $n =$ ca. 20 and ca. 26 for *Kaunea* seem to be the first reasonably representative figures for the genus. Chromosome numbers are now known from 94 of the 180 genera.

A few previously reported numbers are based on vouchers needing corrections of identification. The name *Ageratina aschenborniana* (Schauer) K. & R. used in earlier papers is a synonym of *A. bustamenta*, and *Ophryosporus origanoides* [Meyen & Walp.] Hieron. is a synonym of *O. heptanthus*. The plant reported by Coleman (1968: 235, Brazil: *Coleman 295*) as *Ageratum conyzoides* L. is *Barrosoa betoniciforme* (DC.) K. & R.

The general pattern of chromosome numbers in the tribe was first presented in King et al. (1976). Thirteen of the 18 subtribes had a base of $x = 10$ or clearly derived numbers, such as $x = 15$. The remaining five subtribes show higher base numbers with no remnant of $x = 10$. As elaborated from the chart in King & Robinson (1987), the subtribes have the following numbers with primary bases in **boldface**: Adenostemmatinae 5, **10**; Eupatoriinae **10**, 15, 20; Disynaphiinae **10**; Gyptidinae **10**; Ageratinae **9** (*Acritopappus*), **10**, **11**, **12** (*Microspermum–Piqueria–Stevia* group), 15, 20, 25; Trichocoroninae **15**; Ayapaninae **10**; Alomiinae **9** (*Brickellia* group), **10**; Liatrinae **10**, 20, 30; Fleischmanniinae 4 (*Fleischmannia microstemon*), **10**, 20, 30; Critoniinae **10**, 20; Praxelinae **10**, 20, 29; Hebecliniinae **10**, **16**; Neomirandeinae **17**, 20, 24, 25; Mikaniinae 16, **17**, 18, **19**, 20; Oxylobinae **16**, **17**, ca. 20, 51; Hofmeisteriinae **18**, **19**; Oaxacaniinae **18**. The pattern has not been altered by any of the more recent reports, and it is actually greatly reinforced by numerous new chromosome counts in the subtribes Ageratinae, Fleischmanninae, Hebecliniinae, and Oxylobinae. The only questionable additions since 1977 are in the Critoniinae and Hebecliniinae. Questionable counts have often been overturned by subsequent examination of vouchers, as in the case discussed under *Kaunea* in the Oxylobinae, or by reexamination of the species. The patterns seem well established, and deviations should be carefully rechecked.

The significant new reports are best reviewed in the order of the subtribes established in King & Robinson (1987).

Adenostemmatinae

The new report of $n = 10$ for *Sciadocephala* is the first for that genus and the first in the subtribe outside of *Adenostemma*. Evidently both genera retain the basic number of the tribe. There has been no further evidence in the subtribe for the low $n = 5$ reported by Turner & Irwin (1960) from a plant now determined as *A. involucratum*. Our new report for that species is $n = 10$. The two genera of the subtribe with the anomalous knob-formed pappus have now been counted, but the remaining genus *Gymnocoronis*, which lacks such a pappus, is still unstudied.

Eupatoriinae

The Waisman & Rozenblum (1986) count for *Hatschbachiella* completes the survey of genera in the subtribe. All four genera show a base of $x = 10$, with *Eupatorium* (including *Eupatoriadelphus*) showing some triploids and tetraploids.

Gyptidinae

The new generic reports for *Bahianthus*, *Bejaranoa*, *Litothamnus*, *Platypodanthera*, and *Trichogonia*, and the *Urolepis* counts (Turner et al., 1979; Waisman & Rozenblum, 1986) show that $n = 10$ is basic to the subtribe. The recent cytological study of *Gyptis pinnatifida* Cass. (as *Eupatorium tanacetifolium* Gillies ex Hook. & Arn. by Rozenblum et al., 1988) confirms the triploid condition based on $n = 10$ that is already known to occur in that genus and examines details of the apomixis in the species.

Ageratinae

The many new counts of *Acritopappus*, based on four species, strongly confirm the occurrence of $n = 9$ first noted for one of the species by Coleman (1970) and mentioned by King et al. (1976). The isolated occurrence of $n = 9$ in *Acritopappus* is apparently consistent for the genus, with reports from both viscid-leaved and non-viscid-leaved members. Prior to the discovery of $n = 9$ in *Acritopappus*, the number was known in the tribe from only *Brickellia* and its close relatives in the subtribe Alomiinae.

Other reports of chromosome numbers of Ageratinae since King et al. (1976) confirmed other known patterns. New counts of *Ageratum* spp. show a base of 10. The Dillon & Turner (1982) report of ca. $n = 10$ for *Ascidiogyne sanchez-vegae* Cabrera conforms with the $n = 10$ already known for the type species *A. wurdackii* Cuatr. This further indicates the difference between the latter genus and the members of the *Piqueria* relationship. New reports from *Piqueria* and *Stevia* and the Strother (1983) and Sundberg et al. (1986)

reports for *Microspermum debile* Benth. and *M. nummulariifolium* Lagasca conform to the already known bases of $n = 12$ and $n = 11$ in that group. The South American species reported for *Stevia* all have $n = 11$, and none show the $n = 12$ found in shrubby members of the genus in Central America.

ALOMIINAE

The new generic counts for *Goyazianthus*, *Planaltoa*, and *Pseudokyrsteniopsis*; generic counts by others for *Alomia*, *Flyriella* (Baker & Turner, 1986; Sundberg et al., 1986) and *Kyrsteniopsis* (Sundberg et al., 1986); and the counts for all three species of *Carminatia* (Turner, 1988) extend our knowledge of elements of the subtribe having the base number of 10. The Turner report for his new species, *Carminatia anomala*, is here attributed to the earlier name for the species, *C. alvarezii* Rzed. & Calderón de Rzedowski (1987). Chromosome numbers of the genera could all be anticipated on the basis of their evident relationships within the subtribe. The number $n = 9$ that is notably present in the Alomiinae in *Brickellia* (King et al., 1976; Keil et al., 1988), *Barroetea* (Sundberg et al., 1986), *Pleurocoronis*, and their immediate relatives is unknown in any of the primarily South American genera of the subtribe.

LIATRINAE

The new chromosome count for *Hartwrightia* completes the survey of the six genera of this small subtribe from the southeastern United States. All members of the subtribe have $n = 10$ or polyploids of that number.

FLEISCHMANNIINAE

The numerous new reports for *Fleischmannia* firmly establish $n = 10$ as the base for most of the species. No further examples have been found of the $n = 4$ that is characteristic of the weedy annual *F. microstemon* (Cass.) K. & R. and that has been reported for *F. hymenophyllum* by Grashoff et al. (1972).

The counts reported in the present study formed the basis for statements regarding the polyploid complex first noted by King & Robinson (1978, 1987) in Central America. The geographically restricted Guatemalan species *Fleischmannia bohlmanniana* K. & R., *F. deborabellae* K. & R., and *F. viscidipes* (B. L. Robins.) K. & R. prove to be diploid, while the more widely distributed weedy species *F. pratensis* (Klatt) K. & R. and *F. pycnocephala* (Less.) K. & R. continue to show a consistently polyploid condition.

CRITONIINAE

The three new generic reports for the subtribe (*Bishovia* K. & R., *Cronquistianthus* K. & R., and *Fleischmanniopsis*) and the *Lorentzianthus* count of Bernardello (1986) show the base of $n = 10$ that is characteristic of all previously known members of the group. The only serious suggestion of another base in the subtribe seems to involve the presently uncounted genus *Eupatoriastrum*, which is noted for its paleaceous receptacles. The species belonging to this genus have been associated with a similarly paleaceous species, *Eupatorium corvi* McVaugh (McVaugh, 1972) of Chiapas, which has an $n = 16$ (King et al., 1976). The latter is now recognized as the genus *Matudina* of the subtribe Hebecliniinae, and shows no detailed structural evidence of immediate relationship to *Eupatoriastrum*. In contrast, structural features of *Eupatoriastrum* suggest close relationship to *Koanophyllon*, which has numerous reports of a base of $n = 10$ in this study and in previous studies based on Central and South American material (King et al., 1976; Keil et al., 1988).

Therefore, it is surprising to see a report of $n = 16$ from *Eupatoriastrum nelsonii* Greenman (Sundberg et al., 1986). The voucher cited by Sundberg et al. from Coatepec, Veracruz (*Hernández 320*) has been sought for study, but the specimen is not deposited at TEX as indicated. The actual repository, XAL, has not replied. A specimen of *E. nelsonii* (*Hernández 355* TEX), collected from the same place, is correctly determined. The latter is the voucher for the chemical study by Bohlmann et al. (1985). It is possible that the $n = 16$ reported from *Eupatoriastrum nelsonii* is correct, and that the genus is a member of the Hebecliniinae rather than the Critoniinae. No characteristic of the genus precludes this. In fact, the form and texture of the corollas of *Eupatoriastrum* are rather like that of various members of the *Hebeclinium* group. Structural details indicate that placement within the Hebecliniinae, if correct, would be closer to *Decachaeta* than *Matudina*. Although the structural characters of the Hebecliniinae are less definite than those of most subtribes, there is no reason to believe that $n = 16$ has arisen more than once from $x = 10$.

King et al. (1976) placed *Peteravenia* in the *Hebeclinium* group and reported chromosome numbers of $n = 10$ and $n =$ ca. 17. The genus was transferred to the Critoniinae in King & Rob-

inson (1987), where the report of n = ca. 17 was rejected from the genus as the voucher proved to be *Ageratina subinclusa* (Klatt) K. & R. Two new counts further establish $n = 10$ as the base number for *Peteravenia*.

Praxelinae

New reports for *Chromolaena* and *Praxelis* (Appendix) and reports in recent literature (Sundberg et al., 1986) show the trend already known for high chromosome numbers and irregular meiosis in the subtribe.

Hebecliniinae

King et al. (1976) noted the *Hebeclinium* group for the presence of two distinct base numbers, $x = 10$ and $x = 16$. The members of the subtribe with $n = 10$ were *Hebeclinium* and the South American species of *Bartlettina*. In contrast, the Central American genera *Erythradenia* (Sundberg et al., 1986), *Decachaeta*, and *Matudina*, and the Central American species of *Bartlettina* showed $n = 16$. The geographical pattern seemed to be mostly South America versus Central America, with *Hebeclinium* being basically South American. Subsequent reports have generally confirmed the pattern. Strother (1983) reported $n = 16$ for four Central American species, *Bartlettina breedlovei* K. & R., *B. pansamalensis* (B. L. Robins.) K. & R., *B. pinabetensis* (B. L. Robins.) K. & R., and *B. tuerckheimii* (Klatt) K. & R., and the same number was reported by Sundberg et al. (1986) for *B. hintonii* K. & R. In an apparent exception to the characteristic $n = 16$, two Central American species of *Bartlettina tamaulipanum* (B. Turner) K. & R. and *Eupatorium xalapanum* B. Turner (= *B. brevipetiolata* (Schultz-Bip. ex Klatt) K. & R.) have been reported as $n = 10$ (Turner, 1985). The types have been seen, and they are clearly members of the Central American complex in the genus. The reports of $n = 10$ are greatly in need of confirmation.

The only basically Central American element of the Hebecliniinae presently known with $n = 10$ seems to be *Amolinia heydeana* (B. L. Robins.) K. & R. reported by Strother (1983).

Neomirandeinae

New reports for this monogeneric tribe include one species of each subgenus of *Neomirandea*. The reports of $n = 17$ for *N. eximia* agree with earlier counts. The reports of n = ca. 26 for *N. angularis* are the first of that number in the genus, but they offer limited consistency in a member of the typical subgenus of *Neomirandea*, which has previously been reported variously as $n = 20$, n = ca. 24, n = ca. 25 (King et al., 1976), and the species has recently been reported as $n = 25$ by Sundberg et al. (1986).

Oxylobinae

Reports since King et al. (1976) have provided an expected count of n = ca. 17 for *Piptothrix* (Sundberg et al., 1986) and supported previously known chromosome patterns of $n = 16$ for *Oxylobus* (Turner & Kerr, 1985) and $n = 17$ in *Ageratina* subgenera *Ageratina*, *Neogreenella*, and *Klattiella* (Jansen et al., 1984; Sundberg et al., 1986). Strother (1983) noted a minor departure of $n = 18$ for *Eupatorium subpenninervium* (= *Ageratina subinclusa* (Klatt) K. & R. The present study, Jansen et al. (1984), and Waisman & Rozenblum, (1986) give further examples of the subgenus *Andinia*, i.e., *Ageratina ampla* (Benth.) K. & R., *A. dendroides*, *A. pseudochilca*, *A. popayanensis* (Hieron.) K. & R., *A. angustifolia* (H. B. K.) K. & R., *A. arbutifolia* (Benth.) K. & R., *A. baccharoides* (H. B. K.) K. & R., and *A. elegans* (H. B. K.) K. & R. The counts confirm the consistent n = ca. 40 and n = ca. 42 already seen by King et al. (1976) in the subgenus except for the higher polyploid n = ca. 90 count for *A. angustifolia* by Waisman & Rozenblum (1986).

The new count of n = ca. 20 for *Kaunea ignorata* seems to reinforce the generally high number $2n$ = near 45 found by Royce Oliver in root tips of that species (King & Robinson, 1980). The new report of n = ca. 26 for *Kaunea lasiophthalma* conflicts with an earlier report of $n = 10$ for *Eupatorium lasiophthalmum* Griseb. (Turner et al., 1979), but the voucher for the latter report has been examined and proves to be *Lorentzianthus viscidus*, a species known to have an $n = 10$. It seems that *Kaunea* characteristically has a chromosome number at the level of n = 20–26, which is consistent with higher numbers in other known members of subtribe Oxylobinae. The higher numbers in *Kaunea* are reminiscent of those of another Andean member of the subtribe, *Ageratina* subg. *Andinia*. Nevertheless, the numbers in the two groups do not seem to be the same, and if other aspects of the plants are any indication of relationship, the higher numbers evidently originated separately. Structurally, *Kaunea* seems to be one of the most divergent elements of the Oxylobinae, and it is not now considered close to any part of *Ageratina*.

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Appendix. Chromosome counts and vouchers for species of Eupatorieae. New generic reports are marked **, new species reports *. K numbers represent King collection numbers. Carr counts are marked (C), other counts are by Powell and Weedin unless marked otherwise.

**Acritopappus confertus* (Gardner) K. & R. $2n = 9_{II} + 1_{I}$. Brazil. bahia: 1 km S of Andarai along road to Mucugé. K8708 (C).

**Acritopappus hagei* K. & R. *n* = 9. BRAZIL. BAHIA: ca. 25 km S of Andarai. K8711 (C).

**Acritopappus hagei*. *n* = 9. BRAZIL. BAHIA: 52 km E of Seabra. K8773 (C, and Royce Oliver).

**Acritopappus morii* K. & R., type. *n* = 9. BRAZIL. BAHIA: Mucugé. K8172.

**Acritopappus morii*. *n* = 9. BRAZIL. BAHIA: 9 km N of Mucugé. K8768 (C).

**Acritopappus prunifolius* K. & R. *n* = ca. 9. BRAZIL. BAHIA: 8 km S of Mucugé. K8749 (C).

Adenostemma involucratum K. R. *n* = 10. BRAZIL. RIO DE JANEIRO: grown from seed collected at Botanical Garden. K9701.

Adenostemma platyphylla Cass. *n* = ca. 10. BOLIVIA. COCHABAMBA: 33 km from Colomi. K7694.

Ageratina anisochroma (Klatt) K. & R. *n* = 17. COSTA RICA. SAN JOSÉ: La Palma. K9657 (C).

Ageratina azangaroensis (Schultz-Bip.) K. & R. *n* = 17. BOLIVIA. COCHABAMBA: Challa. K7539.

Ageratina azangaroensis. *n* = 17. BOLIVIA. COCHABAMBA: 46 km from Challa. K7544.

Ageratina azangaroensis. *n* = 17. BOLIVIA. LA PAZ: ca. 30 km from La Paz. K7414.

Ageratina azangaroensis. *n* = ca. 17. PERU. ANCASH: Catac. K9071 (C).

Ageratina azangaroensis. $2n = 17_{II}$ + 2 B chromosomes. BOLIVIA. COCHABAMBA: 4 km W of Epizana. K9646 (C).

Ageratina bustamenta (DC.) K. & R. *n* = 17. GUATEMALA. ALTA VERAPAZ: ca. 22 km W of San Cristóbal Verapaz. K7352.

Ageratina bustamenta. *n* = 17. GUATEMALA. SOLOLA: 13 km SE of Panajachel. K7232.

Ageratina bustamenta. *n* = 17. GUATEMALA. CHIMALTENANGO: 16 km NW of Patzun. K7212.

Ageratina bustamenta. *n* = 17. GUATEMALA. QUEZALTENANGO: 14 km SE of Quezaltenango. K7259.

Ageratina bustamenta. *n* = 17. GUATEMALA. QUEZALTENANGO: 4 km SW of San Mateo. K7266.

Ageratina bustamenta. *n* = 51. GUATEMALA. CHIQUIMULA: 14 km E of Ipala. K7383.

**Ageratina dendroides* (Sprengel) K. & R. *n* = ca. 40. ECUADOR. LOJA: 4 km E of Loja. K7911.

Ageratina mairetiana (DC.) K. & R. *n* = 17. GUATEMALA. HUEHUETENANGO: 5 km N of Chiantla. K7309.

Ageratina mairetiana. *n* = 17. GUATEMALA. HUEHUETENANGO: 7–8 km E of Chiantla. K7313.

**Ageratina pseudochilca* (Benth.) K. & R. *n* = ca. 42. ECUADOR. AZUAY: 5 km S of Cumbe. K7754.

Ageratum fastigiatum (Gardner) K. & R. *n* = 10. BRAZIL. GOIÁS: 25 km NW of Cristallina. K8243.

Ageratum fastigiatum. *n* = 10. BRAZIL. GOIÁS: 2–7 km ESE of Cristallina on the road to Belo Horizonte. K8260.

Ageratum fastigiatum. *n* = 10. BRAZIL. MINAS GERAIS: Serra do Cipó 2 km beyond Chapeu de Sol. K8363.

Ageratum fastigiatum. *n* = 10. BRAZIL. GOIÁS: 5 km NE of Cristallina. K8960 (C).

Ageratum rugosum J. Coulter. *n* = 20 + 1–2 fragments. GUATEMALA. CHIMALTENANGO: 12 km WSW of Chimaltenango. K7199.

**Aristeguietia pseudoarborea* (Hieron.) K. & R. *n* = 10. PERU. AMAZONAS: mountains SE of Chachapoyas. K9208 (C).

Austrobrickellia patens (Don) K. & R. *n* = 10. BOLIVIA. SANTA CRUZ: 1 km from Comarapa. K7629.

Austroeupatorium chaparense (B. L. Robins.) K. & R. *n* = 10. BOLIVIA. COCHABAMBA: 40 km from Comarapa. K7660.

Ayapana amygdalina (Lam.) K. & R. *n* = 10. BOLIVIA. LA PAZ: 27 km from Chulumani. K7456.

***Bahianthus viscidus* (Baker) K. & R. *n* = ca. 12. BRAZIL. BAHIA: A 30 km ao S de Mucugé. Na estrada que vai par Jussiape. K8150.

***Bahianthus viscidus*. *n* = ca. 10. BRAZIL. BAHIA: A 3 km ao S de Mucugé. Na estrada que vai par Jussiape. K8160.

***Bahianthus viscidus*. *n* = 10. BRAZIL. BAHIA: Mucugé. K8169.

***Bejaranoa balansae* (Hieron.) K. & R. *n* = ca. 20. BRAZIL. BAHIA: Trecho Vitoria da Conquista BR 415 Ilheus/Brumado Anagé km 260. K8032.

***Bejaranoa balansae*. *n* = 10. BOLIVIA. SANTA CRUZ: 23 km E of Comarapa. K9654 (C).

***Bishovia bolivensis* K. & R., type. *n* = ca. 10 (possibly $2n = 10_{II} + 1_{I}$ or more than 10_{II}; chromosomes morphologically unusual). BOLIVIA. SANTA CRUZ: 1 km from Comarapa. K7625.

Brickellia argyrolepis B. L. Robins. *n* = 9. GUATEMALA. SOLOLA: 6 km SE of Panajachel. K7230.

Brickellia argyrolepis. *n* = 9. GUATEMALA. JALAPA: ca. 11 km NW of San Luis. K7384.

**Campuloclinium megacephalum* (C. Martius) K. & R. *n* = 20–22. BRAZIL. GOIÁS: 2 km S of Cristallina. K8252.

**Campuloclinium megacephalum*. $2n$ = ca. 10_{II} + ca. 10 B chromosomes. BRAZIL. GOIÁS: 20 km N of Alto Paraiso de Goiás. K8813 (C).

Chromolaena arnottiana (Griseb.) K. & R. *n* = 27–30 univalents. BOLIVIA. SANTA CRUZ: 1 km from Comarapa. K7629.

Chromolaena arnottiana. $2n = 8–9_{II} + 10–12_{I} = 28–30$. ARGENTINA. CATAMARCA: ca. 45 km N of Catamarca. K9461 (C).

Chromolaena collina (DC.) K. & R. *n* = 10. GUATEMALA. ALTA VERAPAZ: ca. 24 km W of San Cristóbal Verapaz. K7355.

**Chromolaena cryptantha* (Schultz-Bip. ex Baker) K. & R. *n* = 10. BRAZIL. GOIÁS: 12 km S of Alto Paraiso de Goiás. K8871 (C).

**Chromolaena cryptantha*. *n* = 10. BRAZIL. GOIÁS: 25 km N of Cristallina. K8944 (C).

**Chromolaena pseudinsignis* K. & R., type. *n* = probably 10. BRAZIL. GOIÁS: Chapada dos Veadeiros, 18 19 km N of Alto Paraiso. K8279.

**Chromolaena tunariensis* (Hieron.) K. & R. $2n = 11_{II} + 1_{I}$. BOLIVIA. COCHABAMBA: Cercado. K9634 (C).

Conocliniopsis prasiifolia (DC.) K. & R. *n* = ca. 10. BRAZIL. BAHIA: com entrada no km 20 da Rodovia Ilhéus/Uruçuca (BA262). K8012.

Conocliniopsis prasiifolia. *n* = 10. BRAZIL. BAHIA: 40 km E of Maracas. K8019.

Conocliniopsis prasiifolia. *n* = 10. BRAZIL. BAHIA: 12 km N of Rio Verde Pequeno. K8588 (C).

Conoclinium coelestinum (L.) DC. *n* = 10. U.S.A. MARYLAND: Montgomery Co., Potomac. K8430.

Critoniella acuminata (H.B.K.) K. & R. *n* = 10. PERU. AMAZONAS: 44 km from Chachapoyas. K9227 (C).

Critoniella acuminata. *n* = 10. PERU. CAJAMARCA: 4 km N of San Ignacio. K9300 (C).

***Cronquistianthus chachapoyensis* K. & R. *n* = ca.

10. PERU. AMAZONAS: 8 km E of Chachapoyas. K9164 (C).

**Disynaphia halimifolia* (DC.) K. & R. *n* = 10. BRAZIL. DISTRITO FEDERAL: vicinity of the University of Brasilia campus. K8227.

Fleischmannia bohlmanniana K. & R., type. *n* = 10. GUATEMALA. CHIMALTENANGO: ca. 9 km NW of Antigua. K7190.

Fleischmannia bohlmanniana. *n* = 10. GUATEMALA. CHIMALTENANGO: 14 km NW of Patzun. K7201.

Fleischmannia bohlmanniana. *n* = 10. GUATEMALA. SOLOLA: 3 km SE of Panajachel. K7220.

Fleischmannia bohlmanniana. *n* = 10. GUATEMALA. SUCHITEPEQUEZ: 20 km N of Patulal. K7238.

Fleischmannia bohlmanniana. *n* = 10. GUATEMALA. QUEZALTENANGO: 28 km S of Quezaltenango. K7255.

Fleischmannia bohlmanniana. *n* = 10. GUATEMALA. QUICHE: 18 km SE of Santa Cruz del Quiche. K7287.

Fleischmannia bohlmanniana. *n* = 10. GUATEMALA. TOTONICAPAN: along the Pan American Highway, ca. 3 km S of Huehuetenango border. K7299.

Fleischmannia deborabellae K. & R. *n* = 10. GUATEMALA. ALTA VERAPAZ: ca. 16 km W of San Cristóbal Verapaz. K7346.

Fleischmannia pastazae (B. L. Robins.) K. & R. *n* = 20. ECUADOR. ZAMORA-CHINCHIPE: 25 km W of Zamora. K7938.

Fleischmannia pratensis (Klatt) K. & R. *n* = 20. GUATEMALA. ALTA VERAPAZ: 5 km WNW of San Cristóbal Verapaz. K7336.

Fleischmannia pratensis. *n* = 20. GUATEMALA. IZABAL: ca. 27 km NE of Gualan. K7371.

Fleischmannia pycnocephala (Less.) K. & R. *n* = ca. 20. GUATEMALA. SACATEPEQUEZ: ca. 24 km N of Escuintla. K7185.

Fleischmannia pycnocephala. *n* = 20. GUATEMALA. SACATEPEQUEZ: 7 km NW of Antigua. K7189.

Fleischmannia pycnocephala. *n* = 20. GUATEMALA. SOLOLA: 5 km SE of Panajachel. K7223.

Fleischmannia pycnocephala. *n* = 40. GUATEMALA. ALTA VERAPAZ: 2 km from Coban. K7331.

Fleischmannia pycnocephala. *n* = 40. GUATEMALA. BAJA VERAPAZ: 4 km S of Purulha. K7362.

Fleischmannia pycnocephaloides (B. L. Robins.) K. & R. *n* = ca. 50. GUATEMALA. CHIMALTENANGO: 16 km NW of Patzun. K7205.

Fleischmannia pycnocephaloides (B. L. Robins.) K. & R. *n* = ca. 50. GUATEMALA. TOTONICAPAN: 33 km N of San Cristóbal Totonicapan. K7294.

Fleischmannia pycnocephaloides var. *glandulipes* (B. L. Robins.) K. & R. *n* = 30. GUATEMALA. TOTONICAPAN: 2 km NE of Totonicapan. K7272.

Fleischmannia pycnocephaloides var. *glandulipes*. *n* = 30. GUATEMALA. TOTONICAPAN: 2 km NE of Totonicapan. K7272.

Fleischmannia sp. *n* = 20 + one univalent. GUATEMALA. SUCHITEPEQUEZ: ca. 3 km W of Cocales. K7242.

**Fleischmannia viscidipes* (B. L. Robins.) K. & R. *n* = 10. GUATEMALA. TOTONICAPAN: 16 km N of San Cristóbal Totonicapan. K7191.

**Fleischmannia viscidipes*. *n* = 10. GUATEMALA. TOTONICAPAN: 18 km NE of Totonicapan. K7282.

***Fleischmanniopsis leucocephala* (Benth.) K. & R. *n* = 10. GUATEMALA. ESCUINTLA: ca. 16 km SW of Amatitlan. K7169.

***Fleischmanniopsis leucocephala*. *n* = 10. GUATEMALA. QUEZALTENANGO: 30 km S of Quezaltenango. K7252.

***Goyazianthus tetrastichus* (B. L. Robins.) K. & R. $2n = 20_1$ erratic, multiple spindles. BRAZIL. GOIÁS: 5–12 km S of Alto Paraiso de Goiás. K8881 (C).

**Grazielia dimorpholepis* Baker. *n* = 10. BRAZIL. MINAS GERAIS: Serra do Cipó 24–28 km due N of the bridge over the Rio Cipó. K8384.

Grazielia intermedia (DC.) K. & R. *n* = 10. BRAZIL. GOIÁS: Chapada dos Veadeiros, 5 km S of Alto Paraiso. K8297.

***Hartwrightia floridana* A. Gray. *n* = 10. U.S.A. FLORIDA: Highlands Co., Hanson, *Wunderlin & Richardson 6420*.

Hebeclinium macrophyllum (L.) DC. *n* = 10. BOLIVIA. LA PAZ: 11 km from Chulumani. K7437.

Isocarpha oppositifolia (L.) Cass. *n* = 10. GUATEMALA. EL PROGRESSO: city limits of El Progresso. K7365.

Kaunea ignorata (Hieron.) K. & R. *n* = ca. 20. BOLIVIA. SANTA CRUZ: one km from Comarapa on road to Cochabamba. K7631.

**Kaunea lasiophthalma* (Griseb.) K. & R. *n* = ca. 26. BOLIVIA. COCHABAMBA: 5 km W of Pojo. K9652 (C).

**Koanophyllon conglobatum* (Gardner) K. & R. *n* = 10–12. BRAZIL. BAHIA: A 2 km a W de Ubatá. K8030.

**Koanophyllon conglobatum*. *n* = 10. BRAZIL. MINAS GERAIS: 27 km NE of Montes Claros. K8575 (C).

Koanophyllon pittieri (Klatt) K. & R. *n* = ca. 30. COSTA RICA. PUNTARENAS: Monteverde. K9685 (C).

**Koanophyllon standleyi* (B. L. Robins.) K. & R. *n* = 10. GUATEMALA. ESCUINTLA: 7 km N of Escuintla. K7173.

**Koanophyllon standleyi*. *n* = 10. GUATEMALA. SACATEPEQUEZ: ca. 13 km N of Escuintla. K7180.

***Litothamnus ellipticus* K. & R. *n* = 10. BRAZIL. BAHIA: 18.7 km N of Porto Seguro. K7988.

Mikania cordifolia (L.f) Willd. *n* = 19. GUATEMALA. ESCUINTLA: 7 km N of Escuintla. K7175.

Mikania cordifolia. *n* = 19. GUATEMALA. SUCHITEPEQUEZ: 10 km E of Mazatenango. K7244.

Mikania cordifolia. *n* = ca. 17. BOLIVIA. COCHABAMBA: 26 km from Comarapa. K7651.

**Mikania goyazensis* (B. L. Robins.) K. & R. *n* = ca. 18. BRAZIL. GOIÁS: Chapada dos Veadeiros, 18–19 km N of Alto Paraiso. K8280.

**Mikania goyazensis*. *n* = 17. BRAZIL. GOIÁS: 20 km N of Alto Paraiso de Goiás. K8814 (C).

Mikania micrantha H.B.K. *n* = 19 ± 1. GUATEMALA. IZABAL: ca. 27 km NE of Gualan. K7370.

**Mikania periplocifolia* Hook. & Arn. *n* = ca. 19. ARGENTINA. CATAMARCA: city limits of Catamarca. K9458 (C).

**Mikania pohlii* (Baker) K. & R. *n* = ca. 34. BRAZIL. GOIÁS: 2 km S of Cristallina. K8254.

**Mikania pohlii*. *n* = ca. 36. BRAZIL. FEDERAL DISTRICT: 18 km from Brasilia. K8928 (C).

**Mikania purpurascens* (Baker) K. & R. *n* = ca. 18 heteromorphic bivalents, one bivalent larger and probably a multivalent, and two univalents or fragments that are consistently not paired. BRAZIL. MINAS GERAIS: Serra do Cipó 24–28 km due N of the bridge over the Rio Cipó. K8376.

**Mikania pyramidata* J. D. Smith *n* = 18–20 + 5 or 6 frag. GUATEMALA. BAJA VERA PAZ: 4 km S of Purulha. K7357.

Neomirandea angularis (B. L. Robins.) K. & R. n = ca. 26. COSTA RICA. CARTAGO: ca. 15 km from Tapanti. K9667 (C).

Neomirandea angularis. n = ca. 26. COSTA RICA. CARTAGO: Volcán Turrialba. K9695 (C).

Neomirandea eximia (B. L. Robins.) K. & R. n = ca. 17. COSTA RICA. SAN JOSÉ: La Palma. K9656 (C).

Neomirandea eximia. n = ca. 17. COSTA RICA. CARTAGO: ca. 15 km from the dam at Tapanti. K9669 (C).

**Ophryosporus angustifolius* B. L. Robins. n = 10. BOLIVIA. SANTA CRUZ: 2 km from Comarapa. K7638.

**Ophryosporus chilca* (H.B.K.) Hieron. n = 10 + one round frag. or univalent. PERU. ANCASH: along the road to Olleros ca. 3 km generally east of the intersection with Peru highway #3. K9042.

**Ophryosporus heptantha* (Schultz-Bip. ex Wedd.) K. & R. n = 20. BOLIVIA. COCHABAMBA: 26 km from Tolata. K7593.

**Peteravenia schultzii* (Schnittsp.) K. & R. n = ca. 10. GUATEMALA. ALTA VERAPAZ: 2 km from Coban. K7332.

**Peteravenia schultzii*. n = 10. GUATEMALA. ALTA VERAPAZ: 19 km W of San Cristóbal Verapaz. K7349.

Piqueria trinervia Cav. n = 24. GUATEMALA. TOTONICAPAN: 33 km N of San Cristóbal Totonicapan. K7295.

Piqueria trinervia. n = 11. GUATEMALA. HUEHUETENANGO: ca. 13 km N of Chiantla. K7311.

***Planaltoa lychnophoroides* G. Barroso. n = 10. BRAZIL. GOIÁS: 12–20 km N of Alto Paraiso de Goiás. K8821 (C).

***Platypodanthera melissifolia* (DC.) K. & R. n = 10. BRAZIL. BAHIA: 10 km N of Livramento do Brumado. K8597 (C).

Polyanthina nemorosa (Klatt) K. & R. n = 10–12 (probably 10). BOLIVIA. LA PAZ: 7 km from Chulumani. K7432.

Praxelis clematidea (Griseb.) K. & R. $n = 32_{I}$. BRAZIL. RIO DE JANEIRO: Rio de Janeiro. Count obtained from progeny of seed collected in botanical garden. K9700.

Praxelis kleinioides (H.B.K.) Schultz-Bip. n = 40 univalents (apomictic). BRAZIL. BAHIA: entre Livramento do Brumado e Rio de Contas, a 5 km do primeiro. K8049.

***Pseudokyrsteniopis perpetiolata* K. & R. n = 10. GUATEMALA. QUICHE: 29 km E of Aguacatan. K7319.

***Sciadocephala schultze-rhonhofiae* Mattf. n = 10. ECUADOR. LOS RÍOS: Río Palenque Biological Station. *C. H. Dodson 5513.*

**Stevia boliviensis* Schultz-Bip. n = 11 (one larger$_{II}$). BOLIVIA. COCHABAMBA: 48 km from Tolata. K7609.

**Stevia boliviensis*. n = 11. BOLIVIA. COCHABAMBA: 23 km from Comarapa. K7641.

**Stevia boliviensis*. n = 11. BOLIVIA. COCHABAMBA: 23 km from Comarapa. K7662.

**Stevia boliviensis*. n = 11. BOLIVIA. COCHABAMBA: 9 km E of Epizana. K9649 (C).

Stevia caracasana DC. $n = 33_{I}$. GUATEMALA. CHIMALTENANGO: 5 km SE of Chimaltenango. K7194.

**Stevia mercedensis* Hieron. n = 11. BOLIVIA. COCHABAMBA: 24 km from Tolata. K7587.

**Stevia mercedensis* Hieron. n = 11. ARGENTINA. CATAMARCA: ca. 45 km N of Catamarca. K9463 (C).

**Stevia obovata* Rusby. n = 11. BOLIVIA. COCHABAMBA: 15 km from Colomi. K7678.

**Stevia polycephala* Bertol. n = 12. GUATEMALA. TOTONICAPAN: 14 km NE of Totonicapan. K7278.

**Stevia polycephala*. n = 12. GUATEMALA. HUEHUETENANGO: ca. 13 km N of Chianta. K7310.

**Stevia samaipatensis* B. L. Robins. n = 11. BOLIVIA. COCHABAMBA: 71 km from Tolata. K7616.

**Stevia samaipatensis*. n = 11. BOLIVIA. COCHABAMBA: 29 km from Cochabamba. K7673.

**Stevia samaipatensis*. n = 10 or 11 (if n = 10 then one larger $_{II}$). BOLIVIA. COCHABAMBA: 29 km from Cochabamba. K7674.

**Stevia samaipatensis*. n = 11. BOLIVIA. COCHABAMBA: ca. 60 km E of the bridge at Punata. K9641 (C).

**Stevia santacruzensis* Hieron. n = 11 + 1 univalent. BOLIVIA. COCHABAMBA: 59 km from Tolata. K7606.

**Stevia sarensis* B. L. Robins. n = 11. BOLIVIA. SANTA CRUZ: 23 km E of Comarapa. K9655 (C).

**Stevia setifera* Rusby. n = 11. BOLIVIA. COCHABAMBA: outskirts of Cochabamba. K7579.

**Stevia tunariensis* Hieron.? n = 11. BOLIVIA. COCHABAMBA: 46 km from Challa. K7541.

**Stevia urticifolia* Billb. in Thunb. n = 11. BOLIVIA. COCHABAMBA: 71 km from Tolata. K7617.

**Stevia yaconensis* Hieron. n = 11. BOLIVIA. COCHABAMBA: ca. 60 km E of the bridge at Punata. K9640 (C).

**Stomatanthes corumbensis* (B. L. Robins.) H. Robins. n = 10. BRAZIL. GOIÁS: ca. 1 km N of Cristallina. K8244.

**Symphyopappus compressus* (Gardner) B. L. Robins. $2n = 10_{II}$ + two univalents or fragments. BRAZIL. GOIÁS: 10 km N of S. Gabriel de Goiás. K8266.

**Symphyopappus compressus*. n = 10. BRAZIL. MINAS GERAIS: 27 km NE of Montes Claros. K8577 (C).

**Symphyopappus decussatus* Turcz. n = 10. BRAZIL. BAHIA: 10 km S of Mucugé. K8753 (C).

**Trichogonia bishopii* K. & R., type. n = 10. BOLIVIA. SANTA CRUZ: 1 km from Comarapa. K7626.

**Trichogonia grazielae* K. & R. n = 10. BRAZIL. GOIÁS: 5 km N of São João d'Alianca. K8271.

**Trichogonia prancii* G. Barroso. n = 10. BRAZIL. GOIÁS: 20 km N of Alto Paraiso de Goiás. K8812 (C).

**Trichogonia salviifolia* Gardner. n = 10 bivalents + one univalent or round fragment. BRAZIL. DISTRITO FEDERAL: 13 km SE of the center of Brasilia about 4 km SW along road from Escola Fazendária. K8183.

**Trichogonia salviifolia*. n = 10 bivalents + two univalents or fragments. BRAZIL. DISTRITO FEDERAL: 32 km N of the bridge at Asa Norte in Brasilia on the road to Alto Paraiso. K8209.

**Trichogonia scottmorii* K. & R., type. n = 10. BRAZIL. BAHIA: 42 km a E de Maracás. K8018.

**Trichogonia villosa* (DC.) Schultz Bip. ex Baker. n = 40, appears to be 20 bivalents. BRAZIL. MINAS GERAIS: Serra do Cipó, 9–11 km beyond Rio Cipó. K8343.

A GEOGRAPHICAL ANALYSIS OF THE FAMILY RANUNCULACEAE

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ABSTRACT

The Ranunculaceae Juss. are distributed worldwide. The primary differentiation of this family apparently took place in the vast territory of Eurasia during the Paleogene at least 50 million years ago or earlier, in Cretaceous time. The western and eastern floristic centers in eastern Asia played the most significant role in the secondary differentiation (i.e., formation of most genera and some groups of species), but important additional centers of ranunculaceous differentiation were in North and South America. The distribution of many groups of this family throughout the world and their local differentiation were associated with the general fall in temperature, development of the temperate floras, and the Alpine rise of mountain ridges (Neogene and more recent epochs).

The aim of this paper is to analyze the role of the Ranunculaceae with respect to floras around the world and to define more precisely some questions concerning the origin and differentiation of this family.

To date, there is no general study of the geographical distribution of the Ranunculaceae as a whole, except those of Tamura (1966–1968), whose data on the presence of species in the various floristic regions of the earth were helpful in preparing this essay. Additionally, we took advantage of our own herbarium studies (examining specimens from KW, LW, LWS, LE, TBI, TAD, BP, and others) and the observations of the senior author during several expeditions through the U.S.S.R. (Ukraine, the Caucasus, the mountains of Middle Asia, and the Altai).

We follow the interpretation of the floristic regions and provinces (Table 1 and map) by Takhtajan (1970, 1978) and the interpretation of endemics in the sense of Tolmachev (1974). Furthermore, we have attempted to recognize local, disjunctive, and widespread endemic species within each province or region.

GEOGRAPHICAL CHARACTERISTICS OF THE RANUNCULACEAE

The Ranunculaceae comprise 55 genera and about 2,200 species (Takhtajan, 1987; Tamura, 1966–1968; Ziman, 1985). About 20 genera[3] and 1,200 species are endemics (Table 2). Some endemic genera, e.g., *Beesia*, *Souliea*, *Kingdonia*, *Asteropyrum*, and *Xanthorhiza*, are morphologically isolated within the Ranunculaceae, and thus we were able to use their areas to discuss peculiarities of the distribution and the differentiation of the family as a whole.

To date, five floristic regions, the Eastern Asiatic, Atlantic North American, Andean, Chile-Patagonian, and Irano-Turanian, contain at least one endemic genus.

Most genera of Ranunculaceae have disjunctive distributions. Some, e.g., *Calathodes*, *Dichocarpum*, *Urophysa*, *Semiaquilegia*, *Beesia*, *Souliea*, and *Kingdonia*, occur within restricted geographic ranges of two to four provinces in one region. Another group, made up of *Helleborus*, *Eranthis*, *Isopyrum*, *Leptopyrum*, *Paropyrum*, *Oxygra-*

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[3] Bibliographic references are numbered. The nomenclature and circumscriptions of ranunculaceous genera follow monographs 4, 20, 74, 183, 187, 213, 264, 333, and others. Authorships for plant taxa follow *Index Kewensis*, Cherepanov (46), the monographs listed above, and regional floras (5 and others).

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phis, *Paraquilegia*, and *Callianthemum*, is characterized by more or less widely disjunctive areas, occupying two to four regions of Eurasia.

Areas of a third group, which includes *Trollius*, *Actaea*, *Cimicifuga*, *Enemion*, *Pulsatilla*, *Hepatica*, *Halerpestes*, and *Trautvetteria*, are represented in three to seven regions of Eurasia and North America. In many cases the disjunctive species of these genera are considered as relicts of the Tertiary temperate flora (Thorne, 1973).

Species of *Caltha* and *Myosurus* are widely distributed in the Northern and Southern hemispheres. It is remarkable that they are widespread in temperate areas but absent in the tropics and subtropics.

The distributional patterns of the remaining 18 genera of Ranunculaceae are unbroken or nearly unbroken. Species of the majority of them occur in two to six regions of Eurasia (*Aconitella* and *Ficaria*), Southeastern Asia (*Naravelia*), South America (*Hamadryas*), Africa (*Knowltonia* and *Clematopsis*), Eurasia, North Africa and North America (*Nigella*, *Aconitum*, *Consolida*, *Aquilegia*, *Adonis*, *Ceratocephalus*, and *Coptis*). *Delphinium* occurs in 11 regions of Eurasia, Africa, North America, and South America; *Thalictrum* occurs in 16 regions on these continents. Species of *Anemone*, *Clematis*, and *Ranunculus* are widespread in both hemispheres in the floras of about 30 regions.

Regional Distribution of the Ranunculaceae

In following Takhtajan (1978) we examined the distribution patterns of the Ranunculaceae in six floristic kingdoms, eight subkingdoms, 34 regions, and about 150 provinces.

HOLARCTIC KINGDOM

Location: territories of the Northern Hemisphere (more than half of the Earth), including Europe, extratropical Asia, North America, and North Africa.

Climate: predominately temperate, partly subtropical, and cold.

Ranunculaceae: 49 genera, 2,000 species.

Boreal Subkingdom

This subkingdom includes four regions: Eastern Asiatic, Circumboreal, Atlantic North American, and Rocky Mountain.

Location: extratropical Eurasia and North America.

Ranunculaceae: 48 genera, 1,500 species.

Eastern Asiatic Region

Location: main part of continental China, northern India, Burma, and Nepal, almost all Japan and Korea, eastern U.S.S.R.

Climate: warm temperate to mostly temperate.

Ranunculaceae: 38 genera, 900 species; 12 endemic genera, 400 endemic species.

Sikang Yunnan Province

Location: highlands; main part of the Chinese provinces Szechwan, Kweichow, and Yunnan, also northeastern Burma and northern Laos.

Characteristic vegetation: mountain coniferous, broad-leaved and rain forest, subalpine, and alpine formations.

Ranunculaceae: 28 genera, 400 species (14, 42, 48, 66, 81, 84, 109, 112, 199, 316).

Related floras: Central Chinese (21/60) and Eastern Himalayan (19/70).

Observations: 8 endemic genera, 180 endemic species. All endemic genera are isolated morphologically within the family. For example, *Asteropyrum* (*A. peltatum*) represents the monotypic tribe Asteropyreae and differs from other species by having simple peltate leaves. One other genus, *Souliea* (*S. vaginata*), belongs to the tribe Cimicifugeae and is distinguished by a unique type of pollen grain which lacks a primary germination apparatus (171). Another endemic monotypic genus, *Kingdonia* (*K. uniflora*), is exceptional by having open dichotomous foliar venation (42). This genus makes up the monogeneric tribe Kingdonieae, subfamily Kingdonioideae.[4] These species, also *Urophysa henryi*, *Beesia calthifolia*, *Calathodes palmata*, *C. polycarpa*, and *C. oxycarpa*, occur in isolated mountain forest locations at 2,000–4,000 m of the Sikang Yunnan, Central Chinese, Eastern Himalayan, and some other provinces.

Disjunct areas of species of *Semiaquilegia* (*S. adoxodoides* and *S. manschurica*) and *Dichocarpum* (*D. fargesii*, *D. dicarpon*, and others) are widely separated in provinces in the west and the east of the Eastern Asiatic Region. These species are also mountain forest plants, restricted to shade locations.

[4] Some systematists consider *Kingdonia* to belong to the Circaeasteraceae or else classified in its own monotypic family, Kingdoniaceae.

TABLE 1. Summary of numbers of genera and species, including endemics, of the Ranunculaceae for the principal floristic regions of the world (after Takhtajan, 297).

Kindgoms, subkingdoms, regions, provinces	Total numbers		Endemics	
	Genera	Species	Genera	Species
I. HOLARCTIC KINGDOM	49	2,000	16	1,000
BOREAL SUBKINGDOM	48	1,500	15	700
Eastern Asiatic Region	38	900	12	400
1. Sikang Yunnan Province	28	400	8	180
2. Central Chinese Province	22	150	7	50
3. North Chinese Province	15	70	—	5
4. Eastern Himalayan Province	23	200	6	90
5. North Burmese Province	14	60	3	10
6. Khasi-Manipur Province	8	25	—	5
7. Wolkano-Bonin Province	2	5		
8. Tokaro-Okinawa Province	2	7		
9. Taiwanian Province	9	40	2	5
10. Manchurian Province	23	160	1	50
11. Japanese-Korean Province	22	130	3	50
12. Sakhalin-Hokkaido Province	17	80	1	20
Circumboreal Region	30	600	—	200
1. Okhotsk-Kamchatka Province	18	90	—	15
2. Northeastern Siberian Province	15	70	—	5
3. Middle Siberian Province	18	100	—	20
4. Western Siberian Province	15	60	—	5
5. Altai-Sayan Province	21	130	—	30
6. Transbaikalian Province	19	100	—	15
7. Eastern European Province	22	110	—	10
8. Central European Province	24	160	—	20
9. Balkan Province	23	140	—	40
10. Atlantic European Province	22	110	—	20
11. North European Province	15	50	—	—
12. Arctic Province	12	80	—	5
13. Caucasian Province	19	160	—	45
14. Euxine Province	18	100	—	35
15. Canadian Province	13	60	—	5
Atlantic North American Region	20	120	3	25
1. North American Prairies Province	12	40	—	1
2. Atlantic-Gulf Coastal Plain Province	7	20	—	5
3. Appalachian Province	20	100	3	20
Rocky Mountain Region	17	100	—	35
1. Sitka-Oregon Province	16	80	—	20
2. Rocky Mountain Province	16	70	—	15
MADREAN SUBKINGDOM	17	130	—	50
Madrean Region	17	130	—	50
1. Californian Province	16	100	—	25
2. Great Basin Province	11	40	—	5
3. Sonoran Province	5	10	—	5
4. Mexican Highlands Province	5	50	—	40
ANCIENT MEDITERRANEAN SUBKINGDOM	30	500	1	250
Saharo-Arabian Region	9	35	—	6
1. Saharan Province	4	10	—	3
2. Egyptian-Arabian Province	9	30	—	3
Macaronesian Region	2	5	—	1
Mediterranean Region	18	130	—	65
1. Liguro-Tyrrhenian Province	17	60	—	20
2. Iberian Province	16	50	—	10
3. East Mediterranean Province	13	50	—	15
4. Southwest Mediterranean Province	9	25	—	5

TABLE 1. Continued.

Kindgoms, subkingdoms, regions, provinces	Total numbers		Endemics	
	Genera	Species	Genera	Species
5. South Mediterranean Province	7	20	—	1
6. Southern Moroccan Province	5	10	—	1
7. Balearic Province	9	15	—	2
8. Adriatic Province	5	15	—	1
9. Krym-Novorossiysk Province	10	30	—	2
Irano-Turanian Region	28	400	1	180
Anterior Asiatic Subregion	28	360	4	360
1. Armeno-Iranian Province	24	220	—	30
2. Hyrcanian Province	14	60	—	5
3. Central Anatolian Province	18	110	—	20
4. Mesopotamian Province	8	40	—	5
5. Turkestanian Province	19	130	—	50
6. Turanian Province	10	50	—	—
7. Western Himalayan Province	19	100	1	35
8. Northern Baluchistanian Province	14	50	—	5
Central Asiatic Subregion	23	200	—	60
1. Dzungaro-Tien Shan Province	21	130	—	40
2. Central Tien Shan Province	19	70	—	25
3. Mongolian Province	18	100	—	5
4. Tibetan Province	20	80	—	10
II. PALAEOTROPICAL KINGDOM	11	100	—	50
INDO-MALESIAN SUBKINGDOM	6	80	—	35
Malesian Region	5	60	—	30
1. Malaccan Province	3	5	—	—
2. Kalimantan Province	3	4	—	—
3. Moluccan Province	1	2	—	
4. Bismarckian Province	1	1	-	
5. Philippinean Province	5	15	—	6
6. South Malesian Province	5	15	—	5
7. Sumatran Province	5	10	—	5
8. Sulawesian Province	2	15	—	12
9. Papuan Province	3	30	—	25
Fijian Region	3	4	—	3
Indo-Chinese Region	6	25	—	3
Indian Region	6	10		3
POLYNESIAN SUBKINGDOM	2	5	—	1
Polynesian Region	1	2	—	—
Hawaiian Region	2	5	—	1
NEOCALEDONIAN SUBKINGDOM	1	1		
Neocaledonian Region	1	1	—	—
AFRICAN SUBKINGDOM	8	50	—	25
Guineo-Congo Region	7	40	—	20
Sudano-Zambesian Region	8	30	—	10
Karro-Namib Region	1	3	—	—
St. Helena and Ascension Region	1	1	—	—
MADAGASCAN SUBKINGDOM	4	10	—	2
Madagascan Region	4	10	—	2
III. CAPE KINGDOM	7	30	—	10
Cape Region	7	30	—	10
IV. NEOTROPICAL KINGDOM	9	70	2	40
Caribbean Region	3	20	—	5
Guayana Highlands Region	2	4		
Amazonian Region	1	2	—	—
Brazilian Region	2	5	—	
Andean Region	9	60	2	30

TABLE 1. Continued.

Kindgoms, subkingdoms, regions, provinces	Total numbers		Endemics	
	Genera	Species	Genera	Species
V. HOLANTARCTIC KINGDOM	8	100	2	80
Chile-Patagonian Region	7	50	2	25
Fernandesian Region	—	—	—	—
South Subantarctic Islands Region	1	5	—	1
Neozeylandic Region	5	60	—	55
VI. AUSTRALIAN KINGDOM	5	50	—	30
East Australian Region	5	45	—	30
Southwest Australian Region	2	5	—	2
Central Australian Region	—	—	—	—

In the flora of the Sikang Yunnan Province, *Aconitum* has about 70 species of which 40 are endemics; *Delphinium* has 70 species and 50 endemics; *Clematis* has 40 and 20; *Anemone* 20 and 15; *Trollius* 10 and 8; and *Aquilegia* 8 and 5 species.

In this province occur species that are important in considering the origin and dispersion of their genera and the family Ranunculaceae as a whole. For example, *Aconitum gymnandrum*, which represents the monotypic subg. *Gymnaconitum*, is found at about 4,000 m in Szechwan and in the Eastern Himalayan Province. Its annual habit is unique within *Aconitum*; this species is characterized by having primitive flowers and is considered a Tertiary relict (181, 241, 284). Another primitive species, *Delphinium aconitoides*, also occurs in this province. The local endemic *Clematis ranunculoides*, occurring there, represents the monotypic sect. *Ranunculoides*, and its life form (rosette-forming perennial herb with tripartite leaves) is regarded (341, 342) as the most primitive within *Clematis*.

There are three monotypic endemic sections of *Anemone*: sect. *Rivularis* (*A. rivularis*), sect. *Anemoclema* (*A. glaucifolia*), and sect. *Begoniifolia* (*A. begoniifolia*). Moreover, the most primitive and simultaneously relict species of *Trollius* (*T. yunnanensis*) (64, 270) and *Aquilegia* (*A. ecalcarata*) occur in the Sikang Yunnan Province (272).

The few species endemic to this province include *Delphinium ceratophorum*, *Ranunculus platypetalus*, and *Thalictrum delavayi*; many other species are shared with adjacent provinces.

Central Chinese Province

Location: Plateau Guichou, Ridges Zinlin-Dabashan and Nanlin, and the southern part of the Yangtze Basin (Kiangsu, Shensi, Hupeh, Anhwei, and Hunan provinces of China).

Characteristic vegetation: mountain forests, subalpine and alpine formations.

Ranunculaceae: 22 genera, 150 species (58, 81, 112, 198, 220, 330, 332).

Related floras: Sikang Yunnan (21/60, e.g., *Aconitum gymnandrum*, *Anemone rivularis*, *Aquilegia ecalcarata*), Eastern Himalayan (18/30, e.g., *Trollius pumilus*, *Aquilegia ecalcarata*, *Anemone obtusiloba*).

Observations: 7 endemic genera, 50 endemic species. (The endemic genera, *Asteropyrum*, *Urophysa*, *Kingdonia*, *Souliea*, *Beesia*, *Calathodes*, and *Dichocarpum*, are shared with the flora of Sikang Yunnan.) Most of the endemic species belong to *Aconitum*, *Delphinium*, *Clematis*, and *Thalictrum*. Endemic *Helleborus chinensis* together with *H. thibeticus* represent the endemic sect. *Dicarpon*. In contrast with the Sikang Yunnan flora, some species of *Pulsatilla*, e.g., *P. chinensis*, and *P. turczaninovii* are distributed here.

North Chinese Province

Location: southeastern part of the Loess Plateau and North Chinese Plain.

Characteristic vegetation: steppe formations and broad-leaved forests.

Ranunculaceae: 15 genera, 70 species (112, 139, 198, 199, 221, 332).

Related floras: Central Chinese (15/30, e.g., *Trollius chinensis*, *Cimicifuga dahurica*, *Delphinium grandiflorum*) and Manchurian (15/20, e.g., *Clematis brevicaudata*, *Thalictrum baicalense*).

Observations: no endemic genera, but 5 endem-

ic species (e.g., *Anemone changtungensis, Clematis nannophila*).

Eastern Himalayan Province

Location: main part of eastern and central Nepal, northern India, and southeastern Tibet.

Characteristic vegetation: mountain forests, subalpine and alpine formations.

Ranunculaceae: 23 genera, 200 species (35, 43, 113, 114, 123, 179, 205, 244, 261, 276, 283, 301).

Related flora: Sikang Yunnan (19/70, including endemic genera *Souliea, Beesia, Calathodes,* and *Dichocarpum*; endemic species, e.g., *Delphinium bonvalotii, Aconitum heterophyllum, Anemone rupicola,* and *Clematis connata*; and disjunct relict species, e.g., *Aconitum gymnandrum, Anemone rivularis,* and *Aquilegia ecalcarata*).

Observations: 6 endemic genera, 190 endemic species. Four of the endemic genera are shared with Sikang Yunnan Province, whereas *Archiclematis* and *Paroxygraphis* are local only. *Archiclematis alternata* grows in central Nepal in bushy border habitats at 2,200 m; *Paroxygraphis sikkimensis* is found in Sikkim in the alpine zone at 4,000 m. There are two endemic, monotypic sections of *Aconitum*: sect. *Fletcherum* (*A. fletcheranum*) and sect. *Alatospermum* (*A. novoluridum*), also the endemic, monotypic *Thalictrum*—sect. *Piuttia* (*T. rotundifolium*). Most endemic species belong to *Delphinium* (in all about 50 species with about 30 endemics, e.g., *D. nepalense*), *Aconitum* (30 and 20, e.g., *A. spicatum*), *Ranunculus* (30 and 10, e.g., *R. hirtellus*), and *Thalictrum* (20 and 10, e.g., *T. elegans*). In contrast with the Sikang Yunnan flora, this flora does consist of some species of *Pulsatilla, Coptis,* and *Hepatica.*

North Burmese Province

Location: between the Eastern Himalayan Province and Southwestern China.

Characteristic vegetation: warm temperate high-mountain forest and meadow formations.

Ranunculaceae: 14 genera, 60 species.

Related floras: Sikang Yunnan and Central Chinese (14/50, e.g., *Anemone vitifolia, A. rivularis, Cimicifuga foetida*).

Observations: 3 endemic genera, *Beesia, Souliea,* and *Dichocarpum,* about 10 endemic species (e.g., *Trollius yunnanensis, Clematis sikkimensis*).

Khasi-Manipur Province

Location: Northeastern India (Shillong Plateau, Khasi, Naga, Manipur, and Patkai Hills).

Characteristic vegetation: most like that of the North Burmese Province.

Ranunculaceae: 8 genera, 25 species.

Related flora: Eastern Himalayan (8/20, e.g., *Anemone rivularis, Clematis buchananiana*).

Observations: no endemic genera, 5 endemic species (e.g., *Trollius pumilus, Delphinium altissimum, Anemone elongata*).

Wolkano-Bonin Province

Location: small islands in Southeastern Asia (Wolkano, Bonin, and others).

Characteristic vegetation: tropical and subtropical formations.

Ranunculaceae: 2 genera, 5 species (215, 216, 299).

Related flora: Japanese-Korean (2/5, e.g., *Clematis pierotii, Ranunculus japonicus*).

Observation: no endemic genera or species.

Tokaro-Okinawa Province

Location: small islands in Southeastern Asia (Ryukyu, Tokara, Okinawa, Amami, and others).

Characteristic vegetation: tropical and subtropical formations.

Ranunculaceae: 2 genera, 7 species.

Related flora: Japanese-Korean (2/7, e.g., *Clematis mejeniana, Ranunculus ternatus*).

Observation: endemic species absent.

Taiwanian Province

Location: Taiwan and some adjacent islands, e.g., Sakisima.

Characteristic vegetation: tropical and subtropical formations, also warm-temperate, high-mountain forests and meadows.

Ranunculaceae: 9 genera, 40 species (216, 331, 339).

Related flora: Japanese-Korean (9/35, e.g., *Anemone stolonifera, Clematis uncinata, Ranunculus cantoniensis*).

Observations: 2 endemic genera, *Calathodes* and *Dichocarpum,* and 5 endemic species (e.g., *Aconitum formosanum, Ranunculus vernyi*).

Manchurian Province

Location: Soviet far east, Northeastern China, North Korea, and Northeastern Mongolia. The main landscape features are more or less level plains,

TABLE 2. The distribution of the genera of the Ranunculaceae in the main floristic regions of the world.

Genera	Regions																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Aconitella						+	+												
Aconitum	+	+	+	+	+	+		+											
Actaea	+	+	+	+	+			+											
Adonis	+	+				+		+											
Alexeya								+											
Anemone	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+
Anemonella			+																
Anemonopsis	+																		
Aquilegia	+	+	+	+	+	+		+											
Archiclematis	+																		
Asteropyrum	+																		
Barneoudia																	+		
Beesia	+																		
Calathodes	+																		
Callianthemum	+	+						+											
Caltha	+	+	+	+	+	+		+								+	+	+	+
Ceratocephalus		+				+		+											
Cimicifuga	+	+	+	+	+			+											
Clematis	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Clematopsis									+	+									
Consolida		+				+	+	+											
Coptis	+	+	+	+	+														
Delphinium	+	+	+	+	+	+	+	+	+	+	+	+		+					
Dichocarpum	+																		
Enemion	+		+	+	+														
Eranthis	+	+				+		+											
Ficaria		+				+		+											
Halerpestes	+	+	+	+	+			+											
Hamadryas																	+		
Helleborus	+	+				+													
Hepatica	+	+	+		+			+											
Hydrastis			+																
Isopyrum	+	+																	
Kingdonia	+																		

TABLE 2. Continued.

Genera	Regions																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Knowltonia									+	+				+					
Laccopetalum																+			
Leptopyrum	+	+						+											
Miyakea	+																		
Myosurus		+	+	+	+	+	+	+								+	+	+	+
Naravelia											+	+	+						
Nigella		+				+	+	+		+									
Oreithales																+			
Oxygraphis	+	+						+											
Paraquilegia	+	+						+											
Paropyrum	+	+						+											
Paroxygraphis	+																		
Pulsatilla	+	+	+	+	+			+											
Ranunculus	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Semiaquilegia	+																		
Souliea	+																		
Thalictrum	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			
Trautvetteria	+	+	+	+															
Trollius	+	+	+	+	+	+		+											
Urophysa	+																		
Xanthorhiza			+																

Conventional designations of the floristic regions:

1—Eastern Asiatic
2—Circumboreal
3—Atlantic North American
4—Rocky Mountain
5 Madrean
6—Mediterranean
7 Saharo-Arabian
8 Irano-Turanian
9—Guineo-Congo
10—Sudano-Zambesian
11—Malesian
12—Indo-Chinese
13 Indian
14—Cape
15—Caribbean
16—Andean
17—Chile-Patagonian
18—Neozeylandic
19—East Australian

but there are some mountainous chains (Sikhote-Alinj and Hingans).

Characteristic vegetation: broad-leaved and coniferous–broad-leaved forest, steppe, and meadow formations.

Ranunculaceae: 23 genera, 160 species (25, 108, 112, 158, 174, 326, 327, 328).

Related floras: Japanese-Korean (18/40, e.g., *Caltha membranacea, Actaea spicata, Enemion raddeanum, Thalictrum filamentosum*) and Okhotsk-Kamchatkian (18/25).

Observations: 1 endemic genus (*Semiaquilegia*) and about 50 endemic species, most of which belong to *Aconitum* (40 species, with about 20 endemics, e.g., *A. desoulavyi*), *Ranunculus* (30 and 5, e.g., *R. tachiroei*), and *Thalictrum* (15 and 5, e.g., *T. amurense*). In contrast to the Sikang Yunnan and other western floras of the Eastern Asiatic Region, this flora includes species of *Enemion, Hepatica, Coptis,* and *Trautvetteria* and few species of *Delphinium* and *Clematis.*

Japanese-Korean Province

Location: Honshu, Shikoku, Kyushu, southern Hokkaido, Iki, Cusima, Goto, additional small islands, and South Korea.

Characteristic vegetation: subtropical and temperate coniferous and broad-leaved forests in lowlands and mountains, also subalpine and alpine formations.

Ranunculaceae: 22 genera, 130 species (208, 216, 271, 299).

Related floras: Manchurian (18/40) and Sakhalin-Hokkaidian (16/25).

Observations: 3 endemic genera, disjunct *Semiaquilegia* and *Dichocarpum*, and local endemic *Anemonopsis* (*A. macrophylla*); these in many mountain forest locations in Honshu. Endemic species are about 50. There are endemic sections of *Anemone* (sect. *Keiskea*), *Coptis* (sect. *Japonocoptis*), *Cimicifuga* (sect. *Pityrosperma*), *Pulsatilla* (sect. *Preonanthopsis*), and *Clematis* (sects. *Patentes* and *Paratragene*). In contrast to the flora of the Manchurian Province, this flora consists of few species of *Aconitum* and lacks species of *Delphinium.*

Sakhalin-Hokkaido Province

Location: South Sakhalin, North Hokkaido, South Kuril Islands (Kunashir, Shikotan, and Iturup).

Characteristic vegetation: predominately coniferous forests.

Ranunculaceae: 17 genera, 80 species (209, 216, 299, 325, 326, 327, 328).

Related floras: Manchurian (16/40, e.g., *Caltha fistulosa, Trollius macropetalus, Aconitum arcuatum*), Japanese-Korean (16/25, e.g., *Aconitum volubile, Anemone raddeana, Adonis amurensis, Trautvetteria japonica*) and Okhotsk-Kamchatkian (14/20, e.g., *Caltha sibirica, Clematis ochotensis*).

Observations: 1 endemic monotypic genus *Miyakea* (*M. integrifolia*) which is related to *Pulsatilla* and 20 endemic species (e.g., *Aconitum miyabei, Anemone yesoensis, Pulsatilla sachalinensis*). In contrast to the Manchurian and Japanese-Korean floras, this flora has no temperate species of *Eranthis, Enemion,* and *Hepatica.*

Circumboreal Region

Location: main part of Europe (except extreme south), the Caucasus, Urals, Siberia, Kamchatka, North Sakhalin, North Kuril, the Aleutian Islands, Alaska, and northern Canada.

Climate: temperate to cold.

Ranunculaceae: 30 genera, 600 species. Endemic genera are absent; there are about 200 endemic species.

Okhotsk-Kamchatka Province

Location: Kamchatka Peninsula, littoral zones along the Okhotsk Sea, North Sakhalin and North Kuril, Komandor and Aleutian Islands.

Characteristic vegetation: predominately coniferous forests.

Ranunculaceae: 18 genera, 90 species (6, 18, 25, 125, 160, 322, 325, 328).

Related floras: most similar to the Manchurian (18/25, e.g., *Caltha fistulosa, Coptis trifolia, Aconitum fischeri*), Sakhalin-Hokkaidian (17/35, e.g., *Trollius macropetalus, Cimicifuga simplex, Aquilegia flabellata*), Northeastern-Siberian (13/30, e.g., *Trollius riederianus, Anemone debilis, Pulsatilla dahurica*), Arctic (10/15, e.g., *Caltha arctica, Trollius membranostylis, Anemone richardsonii*).

Observations: 15 endemic species (e.g., *Aconitum kurilense, Pulsatilla taraoi, Ranunculus recurvatus*). Numbers of species are noteworthy in *Ranunculus* (25), *Aconitum* (10), *Anemone* (10), and *Thalictrum* (10).

Northeastern Siberian Province

Location: northeastern U.S.S.R. (eastern Yakutia, Magadan district; Verkhoyansk, Chersky, and

Suntar-Hayata ridges; Jana-Indigirka, Kolyma, Anadyrj, and Korjakya uplands).

Characteristic vegetation: undersized and thinly growing mountain forests (of *Larix*), sparse groves of trees (e.g., *Pinus*), high-mountain tundras, alpine stone deserts.

Ranunculaceae: 15 genera, 70 species (25, 134, 135, 142, 151, 152, 154, 176).

Related floras: Okhotsk-Kamchatkian (13/30), Manchurian (12/20, e.g., *Actaea erythrocarpa, Aquilegia parviflora, Delphinium cheilanthum*) and Arctic (12/30, e.g., *Caltha arctica, Delphinium brachycentrum, Anemone multiceps*).

Observations: 5 endemic species (e.g., *Trollius chartosepalus, Pulsatilla magadanense, Ranunculus jacuticus*). There are some nemoral Tertiary relicts (*Anemone dichotoma, Pulsatilla dahurica, Ranunculus repens*; 135, 154, 308).

Middle Siberian Province

Location: North Siberia, between the Enisey and Lena rivers (mainly Middle Siberian and Aldan plateaus).

Characteristic vegetation: taiga, composed of coniferous forests (predominately *Larix sibirica*).

Ranunculaceae: 18 genera, 100 species (7, 25, 142, 175, 231).

Related flora: Northeastern Siberian (14/35, e.g., *Cimicifuga simplex, Delphinium crassifolium, Aconitum macrorhynchum, Anemone reflexa*).

Observations: 20 endemic species (e.g., *Aconitum contractum, Ranunculus borealis, R. smirnovii*). There are some nemoral Tertiary relicts (*Anemone altaica, A. sylvestris, Thalictrum foetidum*; 166, 195), Quaternary relicts (*Trollius asiaticus, Aquilegia sibirica, Anemone reflexa, Pulsatilla patens*; 96, 256).

Western Siberian Province

Location: North Siberia, between the Enisey and Obj rivers (Western Siberian Plain).

Characteristic vegetation: taiga (e.g., *Picea alba, Abies sibirica*).

Ranunculaceae: 15 genera, 60 species (25, 168, 169).

Related floras: Middle Siberian (14/30, e.g., *Actaea erythrocarpa, Anemone sylvestris, Ranunculus gmelinii*) and Eastern European (14/10, e.g., *Trollius europaeus, Aconitum septentrionale, Delphinium elatum*).

Observations: 5 endemic species (e.g., *Trollius kytmanovii, Anemone jenisseensis*).

Altai-Sayan Province

Location: south of Western and Middle Siberian provinces (highlands of Altai, Sayan, Kuznetskyi Alatau, Tuva, and others).

Characteristic vegetation: coniferous forests (of *Larix, Abies*, and *Pinus*); broad-leaved forests; subalpine and alpine, steppe, and tundra formations.

Ranunculaceae: 21 genera, 130 species (166, 172, 173, 195, 231, 266, 309).

Related floras: Northeastern Siberian (14/25, e.g., *Aquilegia sibirica, Anemone dichotoma, Pulsatilla flavescens, Adonis sibirica*), Transbaikalian (19/50, e.g., *Trollius lilacinus, Eranthis sibirica, Paraquilegia microphylla*), and Mongolian (18/35, e.g., *Aquilegia glandulosa, Delphinium crassifolium, Oxygraphis glacialis*).

Observations: 30 endemic species (e.g., *Aconitum sajanense, Delphinium sajanense, Pulsatilla ajanensis, Callianthemum sajanense*). Nemoral Tertiary relicts include *Actaea spicata, Cimicifuga foetida, Anemone sylvestris, Eranthis sibirica* (47, 128, 167, 182); high-mountain Quaternary relicts include *Trollius asiaticus, Anemone narcissiflora, Pulsatilla campanella* (194, 232, 256).

Transbaikalian Province

Location: Burjatia, southern parts of the Irkutsk and Chita districts (Khamar-Daban, Baikalyan and some other ridges; Vitim and Stanovoe plateaus; some depressions).

Characteristic vegetation: coniferous forest, and steppe and high-mountain formations.

Ranunculaceae: 19 genera, 100 species (142, 230, 231, 267, 319, 324).

Related floras: Altai-Sayan (19/50) and Mongolian (18/40, e.g., *Trollius ledebourii, Cimicifuga dahurica, Clematis hexapetala*).

Observations: 15 endemic species (e.g., *Aconitum montibaicalense, Aquilegia burjatica, Delphinium korschinskyanum, Ranunculus ajanensis*); large number of species of *Ranunculus* (20), *Aconitum* (15), *Thalictrum* (10), *Pulsatilla* (10), *Aquilegia* (8), and *Delphinium* (8).

Eastern European Province

Location: Southeastern Scandinavia and the European part of U.S.S.R. (mainly Russian Plain but also Crimea, Donetsk, Urals, and other highlands).

Characteristic vegetation: coniferous and broad-leaved forest, forest-steppe and meadow formations.

Ranunculaceae: 22 genera, 110 species (8, 23, 44, 96, 97, 269, 323).

Related floras: Central European (21/70, e.g., *Actaea spicata, Isopyrum thalictroides, Hepatica nobilis*), Western Siberian (14/10), and Manchurian (15/15, e.g., *Actaea erythrocarpa, Anemone reflexa, Thalictrum minus*).

Observations: 10 endemic species (e.g., *Aconitum besserianum, Delphinium sergii, Anemone biarmiensis, Ranunculus crymaeus*). There are disjunct relicts (e.g., *Anemone nemorosa, Aconitum anthora, Isopyrum thalictroides*; 156, 170). *Isopyrum thalictroides* is distributed in Central and Eastern Europe, and western Himalayas; *Pulsatilla grandis* occurs in the Alps, West Carpathians, Balkans, and Crimea, and most species of *Helleborus* (e.g., *H. purpurascens*) are distributed in Europe, but two of them (of sect. *Dicarpon*) occur in western China.

Central European Province

Location: Austria, F.R.G., G.D.R., Poland, and other countries of Central Europe, also western U.S.S.R.

Characteristic vegetation: broad-leaved forests, subalpine and alpine formations.

Ranunculaceae: 24 genera, 160 species (19, 25, 44, 49, 65, 79, 87, 119, 130, 221, 279, 291).

Related floras: Eastern European (21/70), Balkanian (23/80, e.g., *Trollius europaeus, Helleborus odorus, Aconitum paniculatum, Callianthemum coriandrifolium*), and Western Siberian (17/20, e.g., *Aconitum anthora, Anemone sylvestris*).

Observations: 20 endemic species (e.g., *Aconitum firmum, Aquilegia transsilvanica, Ranunculus carpaticus*). Most species belong to *Aconitum* (in all about 20 species, within them 10 endemics), *Aquilegia* (7 and 5), *Ranunculus* (50 and 10). Disjuncts: *Callianthemum coriandrifolium, Aconitum moldavicum*, and others.

Balkan Province

Location: main part of Yugoslavia, almost all Bulgaria, northern Greece, and the European part of Turkey.

Characteristic vegetation: high-mountain formations of forests and meadows.

Ranunculaceae: 23 genera, 140 species (44, 57, 89, 133, 317).

Related floras: Central European (23/80) and Liguro-Tyrrhenian (17/25, e.g., *Delphinium peregrinum, Anemone apennina, Pulsatilla alpina*).

Observations: 40 endemic species (e.g., *Helleborus multifidus, H. cyclophyllus*; bulb plants of the Mediterranean *Ranunculus* sect. *Ranunculastrum, Ranunculus rumelicus, R. millii*). Most species belong to *Ranunculus* (50), *Pulsatilla* (10), *Aquilegia* (8), and *Helleborus* (5 species).

Atlantic European Province

Location: Southwestern Scandinavia, Denmark, Belgium, Holland, Great Britain, Ireland, main part of France, northern F.R.G. and G.D.R., northern Spain.

Characteristic vegetation: coniferous and mostly broad-leaved forests, high-mountain formations with mixture of arctic, boreal, and nemoral elements.

Ranunculaceae: 22 genera, 110 species (44).

Related floras: Central European (22/50, e.g., *Ranunculus auricomus, R. platanifolius*) and Arctic (12/20, e.g., *Ranunculus sulphureus, R. hyperboreus*).

Observations: 20 endemic species (most of them restricted to dry rocky mountain places, e.g., *Aquilegia pyrenaica, Thalictrum tuberosum, Ranunculus pyrenaeus, R. gramineus*), including warmth-loving (e.g., *Helleborus foetidus, H. niger, Hepatica nobilis*), cold-tolerant (e.g., *Oxygraphis glacialis, Ranunculus pygmaeus*), and xerophytic (e.g., *Nigella gallica, Consolida regalis, Adonis pyrenaica*) elements.

North European Province

Location: main part of Scandinavia, northwestern U.S.S.R. (except Arctica).

Characteristic vegetation: coniferous forests (of *Picea abies* and *Pinus sylvestris*).

Ranunculaceae: 15 genera, 50 species (25, 44, 197, 207, 240).

Related floras: Atlantic and Central European.

Observations: no endemic species; most genera are represented with one or two species, except *Ranunculus* (about 25 species).

Arctic Province

Location: extreme northern Eurasia and North America.

Characteristic vegetation: tundra formations.

Ranunculaceae: 12 genera, 80 species (126, 136, 153, 164, 176, 197, 234, 313).

Related floras: Eurasiatic and Canadian taiga

(10/50, e.g., *Aquilegia sibirica, Anemone sylvestris, Ranunculus monophyllus*), also high-mountain zones (12/40, e.g., *Anemone narcissiflora, Oxygraphis glacialis, Thalictrum alpinum*).

Observations: few endemic species. About 50 species are widely distributed in Eurasia, and about 30 species occur in Eurasia and North America (e.g., *Delphinium chamissonis, Anemone richardsonii, Ranunculus affinis*). Hypoarctic elements include *Delphinium middendorffii, Ranunculus gmelinii*, and others); arctic elements include *Caltha caespitosa, Ranunculus sabinii, R. punctatus*, and others.

Caucasian Province

Location: Big and Little Caucasus mountains, Dagestan and Stavropolje hills and adjacent territories.

Characteristic vegetation: coniferous and broad-leaved (*Quercus* and *Fagus*) forests, mountain-steppe, subalpine and alpine formations.

Ranunculaceae: 19 genera, 160 species (90, 101, 102, 103, 149, 150).

Related floras: Euxinian (16/65, e.g., endemics *Trollius ranunculinus, Helleborus caucasicus, Delphinium dasycarpum, Ranunculus helenae, Ranunculus loykae, R. abchasisus*, and others), Armeno-Iranian (17/40, e.g., *Delphinium foetidum, Aconitum orientale, Pulsatilla albana, Ranunculus brutius*) and Central European (17/10, e.g., *Anemone nemorosa, Ranunculus repens*).

Observations: 45 endemic species, with most occurring in subalpine and alpine zones (e.g., *Pulsatilla aurea, Delphinium caucasicum, D. speciosum, Ranunculus baidarae, R. acutilobus*).

Euxine Province

Location: western part of the Caucasian Isthmus (Abkhasia, Adjaria, and adjacent territories).

Characteristic vegetation: like the Caucasian Province.

Ranunculaceae: 18 genera, 100 species (57, 103, 149, 157).

Related flora: Caucasian (16/65, including 25 endemic species).

Observations: 35 endemic species. In contrast to the Caucasian flora, this flora does not possess annuals of *Myosurus* and *Ceratocephalus* but does include a few perennials of *Anemone, Clematis, Delphinium* (sect. *Diedropetala*), and *Ranunculus* sect. *Ranunculastrum*).

Canadian Province

Location: Canada (Labrador, Hudson Bay, and Mackenzie districts) and Alaska.

Characteristic vegetation: coniferous forests (mainly of *Pinus, Picea*, and *Larix*).

Ranunculaceae: 13 genera, 60 species (26, 86, 99, 100, 115, 245, 315).

Related floras: Sitka-Oregonian (13/25, e.g., *Aconitum columbianum, Aquilegia formosa, Ranunculus macounii*), Appalachian (13/15, e.g., *Actaea rubra, Aquilegia canadensis, Ranunculus cymbalaria*), and Arctic (13/10, e.g., *Aconitum delphinifolium, Delphinium brachycentrum, Anemone multifida*).

Observations: few endemic species (e.g., *Ranunculus occidentalis, Thalictrum occidentalis*).

Atlantic North American Region

Location: eastern North America (from the coast of the Atlantic Ocean to the Great Basin and from southern districts of Canada to the Gulf of Mexico).

Climate: mainly temperate.

Ranunculaceae: 20 genera, 120 species (15a, 32, 33, 55, 116, 132, 144–148, 223, 290, 305, 315).

North American Prairies Province

Location: vast treeless plain in the middle of North America (Saskatchewan and Manitoba provinces of Canada, Nebraska, Iowa, Kansas, North and South Dakota, Oklahoma, and Texas states of U.S.A.).

Characteristic vegetation: grass formations (mainly of *Andropogon, Buchloë, Stipa*, and other genera).

Ranunculaceae: 12 genera, 40 species.

Related flora: Appalachian (11/18, e.g., *Aquilegia canadensis, Clematis virginiana, Thalictrum revolutum*).

Observations: 1 endemic species (*Clematis fremontii*).

Atlantic-Gulf Coastal Plain Province

Location: Coastal Plain territories in southeastern U.S.A. (parts of North Carolina, Virginia, Florida, Alabama, Mississippi, Arkansas, and Louisiana).

Characteristic vegetation: salt strands, dune, pine barrens, bog, marsh, beach and sea coast formations.

Ranunculaceae: 7 genera, 20 species.

Related flora: Appalachian (7/15, e.g., *Actaea pachypoda, Clematis virginiana*).

Observations: few endemic species (e.g., *Thalictrum cooleyi*).

Appalachian Province

Location: southeastern and south-central Canada (Ontario, Manitoba, and Quebec) and northeastern and central states of U.S.A. (Minnesota, Wisconsin, New York, Pennsylvania, Kentucky, Tennessee, and others). Mainly mountain territories (Piedmont Uplands, Alleghany, Blue Ridge, Catskill, Cumberland, Green, White mountains, Ozark Plateau, and others).

Characteristic vegetation: broad-leaved forests (*Fagus*, *Quercus*, *Acer*), with less representation of coniferous forests (*Pinus*, *Picea*, *Abies*, and other genera).

Ranunculaceae: 20 genera, 100 species.

Related floras: Canadian (13/15), Manchurian (16/5).

Observations: 3 endemic genera, 20 endemic species. All endemic genera are monotypic and are isolated morphologically within the family, e.g., *Hydrastis* (*H. canadensis*), *Xanthorhiza* (*X. simplicissima*) (stands apart from *Coptis*), and *Anemonella* (*A. thalictroides*). Endemic species belong mainly to *Clematis* (e.g., *C. addisonii*, *C. coactilis*), *Thalictrum* (*T. cooleyi*, *T. subrotundum*, and others), and *Ranunculus* (e.g., *R. harveyi*, *R. alleghaniensis*).

Rocky Mountain Region

Location: western North America (western Canada, also Washington, Oregon, Wyoming, California, and other states).

Climate: temperate to rather xerophytic.

Ranunculaceae: 17 genera, 100 species (1, 54, 55, 116, 122, 228, 259, 265, 315).

Sitka-Oregon Province

Location: western islands (e.g., Vancouver), main part of British Columbia, Washington, Oregon, and northeastern California (Selkirks, Gold Russell, and Cascade mountains).

Characteristic vegetation: predominately coniferous forests (*Picea*, *Pseudotsuga*, *Abies*, and others), subalpine and alpine formations.

Ranunculaceae: 16 genera, 80 species (mainly *Caltha*, *Coptis*, *Anemone*, *Delphinium*, and *Ranunculus*).

Related flora: Rocky Mountain (15/60, e.g., *Caltha leptosepala*, *Actaea arguta*, *Pulsatilla occidentalis*, *Trautvetteria carolinensis*).

Observations: 20 endemic species (e.g., *Caltha asarifolia*, *Coptis asplenifolia*, *Delphinium oreganum*).

Rocky Mountain Province

Location: southern Wyoming, central Colorado, and northern New Mexico (Rocky Mountains).

Characteristic vegetation: like the Sitka-Oregonian but more xerophytic.

Ranunculaceae: 16 genera, 70 species (mainly *Delphinium*, about 20 species, and *Ranunculus*, about 30 species).

Related floras: Sitka-Oregonian (15/60) and Californian (15/40, e.g., *Aquilegia chrysantha*, *Enemion stipitatum*, *Delphinium andersonii*).

Observations: 15 endemic species (e.g., *Delphinium decorum*, *Ranunculus inamoenus*, *R. oresterus*). In contrast to the Sitka-Oregonian flora, this flora includes some species of *Enemion* and few species of *Caltha* and *Coptis*. *Trollius* is absent.

Madrean Subkingdom

This subkingdom includes only the Madrean Region.

Madrean Region

Location: southwestern U.S.A. (California, Nevada, Utah, New Mexico, and other states) and almost all of Mexico.

Climate: warm and hot, dry.

Ranunculaceae: 17 genera, 130 species which are restricted to mountains and are absent in deserts and chaparral formations (1, 73, 116, 214, 273, 286, 306, 315).

Californian Province

Location: main part of California.

Characteristic vegetation: predominately coniferous (*Pinus*, *Sequoia*) and broad-leaved forest (*Quercus* and other genera), also subalpine and alpine formations and chaparral.

Ranunculaceae: 16 genera, 100 species.

Related flora: Rocky Mountain (16/40).

Observations: about 25 endemic species, mostly *Delphinium* (e.g., *D. californicum*, *D. luteum*, *D. uliginosum*). In contrast to the Rocky Mountain flora, this flora includes many species of *Delphinium* (in all about 40) and several species of *Aquilegia*, and *Myosurus*.

Great Basin Province

Location: Great Plain and Colorado Plateau (western parts of Washington, Oregon, and Cali-

fornia, almost all of Nevada, Utah, northern parts of Arizona and New Mexico).

Characteristic vegetation: predominately chaparral (of *Cercocarpus* and others), few high-mountain formations.

Ranunculaceae: 11 genera, 40 species.

Related floras: Californian (11/30, e.g., *Actaea arguta, Delphinium menziesii, Anemone globosa, A. drummondii*).

Observations: few endemic species (e.g., *Delphinium depauperatum, Anemone tuberosa*).

Sonoran Province

Location: Southeastern California, partly Arizona, New Mexico, and Texas, central Mexico.

Characteristic vegetation: desert formations.

Ranunculaceae: 5 genera, about 10 species.

Related flora: Great Basin (5/5, e.g., *Delphinium parishii, Clematis lasiantha*).

Observations: endemic species are *Delphinium parryi, Anemone sphoenophylla, Clematis pauciflora, Myosurus sessilis,* and *Ranunculus andersonii.*

Province of Mexican Highlands

Location: western and eastern Mexico (Sierra Madre Mountains, United Cordilleras).

Characteristic vegetation: predominately rather xerophytic high-mountain formations.

Ranunculaceae: 5 genera, 50 species.

Related flora: Californian (all five genera, but common species are absent).

Observations: about 40 endemic species, of which most belong to *Thalictrum* (e.g., *T. peltatum, T. lanatum, T. pubigerum*), also to *Delphinium* (e.g., *D. scopulorum*) and *Anemone* (*A. mexicana,* and others).

Ancient Mediterranean Subkingdom

This subkingdom includes four regions (Saharo-Arabian, Macaronesian, Mediterranean, and Irano-Turanian).

Location: Southern Europe, Northern Africa, and Western Asia.

Ranunculaceae: 30 genera, 500 species.

Saharo-Arabian Region

Location: extratropical Sahara, main parts of the Arabian and Sinai peninsulas and adjacent territories.

Climate: warm-temperate and hot xerophytic.

Ranunculaceae: 9 genera, 35 species (23, 29, 191, 237, 292).

Saharan Province

Location: Sahara Desert from the Atlantic coast to Egypt.

Characteristic vegetation: predominately desert formations.

Ranunculaceae: 4 genera, 10 species (e.g., *Delphinium bovei, Consolida deserti, Adonis dentata*).

Related flora: Egyptian-Arabian (4/6).

Observations: few endemic species.

Egyptian-Arabian Province

Location: eastern Egypt, Arabia, and Sinai.

Characteristic vegetation: predominately desert formations, also some mountain formations.

Ranunculaceae: 9 genera, 30 species (mainly species of *Ranunculus, Consolida,* and *Delphinium*).

Related floras: Saharan (4/6, e.g., *Adonis dentata, Nigella deserti*).

Observations: few endemic species (e.g., *Nigella assyriaca, Adonis palaestina*).

Macaronesian Region

Location: Azores, Madeira, Canary and Cape Verde islands.

Ranunculaceae: 2 genera: *Clematis* (5 species) and *Ranunculus* (30 species).

Mediterranean Region

This region includes nine provinces.

Location: southern Europe, northern Africa, and western Asia Minor.

Climate: mainly subtropical and rather arid.

Ranunculaceae: 18 genera, 130 species (23, 44, 57, 191, 200, 237, 238).

Liguro-Tyrrhenian Province

Location: southern France, southwestern Italy, islands in the Tyrrhenian and Ligurian seas (e.g., Corso, Sicily, Sardinia).

Characteristic vegetation: evergreen forest and shrub formations.

Ranunculaceae: 17 genera, 60 species.

Related floras: Iberian (16/25, e.g., *Pulsatilla rubra, Clematis cirrhosa, Hepatica nobilis*) and Balkanian (15/20, e.g., *Helleborus lividus, Aconitum anthora, Pulsatilla alpina*).

Observations: about 20 endemic species, most of which are high-mountain representatives of *Aquilegia* (e.g., *A. bernardii, A. litardieri*) and *Ranunculus* (e.g., *R. cordigerus, R. rupestris*). In contrast to the Balkanian flora, this flora has

no mesophytic species of *Caltha*, *Trollius*, *Actaea*, or *Cimicifuga*. Like other Mediterranean floras, the Liguro-Tyrrhenian flora includes a large number of annuals (about 20 species, e.g., *Delphinium halteratum*, *D. pictum*, *Nigella damascena*).

Iberian Province

Location: main parts of Pyrenees Peninsula (including Cantabrian Mountains, Sierra Nevada, Central Cordilleras).

Characteristic vegetation: like the Liguro-Tyrrhenian, but also steppe formations.

Ranunculaceae: 16 genera, 50 species.

Related flora: Liguro-Tyrrhenian (16/25).

Observations: about 10 endemic species, mostly *Aconitum* (e.g., *A. nevadense*), *Delphinium* (e.g., *D. nevadense*, *D. obcordatum*), and *Ranunculus* (e.g., *R. gramineus*, *R. abnormis*). This flora differs from the former by lacking *Eranthis*, possessing fewer species of *Helleborus* and *Aquilegia*, and having more species of *Anemone* and *Pulsatilla*.

East Mediterranean Province

Location: about all of Greece, west of Asia Minor, and adjacent parts of Syria, Lebanon, and Israel.

Characteristic vegetation: predominately shrub formations (*Arbutus*, *Spartium*, and others), partly semideserts.

Ranunculaceae: 13 genera, about 50 species.

Related flora: Mesopotamian (8/25, e.g., *Consolida regalis*, *Adonis annuus*).

Observations: about 15 endemic species (e.g., *Nigella cretica*, *N. doerfleri*, *Consolida hellespontica*, *Myosurus heldreichii*, *Ranunculus creticus*). Almost all endemics and half of the ranunculaceous species are annuals. In contrast to the previously mentioned floras, this flora has no species of *Aconitum*, *Pulsatilla*, or *Hepatica* but possesses species of *Aconitella*.

Southwest Mediterranean Province

Location: southern Pyrenees Peninsula, also northwestern Africa (mainly Morocco).

Characteristic vegetation: coniferous and broad-leaved forests (mainly cut down), shrub and grass formations.

Ranunculaceae: 9 genera, about 25 species.

Related floras: South Mediterranean (7/15, e.g., *Anemone coronaria*, *Consolida orientalis*, *Delphinium staphisagria*).

Observations: few endemic species (e.g., *Clematis campaniflora*, *Delphinium sylvaticum*). Some species (e.g., *Aconitum lamarckii*, *Helleborus foetidus*) show temperate Eurasiatic affinities.

South Mediterranean Province

Location: mainly northern Algeria and Tunis.

Characteristic vegetation: like the Southwest Mediterranean.

Ranunculaceae: 7 genera, about 20 species.

Related flora: Southwest Mediterranean (7/15).

Observations: Virtually no endemic species.

Southern Moroccan Province

Location: southern Morocco.

Characteristic vegetation: shrub and grass formations of a mixture of Mediterranean and Saharan elements.

Ranunculaceae: 5 genera, about 10 species.

Related floras: Southwest Mediterranean (5/5) and Saharan (4/4).

Observations: virtually no endemic species; species are predominately annuals (e.g., *Consolida mauritanica*, *Ranunculus muricatus*).

Balearic Province

Location: islands of Majorca, Minorca, and Pitius.

Characteristic vegetation: similar to the Iberian Province.

Ranunculaceae: 9 genera, 15 species.

Related flora: Iberian (9/10, e.g., *Helleborus lividus*, *Anemone coronaria*, *Delphinium staphisagria*, *Ranunculus bullatus*).

Observations: endemic species are only *Clematis balearica* and *Ranunculus balearicus*.

Adriatic Province

Location: coastal districts of Italy, Yugoslavia, and Albania.

Characteristic vegetation: evergreen forest and shrub formations.

Ranunculaceae: 7 genera, about 15 species.

Related floras: Balkanian (5/10, e.g., *Anemone coronaria*, *Nigella damascena*), also Liguro-Tyrrhenian (7/8).

Observations: 1 endemic species, *Ranunculus garganicus*.

Krym-Novorossiysk Province

Location: small territory of the South Crimea and the northeastern Caucasus.

Characteristic vegetation: similar to most of the Mediterranean provinces.

Ranunculaceae: 10 genera, about 30 species (25, 44, 103, 258, 269).

Related floras: Eastern European (10/25, e.g., *Aquilegia vulgaris, Adonis flammea, Ranunculus sceleratus*).

Observations: virtually no endemic species.

Irano-Turanian Region

This region includes 11 provinces.

Location: vast area of Asia Minor and Anterior, Middle, and Central Asia.

Climate: temperate, but mainly arid.

Ranunculaceae: 28 genera, 400 species. One endemic genus (*Alexeya*), 180 endemic species.

Anterior Asiatic Subregion

Location: western Irano-Turanian Region.

Ranunculaceae: 28 genera, 360 species, including about 150 endemic species.

Armeno-Iranian Province

Location: Armenia, Azerbaijan, part of Turkmenia, Southeastern Turkey, Iran, Iraq, and western Afghanistan.

Characteristic vegetation: steppe, semidesert, and desert formations, scrubs, sparse growth of trees (e.g., *Juniperus, Pistacia*), also high-mountain formations.

Ranunculaceae: 24 genera, 220 species (50, 56, 57, 91, 92, 103, 149, 225, 260, 294).

Related floras: Caucasian (19/40, e.g., *Caltha polypetala, Helleborus orientalis, Delphinium foetidum, Aquilegia olympica*), Hyrcanian (12/30, e.g., *Aconitella hohenackeri, Delphinium flexuosum*), and especially Central Anatolian (18/50, *Actaea spicata, Eranthis hyemalis, Aconitum orientale, Anemone blanda*).

Observations: about 30 endemic species, of which most belong to *Ranunculus* (in all about 80 species—10 endemic, e.g., *R. crateris, R. sintenisii*), *Delphinium* (35 and 10, e.g., *D. araraticum, D. carduchorum*), and *Consolida* (30 and 5, e.g., *C. armeniaca, C. olopetala*). All these species are restricted to open limestone high-mountain locations. There are about 60 species of annuals, mainly species of *Nigella, Consolida, Adonis*, and *Myosurus*. In contrast to the Caucasian and Hyrcanian flora, this flora consists of some species with boreal and nemoral affinities in the floras of Eastern Asia (e.g., *Paropyrum anemonoides, Isopyrum thalictroides, Actaea spicata*).

Hyrcanian Province

Location: small southeastern part of the Caucasian Isthmus (Talysh Chain).

Characteristic vegetation: relict broad-leaved forests (mainly of *Quercus castaneifolia* and *Zelkova carpinifolia*).

Ranunculaceae: 14 genera, 60 species (88, 103, 260).

Related floras: Caucasian (13/40, e.g., *Delphinium foetidum, Helleborus orientalis, Trollius ranunculinus*) and Armeno-Iranian (12/30).

Observations: 5 endemic species (among them, *Ranunculus hyrcanus, Anemone caucasica*, and *Delphinium ochroleucum*). In contrast to the previous floras, there are no species of *Actaea, Aconitum, Pulsatilla*; there are many species of *Nigella* and *Consolida*.

Central Anatolian Province

Location: northwestern Asia Minor (about half of the territory of Turkey, including the Anatolian Plateau).

Characteristic vegetation: semiarid and arid grass formations.

Ranunculaceae: 18 genera, 110 species (57).

Related floras: Armeno-Iranian (18/50) and East Mediterranean (13/20, e.g., *Thalictrum orientalis, Anemone blanda, Ranunculus asiaticus*).

Observations: about 20 endemic species, of which most belong, like the Armeno-Iranian endemics, to *Ranunculus* (in all about 50 of which 5 are endemics, e.g., *R. demissus, R. fibrillosus*), *Delphinium* (10 and 5, e.g., *D. venulosum, D. ilgarense*), and *Consolida* (10 and 5, e.g., *C. raveyi, C. thirkeana*).

Mesopotamian Province

Location: mainly Syria, Iran, Iraq, Israel.

Characteristic vegetation: semidesert and desert formations.

Ranunculaceae: 8 genera, 40 species (23, 57, 225, 237, 292).

Related floras: East Mediterranean (8/25) and Egyptian-Arabian (8/15, e.g., *Nigella deserti, Adonis palaestina*).

Observations: few endemic species (e.g., *Delphinium chodatum*). Most of species are annuals.

Turkestanian Province

Location: mountain ridges and highlands within Middle Asia (Paropamiz, Badkhyz, Karabylj, Badakhshan, Gyssar, Karatau, Nuratau, Mogoltau).

Characteristic vegetation: arid high-mountain forest, shrub and grass formations.

Ranunculaceae: 19 genera, 130 species (25, 39, 140, 141, 143, 163, 219).

Related floras: Dzungaro-Tien Shanian (19/50, e.g., endemics *Ranunculus rubrocalyx, Delphinium oreophylum, Aquilegia atrovinosa, Callianthemum alatavicum*) and Armeno-Iranian (17/20, e.g., *Eranthis longistipitata, Delphinium semibarbatum, Clematis asplenifolia*).

Observations: about 50 endemic species, including *Pulsatilla kostyczewii* of the monotypic sect. *Jostemon,* also about 10 species of *Delphinium* (e.g., *D. lipskyi, D. karategini*), 25 species of *Ranunculus* (e.g., *R. mogoltavicus, R. komarovii*), 8 species of *Aquilegia* (e.g., *A. vicaria, A. darwasi*) and *Anemone* (*A. eranthioides, A. seravshanica*—in all 10). In contrast to the Armeno-Iranian flora, this flora includes only about 10 annual species and lacks *Caltha, Actaea, Helleborus,* and *Isopyrum.* Besides that, this flora includes some alpine disjuncts (e.g., *Trollius lilacinus, Delphinium brunonianum, Paraquilegia microphylla*) that are regarded as Tertiary relicts (218).

Turanian Province

Location: eastern Transcaucasia, Caspian lowland and vast plain territories of the middle asiatic republics of U.S.S.R.

Characteristic vegetation: desert, semidesert, and dry steppe formations.

Ranunculaceae: 10 genera, 50 species (25, 39, 94, 129, 162, 163, 226).

Related floras: Turkestanian (9/25, e.g., *Anemone gortschakovii, Clematis tangutica, Thalictrum isopyroides*) and Armeno-Iranian (8/15, e.g., annuals *Consolida stocksiana, Ceratocephalus falcatus, Adonis parviflora*).

Observations: no endemic species.

Western Himalayan Province

Location: northern parts of Afghanistan, Pakistan, India, and northwestern China (Nuristan, Vasiristan, Kashmir, Simla, and other highlands).

Characteristic vegetation: subtropical formations in low zones, temperate forest, subalpine and alpine formations in high zones.

Ranunculaceae: 19 genera, 100 species (123, 179, 180, 243, 257, 283, 299).

Related floras: Eastern Himalayan (17/35, including endemics *Caltha gowaniana, Trollius acaulis, Delphinium coeruleum, Thalictrum glareosum,* and others) and Dzungaro-Tien Shanian (15/25, e.g., *Trollius dschungaricus, Hepatica falconeri, Ranunculus brotherusii, R. popovii*).

Observations: 1 local endemic genus, *Alexeya* (*A. vvedenskyi*), which is closely related to *Paraquilegia* and separated from the latter (222). Endemic species are about 35 (e.g., *Aconitum heterophyllum, Clematis barbellata, Anemone tetrasepala*). There are some disjunct relicts (e.g., *Anemone vitifolia, Actaea spicata, Isopyrum thalictroides*), which are absent in other provincial floras of the Irano-Turanian Region.

Northern Baluchistanian Province

Location: parts of Iran, Afghanistan, and Pakistan (Suleyman, Toba-Kakar, Kweta-Pishin, and other ridges).

Characteristic vegetation: high-mountain arid formations.

Ranunculaceae: 14 genera, about 50 species (91, 123, 225, 299).

Related floras: Western Himalayan (12/20, e.g., *Delphinium brunonianum, Oxygraphis involucratum, Anemone narcissiflora*) and Armeno-Iranian (14/20, e.g., *Consolida rugulosa, Clematis orientalis, Thalictrum isopyroides*).

Observations: about 5 endemic species (e.g., *Delphinium incanum, Thalictrum afghanicus*).

Central Asiatic Subregion

Location: vast territories from central Tien Shan to Big Hingan (part of territory of middle asiatic republics of U.S.S.R., Mongolia, Tibet, and North China).

Climate: temperate but rather arid.

Ranunculaceae: 23 genera, 200 species, including about 60 endemic species.

Dzungaro-Tien Shan Province

Location: a part of the territory of the Kazakh Republic (Talass, Dzungar, Tarbagatai, and other ridges, also the Kazakh small ridges).

Characteristic vegetation: high-mountain forest and grass formations, also rocky desert and dry steppe formations.

Ranunculaceae: 21 genera, 130 species (25, 39, 94, 140, 163, 226).

Related floras: Central Tien Shanian (19/60, including 25 endemic species, e.g., *Trollius dschungaricus, Aconitum karakolicum, Delphinium turkestanicum, Ranunculus gelidus*), Turkestanian (19/50), and Western Himalayan (15/25).

Observations: about 40 endemic species, of which most belong to *Aquilegia* (e.g., *A. tianschanica*), *Aconitum* (e.g., *A. nemorum*), *Delphinium* (e.g., *D. batalinii*), *Anemone* (e.g., *A. almaatensis*), and *Ranunculus* (e.g., *R. regelianus*). In contrast to the Turkestanian flora, this flora includes more species of *Aconitum*, *Callianthemum*, and *Adonis* but fewer species of *Ranunculus*, *Nigella*, and *Consolida*.

Central Tien Shan Province

Location: west of the Dzungaro-Tien Shan Terskey and Kungey Alatau, also Kirgiz and Fergana ridges.

Characteristic vegetation: like the Dzungaro-Tien Shanian, but mostly steppe formations.

Ranunculaceae: 19 genera, 70 species.

Related flora: Dzungaro-Tien Shanian (19/60).

Observations: All 25 endemic species are shared with the Dzungaro-Tien Shanian flora.

Mongolian Province

Location: Mongolia, the Kashgarian and Tsaidam hollows.

Characteristic vegetation: in the northern outlying districts (Khubsugul, Khentei, Khangai, and Mongolian Altai) predominately high-mountain forest and grass formations, in the central and southern parts predominately steppe and desert formations.

Ranunculaceae: 18 genera, about 100 species (105, 106, 108).

Related floras: Transbaikalian (18/40) and Altai-Sayan (18/35).

Observations: few endemic species (e.g., *Clematis intricata*, *Adonis mongolica*, *Ranunculus mongolicus*). Several species belong to *Aconitum*, *Clematis*, and *Ranunculus*.

Tibetan Province

Location: Pamir, Tibetan, and Tsinkhai plateaus.

Characteristic vegetation: predominately high-mountain stone tundra and desert formations.

Ranunculaceae: 20 genera, about 80 species.

Related floras: Turkestanian (16/30, e.g., *Trollius micranthus*, *Callianthemum alatavicum*, *Pulsatilla kostyczewii*) and Sikang Yunnanian (13/15, e.g., *Aconitum franchetii*, *Anemone imbricata*, *Delphinium albocoeruleum*).

Observations: 10 endemic species (e.g., *Delphinium propinquum*, *Ranunculus pamiri*, *Thalictrum ruthifolium*).

The flora of the Eastern Asiatic Region is an extraordinary mixture of tropical and temperate elements, and is considered (296, 297) as the most significant center of development of the Angiosperms, possibly the area of origin.

Within this region the flora of the Sikang Yunnan Province is extremely rich with Angiosperms; therefore, some Soviet plant geographers (159, 295, 338) regarded Southwestern China as the cradle of the modern temperate flora of Eurasia and considered the latter as derived from an ancient tropical flora. Other botanists (78, 107, 109) suggested that the primary development of the temperate mesophytic forest flora of Eurasia took place within the Eurasiatic tropical flora, possibly within Southwestern China, which has been the greatest refugium for this temperate flora.

According to the paleobotanical data (131), since Late Cretaceous time the Sikang Yunnan flora was mainly a high-mountain one, which included many temperate elements. The Yunnan Plateau is one of the most ancient mountain systems, formed in the Late Cretaceous (Yanshan movement of the earth crust—224), while the Himalayas are much more recent and belong to the alpine stage of mountain development (192). Therefore, the Eastern Himalayan flora is considered young (297).

Some plant geographers (13, 280) claim that the Manchurian flora was a significant refugium of the Tertiary warm temperate forest flora and suggest that the former coniferous–broad-leaved mesophytic forests, in which temperate elements now predominate, migrated there during the Miocene and that the flora of Manchuria has scarcely changed since.

According to Maekawa (190), a warm temperate flora developed in Japan and Korea since the Oligocene-Miocene. Tanai (304) claimed that the mesophytic coniferous–broad-leaved forests that survived there are quite similar to those in Manchuria.

Our analysis of the role of the Ranunculaceae in the provincial floras of the Eastern Asiatic Region led us to postulate that the initial differentiation of many groups of this family took place there in two diverse floristic centers, western and eastern ones. The former includes the Sikang Yunnan, Eastern Himalaya, and adjacent territories, the latter coincides with Manchuria, Japan, and Sakhalin.

The western floristic center consists of ten endemic genera and about 300 endemic species of the Ranunculaceae. Most of the endemic genera *Asteropyrum*, *Urophysa*, *Kingdonia*, *Souliea*, *Beesia*, *Calathodes*, *Semiaquilegia*, and *Dichocarpum*, are distributed disjunctively in two to four

provinces of eastern Asia and only *Archiclematis* and *Paroxygraphis* are local Eastern Himalayan endemics.

Most of the endemic ranunculaceous species within the western floristic center of eastern Asia are high mountain plants, and in this area a number of species are shared with two or three adjacent provincial floras. There are 22 genera and about 60 species (including about 20 endemics) in common with the Sikang Yunnanian, Eastern Himalayan, and Central Chinese provincial floras. These floras consist of the most primitive species of *Trollius* (*T. yunnanensis*), *Anemone* (*A. rivularis*), *Clematis* (*C. ranunculoides*), and *Aquilegia* (*A. ecalcarata*), and all of these genera include sections endemic to the western part of eastern Asia. Compared with the eastern floristic center, the western one is home to species of the disjunctive Eurasiatic genera *Helleborus*, *Paropyrum*, *Paraquilegia*, and *Oxygraphis*.

All these facts confirm our opinion concerning the close connections of the floras of the previously mentioned western provinces of eastern Asia. In the region of these western provinces during past geological periods a single high-mountain flora existed which became a center of development for several genera of the Ranunculaceae (all ten endemic genera, also *Trollius*, *Aconitum*, *Aquilegia*, *Anemone*, and *Clematis*). We do not consider the Ranunculaceae in the Eastern Himalayan Province as consisting of young species; rather, we support the opinion of van Steenis (289) about their antiquity.

The eastern floristic center in eastern Asia consists of four endemic ranunculaceous genera and about 120 endemic species. Two endemic genera, *Semiaquilegia* and *Dichocarpum*, are shared with the western center and the other two genera, *Anemonopsis* and *Miyakea*, are local endemics.

Most endemic species of Ranunculaceae in the eastern part of eastern Asia are montane forest plants. There are 17 genera and about 25 species shared by Manchuria, Japan, and Sakhalin, but there are almost no endemic species shared by two or three provinces. These floras consist of endemic sections of *Cimicifuga*, *Anemone*, *Pulsatilla*, *Clematis*, and *Coptis*. In contrast to the western floristic center, in the eastern center occur species of the disjunctive Palearctic genera *Enemion* and *Trautvetteria*, comparatively few species of *Delphinium* (absent in Japan and Sakhalin), and comparatively few *Clematis* species (especially few in Manchuria).

A comparison of the roles of the Ranunculaceae in the provincial floras of the western and eastern parts of eastern Asia indicated that only one-third of the ranunculaceous genera are common to both areas (*Caltha*, *Trollius*, *Actaea*, *Cimicifuga*, *Aconitum*, *Delphinium*, *Aquilegia*, *Anemone*, *Pulsatilla*, *Adonis*, *Thalictrum*, *Ranunculus*), and all of them are shared with the flora of the Circumboreal Region.

The facts obtained as a result of our analysis are probably best explained on the basis of the hypothesis that the Ranunculaceae probably originated in the vast land mass of Eurasia, with eastern Asia as a most significant center of secondary differentiation and conservation of many ranunculaceous genera. There were two centers of formation for genera and species of Ranunculaceae, western and eastern, which developed rather independently, though some groups migrated from one to the other. In our opinion, in the high-mountain flora of Sikang Yunnan, the Eastern Himalayas, and adjacent territories the endemic genera *Asteropyrum*, *Beesia*, *Calathodes*, *Souliea*, *Urophysa*, *Kingdonia*, *Archiclematis*, and *Paroxygraphis* evolved, as did such genera as *Trollius*, *Aquilegia*, *Anemone*, and *Clematis*. Meanwhile, in the montane forest flora of Manchuria, Japan, and adjacent territories, the endemic genera *Anemonopsis*, *Miyakea*, *Semiaquilegia*, and *Dichocarpum* evolved.

Plant geographers (77, 136, 166) regarded the Altai as the refugium of the Tertiary nemoral relicts and one of the important centers of development of the high-mountain Eurasiatic flora. They proposed that many ancient Eastern Asiatic species migrated westward through the Altai. Our data on the Ranunculaceae confirm the importance of the Altai flora in the development and distribution of many Eurasiatic groups of Angiosperms. Furthermore, endemic genera and sections of the Ranunculaceae in the Siberian provincial floras are absent, and moreover, almost no species occur in all provincial floras of Siberia. These facts can be explained if one is to suppose that contacts of Siberian floras were not close.

According to Tikhomirov (308) and Vasiljev (321), the origin of Siberian taiga floristic complexes are recent (Pleistocene), but Tolmachev (310) claimed that these complexes were more ancient (Early Pliocene). Our data support the latter opinion but show that the floristic elements of the Ranunculaceae of the northern Siberian taiga were derived from Eastern Asiatic ones. Consequently, some Siberian species of *Trollius*, *Aconitum*, *Delphinium*, *Anemone*, *Ranunculus*, and *Thalictrum* are considered today as boreal or taiga elements, but they are really related to the nemoral high-

mountain elements of the more warmth-loving floras of Manchuria and western China.

Our analysis of the Ranunculaceae of the provincial floras of Europe shows the presence of 25 genera and about 250 species. Endemic ranunculaceous genera are absent, but there are about 75 endemic species restricted mainly to the Alps, Carpathians, Pyrenees, and other highlands, and include species of *Aquilegia*, *Aconitum*, *Delphinium*, *Ranunculus*, and *Thalictrum*.

The distinctive features of the European provincial floras include not only the presence within them of many common ranunculaceous species but also historical connections with the Siberian and especially with the Eastern Asiatic floras. According to Popov (236), the Eastern Asiatic and European floras have the same age, but our data show that the latter are derivative from the former. In our opinion, therefore, the majority of the Tertiary ranunculaceous groups have migrated into Europe from the east during the Pliocene and became preserved there in the Alps, Carpathians, and other mountains. More recently, in these territories intensive radiation of new groups of *Aconitum*, *Delphinium*, and *Aquilegia* took place.

Our data from analysis of the role of the Ranunculaceae in arctic regions uphold the opinion of Tolmachev (312) and Budantsev (36) concerning the comparatively recent age of the arctic floristic complexes and their derivation from boreal and partly from nemoral complexes. Contrary to some plant geographers (95, 314, 320) who consider the territory of the Arctic Province as a floristic region or a special zone without division into regions and provinces, we follow Takhtajan's (297) interpretation of this province.

The Caucasus was a remarkable center in the formation of some high-mountain groups of Angiosperms in the Late Pliocene and Pleistocene (77, 101, 102, 193, 293). These groups originated out of subtropical-forest species (complexes of the Poltava flora—170), but some of them migrated there from the east, mainly from eastern Asia.

We note also the presence within the modern Caucasian flora of 22 genera and about 230 species of Ranunculaceae (about 60 endemic). Almost all ranunculaceous genera in the Caucasian provincial floras are shared with those in the European and Siberian floras of the Circumboreal Region. Most species of these genera (*Aquilegia*, *Aconitum*, *Delphinium*, *Anemone*, *Pulsatilla*, *Clematis*, and *Thalictrum*) occur in eastern Asia and Siberia.

Some genera (e.g., *Nigella*, *Consolida*, *Ceratocephalus*) occurring in the Caucasian floras are shared with the floras of the Mediterranean Region. In the flora of the Caucasus, there are some Eurasiatic disjuncts (e.g., *Actaea spicata*, *Anemone nemorosa*), which are generally accepted as Tertiary relicts. These data led us to hypothesize close connections among the ranunculaceous groups in Eurasia (including the Caucasus) during past periods and to hypothesize possible migrations of their ancestral groups into the Caucasus from the east.

The membership within the Ranunculaceae of large numbers of Caucasian endemics indicates local differentiation of this family in the high-mountain zones, especially within *Delphinium* and *Ranunculus*. Most of the Caucasian endemic species (e.g., *Aquilegia colchica*, *Delphinium pyramidatum*, *Anemone speciosa*, *Aconitum pubiceps*, *Ranunculus helenae*) originated in the Western Caucasus (or Colkhis), which is considered to be a significant refugium of the Late Tertiary warm-temperate forest flora. Another large Tertiary floristic refugium, which was in the Eastern Caucasus (Hyrcan or Talysh), did not play a large role in the differentiation of the Ranunculaceae and hence the Talysh endemic species of this family are not numerous. The evolution of the ranunculaceous flora of these two centers developed independently, and shared endemics as well as vicariant species of Ranunculaceae are almost absent.

Some species of Ranunculaceae in the Caucasian floras are shared with the Mediterranean Region or are closely related to species there. They are predominately annual xerophytes (e.g., *Nigella arvensis*, *Consolida ambigua*, *Ceratocephalus testiculatus*, *Adonis aestivalis*). The Caucasian ranunculaceous species with connections in Anterior Asia are xerophytic and mainly annual (e.g., *Delphinium cyphoplectrum*, *Consolida divaricata*, *Nigella orientalis*, *Aconitella hohenackeri*, *Thalictrum sultabadense*). At the same time, within the ranunculaceous species shared between the Caucasus and Asia Minor, many are high-mountain, mesophytic, mainly forest plants (e.g., *Caltha polypetala*, *Trollius ranunculinus*, *Aquilegia caucasica*, *Anemone impexa*, *Pulsatilla violacea*).

All previously mentioned data led us to suggest close connections of the ranunculaceous groups in Eurasia (including the Caucasus) in past periods; possible migration into the Caucasus of some ancestral groups of this family from the east through Asia Minor and some xerophytic groups from the Mediterranean Region; evolution of some groups within the Caucasian flora itself.

According to the literature, the flora of the Appalachian Province of the Atlantic North American Region is ancient (mainly Tertiary), whereas the

flora of the North American Prairies and the Atlantic-Gulf Coastal Plain provinces are comparatively recent and derivative. Our data support this conjecture, including close relationships of the boreal floras of Eurasia with those of North America while, on the other hand, maintaining that there were relatively prolonged disconnections of the floras in the western and eastern parts of both continents (31, 98, 184). These floristic events were promoted by means of sea barriers (ancient Siberian Sea and the Straits of Mexico) and Miocene and more recent land bridges between Eurasia and North America through the Pacific and Atlantic oceans (135, 251).

Seventeen ranunculaceous genera are shared by North American and Eurasian boreal floras. It is remarkable that more than half of them (*Caltha*, *Actaea*, *Cimicifuga*, *Aconitum*, *Delphinium*, *Clematis*, *Anemone*, *Pulsatilla*, *Ranunculus*, and *Thalictrum*) consist of sections with Eurasiatic–North American distributions. Although species in common to these floras are few (e.g., *Anemone narcissiflora*, *Thalictrum alpinum*, *Ranunculus pedatifidus*), pairs of corresponding or closely related species are numerous (e.g., *Actaea spicata–A. rubra*, *Trautvetteria japonica–T. grandis*, *Enemion raddeanum–E. biternatum*).

Our analysis showed that the territories of the Appalachian and Rocky Mountain provinces were important centers of North American differentiation of the Ranunculaceae. Within the former, the relict genera *Hydrastis*, *Xanthorhiza*, and *Anemonella* evolved, and within both of them, some sections of *Trollius*, *Aquilegia*, *Ranunculus*, *Thalictrum*, *Enemion*, and *Cimicifuga*. Possibly, the two last-mentioned genera originated within these floras. Compared with the peculiarities of distribution of species of *Hydrastis*, *Xanthorhiza*, and *Anemonella* (they occur disjunctively through about ten states in the Appalachian province, e.g., Illinois, Tennessee, Virginia, and others), we regard the age of these genera (at least that of *Enemion*) as more recent than the Eastern Asiatic endemic genera (e.g., *Beesia*, *Calathodes*).

A comparison of the distribution of the Ranunculaceae in all four regions of the Boreal Subkingdom (Eastern Asiatic, Circumboreal, Atlantic North American, and Rocky Mountain) showed the considerable floristic role of this family in each. These data form the basis of our supposition that the development of the Ranunculaceae took place over a long period of time within the Tertiary warm-temperate flora which was in common to all circumpolar territories of the Northern Hemisphere (31, 296). We regard western and eastern parts of eastern Asia and eastern North America (Appalachians) as significant refugia of this ancient flora. The Altai-Sayan Ridges, Alps, Carpathians, Pyrenees, Caucasus, and the Rocky Mountains were, in our opinion, secondary centers of the differentiation of some groups of the Ranunculaceae.

In the Madrean Region of the Madrean Subkingdom all ranunculaceous species are concentrated on mountain slopes, and they are mainly members of the Californian and Mexican Highland provinces. These species are scanty in chaparral formations and absent in deserts. All genera of the Ranunculaceae are in common to those in both Eurasiatic and North American floras of the Boreal Subkingdom, but species in common are few and most of them are relict disjuncts. The mountains of California were one of the secondary centers of differentiation of *Delphinium*, and some groups of *Thalictrum* evolved in the Mexican Highlands.

Our analysis of the Ranunculaceae within the Madrean Region upholds the suspected (251, 286) relationships of many northern Californian groups of species with those in the boreal floras in both western and eastern North America, and, moreover, with those in boreal Eurasia. Stebbins & Major (251) regarded *Trautvetteria grandis*, *Delphinium californicum*, *Clematis occidentalis*, *Anemone quinquefolia*, and some other disjuncts as relicts of Tertiary deciduous mesophytic forests, although most endemic species of *Delphinium* have a more recent age, and our data confirm that hypothesis. It is remarkable that 15 genera of the Ranunculaceae are in common to the floras in the above-mentioned regions of the Boreal and Madrean subkingdoms.

The modern flora of the regions of the Ancient Mediterranean Subkingdom is rather xerophytic, but the Ancient Mediterranean flora developed as a derivative and mainly migratory one from boreal and tropical mesophytic floras. Most of the Angiosperms in the Mediterranean flora are related to corresponding Eastern Asiatic groups (Popov—235).

Within the Mediterranean Region the floras of the Liguro–Tyrrhenian and Iberian provinces are quite rich with Ranunculaceae. They are similar to the Balkanian flora of the Circumboreal Region but much different from the rest of the Mediterranean provincial floras. At the same time, the flora of the East Mediterranean Province is related to the most xerophytic provincial floras of the Irano-Turanian Region (e.g., Mesopotamian), and within the former about half of the species of Ranunculaceae are annuals.

Our analysis of the Ranunculaceae within the Mediterranean floristic provinces showed their xerophytic features (presence of many annuals and bulb plants) and clear connections with mesophytic groups of this family in the floras of the Boreal Subkingdom, especially with those in the high-mountain floras of Southern Europe.

Within the Irano-Turanian Region, most Ranunculaceae belong to the provincial floras of the Anterior Asiatic Subregion, while in the floras of the Central Asiatic Subregion there are relatively few Ranunculaceae. Most ranunculaceous representatives are concentrated in the flora of the Armeno-Iranian Province, which is surpassed worldwide for the richness of the Ranunculaceae only by the Sikang Yunnan Province. Nevertheless, the number of endemic species is remarkably low, especially as compared with the flora of the Sikang Yunnan Province (30/220 vs. 180/400—see Table 1). Within Ranunculaceae predominate species with boreal and nemoral affinities predominate in the floras of eastern Asia and South Siberia. These phenomena confirm the close connections between the Armeno-Iranian, South Siberian, and Eastern Asiatic floras and might reflect that the ancient flora of Anterior Asia was once more mesophytic.

From an analysis of the role of the Ranunculaceae in the provincial floras of the Irano-Turanian Region, we note that the highlands of Middle Asia (Pamiro-Alai, Tien Shan, and others) were sites of secondary formation of some groups of this family (more than 100 endemic species of *Aconitum*, *Delphinium*, *Aquilegia*, *Anemone*, and *Ranunculus*). The floras of the Turkestanian, Dzungaro-Tien Shan, and Central Tien Shan provinces are very similar in terms of Ranunculaceae. This phenomenon reflects the autochthonous development of the Mountain Middle Asiatic flora on the base of the ancient boreal groups of Angiosperms (Kamelin, 140, called them the Turkmenian and the Himalayan-Mediterranean branches). According to Pavlov (227) and Vykhodtsev (329), most of the Middle Asiatic mountain endemics are recent (Quaternary) and progressive, while Ovchinnikov (218) claimed that within them are some relict elements of nemoral complexes with certain Eastern Asiatic relatives (e.g., disjuncts *Trollius lilacinus*, *Delphinium brunonianum*, *Hepatica falconeri*, *Paropyrum anemonoides*). We agree therefore with Kamelin (140) that the Mountain Middle Asiatic flora, including the floras of the Tien Shan, is a single unit.

The Armeno-Iranian and Central Anatolian provincial floras are similar to the flora of the Mediterranean Region and are much different from the floras of Mountain Middle Asia. There are many annuals (species of *Consolida*, *Nigella*, and others), but almost no endemic species of the Ranunculaceae. Species in common to the floras of Mountain Middle Asia, Armeno-Iranian, and Central Anatolian provinces are few, especially within *Aconitum*, *Delphinium*, *Aquilegia*, *Anemone*, and *Pulsatilla*. Meanwhile, the two last-mentioned floras include some genera and many species shared with those in the Caucasian floras but absent in both the Middle Asiatic and Mediterranean floras (e.g., *Caltha polypetala*, *Helleborus orientalis*, *Actaea spicata*, *Isopyrum thalictroides*). It is remarkable that *Caltha*, *Helleborus*, *Actaea*, and *Isopyrum* are boreal mesophytes with many species in both the floras of the Eastern Asiatic and Circumboreal regions.

The floristic richness of the Ranunculaceae in the floras of the Western Himalayan and North Baluchistanian provinces is intermediate between the high-mountain floras of Middle and Eastern Asia.

The Ranunculaceae in the Central Asiatic provincial floras, both Mongolian and Tibetan, consist of few endemic species. The outlying northeastern districts are related to those in the Altai-Sayanian and West Chinese floras.

We conclude that the flora of the Ancient Mediterranean Subkingdom played a noteworthy role in the differentiation of the Ranunculaceae largely because of the evolution of annual (*Nigella*, *Consolida*, and *Aconitella*) and bulb plants (species of *Anemone* and *Ranunculus*). Within the high-mountain floras, some groups of ranunculaceous endemic species recently evolved.

PALAEOTROPICAL KINGDOM

Location: territories of Southeastern Asia and Africa, also adjacent islands.

Climate: mainly tropical.

Ranunculaceae: 11 genera, 100 species.

Indo-Malesian Subkingdom

This subkingdom includes four regions: Malesian, Fijian, Indo-Chinese, and Indian.

Location: Hindustan and Indo-China, also numerous islands in the Indian and Pacific oceans.

Ranunculaceae: 6 genera, 80 species.

Malesian Region

Location: south of the Malacca Peninsula, the Malaya Archipelago, New Guinea, and adjacent little islands.

Ranunculaceae: 5 genera, 60 species (12, 51, 70, 177, 178, 202, 203, 204, 287, 288, 289).

Characteristic vegetation: tropical forests in lowlands, also insular high-mountain formations.

Malaccan Province

Location: Malacca Peninsula and some little islands.

Ranunculaceae: 3 genera, 5 species (*Anemone sumatrana, Clematis smilacifolia, C. meyeniana, Naravelia dasyneura, N. laurifolia*).

Related floras: South Malesian (3/5) and Kalimantanian (2/3).

Observations: no endemic species.

Kalimantan, Moluccan, and Bismarckian Provinces

Ranunculaceae: 3/4, 1/2, and 1/1. Endemic species are few (e.g., *Ranunculus lowii*).

Philippinean Province

Ranunculaceae: 5 genera, 15 species.

Related floras: South Malesian (5/3, e.g., *Naravelia laurifolia, Clematis lechenaultiana*).

Observations: 6 endemic species (e.g., *Naravelia pauciflora, Clematis antonii, Ranunculus philippinense, Thalictrum philippinense*).

South Malesian Province

Ranunculaceae: 5 genera, 15 species.

Related floras: Malaccan (3/5) and Philippinean (5/3).

Observations: 5 endemic species (e.g., *Clematis korthalsii, Ranunculus javanicus, Thalictrum javanicum*).

Sumatran Province

Ranunculaceae: 5 genera, 10 species.

Related flora: South Malesian (5/8, e.g., common endemics *Ranunculus javanicus, Clematis javanica*, and others).

Observations: 5 endemic species (e.g., *Anemone angustiloba, Ranunculus sundaicus*).

Sulawesian Province

Ranunculaceae: 2 genera, 15 species.

Related floras: South Malesian (2/2, e.g., *Ranunculus blumei*).

Observations: about 15 endemic species (e.g., *Clematis molissima, Ranunculus celebicus, R. frigidurbis*).

Papuan Province

Ranunculaceae: 3 genera, 30 species.

Related flora: Sulawesian (2/2, e.g., *Clematis pickeringii*).

Observations: about 30 endemic species (e.g., *Clematis papuasica, C. phanerophlebia, Ranunculus bellus, R. brassii*).

Fijian Region

Location: Fiji, New Hebrides, Samoa, Tonga, and adjacent small archipelagoes.

Ranunculaceae: 3 genera, 4 species (*Clematis pickeringii, Ranunculus perindutus, R. keysseri, Thalictrum papuanum*—274).

Related flora: Papuan (2/2, e.g., *Clematis pickeringii, Thalictrum papuanum*).

This region includes the Fijian and Hebridean provinces.

Indo-Chinese Region

Location: peninsular Indo-China, adjacent continental territories (Southeastern Bangladesh, Southeastern Burma, South China, Thailand, Laos, Kampuchia, and Vietnam), also Andaman and Hainan islands.

Ranunculaceae: 6 genera, 25 species (21, 70, 277, 299, 302).

Related floras: Eastern Asiatic (6/10, e.g., *Clematis acuminata, Ranunculus chinensis, Thalictrum punduanus*) and Malesian (5/5, e.g., *Clematis smilacifolia, Naravelia laurifolia*).

Observations: few endemic species (e.g., *Clematis thaiana, Thalictrum siamense*).

Indian Region

Location: peninsular Hindustan, Ganges Plain, South Foothills of the Himalayas, and some islands (e.g., Sri Lanka).

Ranunculaceae: 6 genera, about 10 species (123, 262); all ranunculaceous species are concentrated in the high-mountain flora of the Deccan Plateau, West and East Gaty ridges.

Related floras: Eastern Himalayan (5/5, e.g., *Anemone rivularis, Clematis nutans, C. grewiaflora*), Malesian (5/3, e.g., *Anemone vitifolia, Naravelia laurifolia*), and African (5/2, e.g., *Delphinium dasycaulon* and *Clematis grata*).

Observations: few endemic species (e.g., *Clematis triloba, Naravelia zeylanica, Thalictrum dalzellii*).

Polynesian Subkingdom

Location: many islands of Polynesia, Hawaii, and Micronesia.

This subkingdom includes two regions—Polynesian and Hawaiian—and three provinces—Micronesian, Polynesian, and Hawaiian.

Ranunculaceae: 1 genus and 2 species (*Ranunculus hawaiensis* and *R. mauensis*—45).

Neocaledonian Subkingdom

This subkingdom includes only the Neocaledonian Region and the Neocaledonian Province.

Location: New Caledonia.

Climate: tropical.

Ranunculaceae: only *Clematis pickeringii* (110).

African Subkingdom

This subkingdom includes four regions—Guineo-Congo, Sudano-Zambesian, Karroo-Namib, and St. Helena and Ascension islands.

Location: main part of the African continent to latitude 20°S, also tropical deserts in the south of the Arabian Peninsula and in Anterior Asia.

Climate: tropical, but in highlands more or less temperate.

Ranunculaceae: 8 genera, 50 species (3, 34, 69, 72, 117, 121, 127, 206, 217, 242, 252, 282, 318). The Ranunculaceae are absent in tropical deserts and semideserts; are scarce in tropical rainforests and arboreal woodlands in low places of northern, western, and central tropical Africa; and are important in tropical mountain and afroalpine floras (117, 118).

Guineo-Congo Region

Location: territories adjacent to the Guinean Bay, including North Angola and the Congo Basin, and western Kenya, Tanzania, and Uganda.

Characteristic vegetation: predominately tropical forests and savannas, also highland formations in the extreme east.

Ranunculaceae: 7 genera, 40 species concentrated in the Congo Province, but absent in the Guinea Province.

Related floras: Sudano-Zambesian (6/15, e.g., *Anemone thomsonii, Clematis simensis, Delphinium leroyi, Thalictrum rhynchocarpum*), Cape (7/10, e.g., *Knowltonia transvaalensis, Delphinium leroyi, Clematopsis hombleyi, Ranunculus multifidus*), and Western Chinese (5/2, e.g., *Clematis grata* and *Delphinium dasycaulon*).

Observations: about 20 endemic species (e.g., *Delphinium macrocentron, Clematis dolichopoda, Thalictrum zernyi, Ranunculus aberdaricus*). Most species belong to *Clematis* (about 15) and *Ranunculus* (about 20). Endemic species occur mainly in the upper belts of Elgon, Kilimanjaro, Aberdare, and other mountains at elevations of 2,500–4,500 m.

Sudano-Zambesian Region

Location: vast territories of western, central, eastern, and southern Africa, also territories in the Arabian Peninsula and southwestern Asia.

Characteristic vegetation: predominately savanna and desert formations, some high-mountain areas.

This region includes the Sahelian, Nubo-Arabian, Omano-Rajastanian, Socotran, South Arabian, Sudanian, Somalo-Aethiopian, and Zambesian provinces.

Ranunculaceae: 8 genera, about 30 species mostly in the two last-mentioned provinces.

Related floras: Guineo-Congo (6/15) and Cape (6/5, e.g., *Clematis welwitchii, Clematopsis scabiosifolia, Thalictrum rhynchocarpum*).

Observations: about 10 endemic species (e.g., *Clematis inciso-dentata, Delphinium wellbyi, Ranunculus oligocarpus*).

In the floras of the Karroo-Namib Region and the region of the St. Helena and Ascension islands, Ranunculaceae are almost absent.

Madagascan Subkingdom

This subkingdom includes only the Madagascan Region.

Location: Madagascar and adjacent islands (e.g., Komory, Seychelles, and others) to the east of the African continent.

Madagascan Region

Location: Madagascar.

Characteristic vegetation: predominately tropical forests.

Ranunculaceae: 4 genera, about 10 species (e.g., *Clematis stanleyi, Clematopsis bojeri, Ranunculus madagascarensis, Knowltonia vesicatoria*—16, 252).

Related floras: Sudano-Zambesian (4/2).

Observations: few endemic species.

The Indo-Malesian Subkingdom is regarded as the greatest refugium of the Palaeotropical Angiosperms in which were preserved many endemic and relict families and genera (10, 296, 337). There are few ranunculaceous representatives, and they occur mainly in the mountain flora of this subkingdom. Lam (177) and van Steenis (287) regarded *Anemone*, *Ranunculus*, and *Thalictrum* as examples of temperate genera that penetrated the Malesian tropical mountain flora from temperate eastern Asia through ancient mountain ridges. Our data do not challenge this idea. Possibly, the Ranunculaceae migrated through Malesia in the Southern Hemisphere by two different routes. The western route went through Sumatra, Kalimantan, and Java, and the eastern one passed through the Philippines, Molucca, Sulavesi, and New Guinea. Van Steenis (288) and Aubreville (9) supposed these groups of islands to be the distinct centers of development and dispersal of the Angiosperms: the former island group was related to the Southeastern Asiatic floristic center, while the latter group was home to part of the Australo-Papuan flora.

The formation of uplands in New Guinea in the Late Oligocene limited north-to-south penetration by high-mountain Ranunculaceae (201, 202, 248). After that time some endemic groups of *Clematis* and *Ranunculus* evolved in the highlands of Malesia. Areas of some species (e.g., *Naravelia dasyneura*, *Anemone sumatrana*, *Clematis lechenaultiana*) occur in the adjacent Indo-Chinese, Malesian, and Indian regions, while some other species (e.g., *Anemone vitifolia*, *Clematis meyeniana*) occur disjunctively also in the highlands of West China, the Himalayas, and Japan. The most interesting area has *Clematis pickeringii* because it includes Malesia, New Caledonia, and northeastern Australia.

In the flora of the African Subkingdom only two genera are restricted to Africa and Madagascar: *Clematopsis*, which is related to *Clematis*, and *Knowltonia*, which is related to *Anemone*. The rest of the ranunculaceous genera (*Anemone*, *Clematis*, *Delphinium*, *Nigella*, *Ranunculus*, and *Thalictrum*) are shared by the floras of the Boreal and Ancient Mediterranean subkingdoms, and many species of them are related to the species of the latter subkingdom. For example, *Anemone thomsonii* is distributed in the alpine and subalpine belts of Mount Kilimanjaro and a related species, *A. glaucifolia*, grows in high mountains of western China. *Clematis grata* and *Delphinium dasycaulon* are common to the floras of western China, the Himalayas, and in Hindustan.

Our analysis of the distribution of the Ranunculaceae in Africa confirms Hedberg's (117, 118) and Boughey's (27) suggested existence of the Ancient Tropical Mountain flora in Africa and the possible connections between the Afro-Alpine and Boreal floras of Africa and Eurasia in past periods. We suppose that the ranunculaceous representatives migrated into Africa from Eurasia by means of some ancient land bridges (e.g., Sunda, Arabian) that existed there until the Late Cretaceous and early Quaternary (246, 250, 335). Afterwards, formation of the mountain ridges in eastern Africa (dated as Miocene) promoted development of the high-mountain groups of Ranunculaceae and migration of some of them into South Africa, where cold and temperate conditions existed until the Cretaceous (53). Few groups (e.g., species of *Clematis*, *Clematopsis*, and *Knowltonia*) migrated southward and secondarily became adapted to the tropical conditions of Africa.

CAPE KINGDOM

Location: southern tip of Africa.

This subkingdom includes only the Cape Region.

Characteristic vegetation: predominately sclerophyllous scrub and forest formations.

Ranunculaceae: 7 genera, about 30 species.

Related floras: Guineo-Congo (7/10) and Sudano-Zambesian (6/5).

Observations: about 10 endemic species (e.g., *Clematis brachiata*, *Knowltonia hirsuta*, *Ranunculus cooperi*). Some endemics (e.g., *Anemone capensis* and *A. alchemillifolia*) are related to endemics in the floras of the Eastern Asiatic Region.

The Cape flora is extraordinarily rich and distinctive (297), but the Ranunculaceae in it are rather few and are related to those in the floras of the African and Boreal subkingdoms.

NEOTROPICAL KINGDOM

Location: southern Florida in North America, lowlands of Mexico, Central America, and South America (except the extreme south), also adjacent islands.

Climate: tropical in lowlands, temperate in highlands.

Ranunculaceae: 9 genera, 70 species.

This kingdom includes five regions: Caribbean, Amazonian, Brazilian, Andean, and the Guayana Highlands.

Caribbean Region

Location: extreme southern North America (tropical Florida), almost all Central America, and some islands mainly in the Caribbean Sea.

Ranunculaceae: 3 genera, about 20 species (2, 67, 281).

Galapageian Province

Location: Galapagos Islands.

Ranunculaceae: absent.

West Indian Province

Location: Cuba, Jamaica, and other Caribbean islands.

Ranunculaceae: 2 genera, 5 species (e.g., *Clematis dioica, C. havanensis, Ranunculus cubensis*).

Central American Province

Location: Guatemala, Honduras, Nicaragua, Costa Rica, and Panama.

Ranunculaceae: 3 genera, about 20 species.

Related floras: Mexican Highlands (3/5, e.g., *Clematis haenkeana, Ranunculus donianus, Thalictrum hintonii*) and Andean (3/10, e.g., *Ranunculus flagelliformis, R. peruvianus, Thalictrum panamense*).

Observations: 6 endemic species, all *Thalictrum* (e.g., *T. guatemalense, T. standleyi*).

Region of the Guayana Highlands

Location: Guayana Plateau (southern Venezuela, western Guyana, western Colombia, and northern Brazil).

Characteristic vegetation: as in the previous and next two regions, predominately tropical forests, savannas, hylaeas, campo limpo, and chaco formations.

Ranunculaceae: 2 genera, 4 species (e.g., *Clematis dioica, Ranunculus apiifolius*).

Amazonian Region

Location: Amazon Basin in Brazil.

Ranunculaceae: 1 genus, 2 species (e.g., *Clematis brasiliana*).

Brazilian Region

Location: main part of Brazil, eastern Paraguay, Bolivia, and northern Argentina.

Ranunculaceae: 2 genera, 5 species (e.g., *Clematis hilarii, Ranunculus platensis*—186, 187, 188).

Andean Region

Location: Andean ridges from Venezuela to northern Chile. Predominately highlands with summits (e.g., Chimboraso and Christóbal Colón) of about 5,000–6,000 m.

Characteristic vegetation: predominately high-mountain formations of temperate elements.

Ranunculaceae: 9 genera, 60 species (59, 71, 83, 186, 189).

Related floras: Mexican Highlands (5/20, e.g., *Clematis sericea, Anemone decapetala, Myosurus apetalus, Thalictrum podocarpum*) and Chile-Patagonian (5/10, e.g., *Caltha sagittata, Myosurus aristatus, Anemone helleborifolia*).

Observations: 2 endemic genera and about 30 endemic species. The endemic genera, local and monotypic, are represented by *Oreithales integrifolia* and *Laccopetalum giganteum*, which are distributed in Peru, Bolivia, and Ecuador at about 4,000 m. Endemic species belong mainly to *Ranunculus* (about 20—e.g., *R. pilosus*), but some endemics include *Clematis* (e.g., *C. albo-rosea*), *Anemone* (e.g., *A. jamesonii*), and *Thalictrum* (e.g., *T. longistylum*).

Summing the data of the analysis of the Ranunculaceae in the floras of the Neotropical Kingdom, we must keep in mind that North America was separated from South America with a relatively wide sea space during Cretaceous and Paleogene time (250). On the other hand, until the Oligocene South America was joined through the subantarctic bridge with Antarctica which at that time was covered with cool temperate forests (246, 248). The Andes were formed in the Pleistocene and after that they became an important transtropical bridge for the migration of temperate floristic elements from North America to South America and vice versa (211, 246).

Species of *Thalictrum* and *Anemone multifida* migrated through the Andes from the north. In fact, most of the species allied to the Andean species are distributed in North and Central America (e.g., species of *Thalictrum*, sects. *Camptogastrum* and *Pelteria*, species of *Anemone*, series *Multifida*). But some species of *Clematis* sect. *Clematis*, subsect. *Dioicae* and *Aristatae*, *Anemone* sect. *Rivularidium*, *Caltha* sect. *Psychrophila*, and *Ranunculus* sect. *Trollianthoidea* were found almost exclusively in South America, richly represented

in the Andes and with relatives in the extreme south of the Southern Hemisphere.

The Andean high-mountain flora was one of the important centers of ranunculaceous differentiation. There are two distinct monotypic endemic genera in this flora, *Oreithales* and *Laccopetalum*. The former is hexaploid and seems to be derived from *Anemone* (32, 68); the latter differs from other Ranunculaceae by possessing a large number of nectary glands and possessing large unbroken leaves (length over 40 cm).

HOLANTARCTIC KINGDOM

Location: territory of South America to latitude 30°S, some islands in the southern extremity and New Zealand.

Climate: temperate and mainly cold.

Ranunculaceae: 8 genera, 100 species.

This kingdom includes four regions: Chile-Patagonian, Fernandezian, Neozeylandic, and South Subantarctic islands.

Chile-Patagonian Region

Location: Chile, Uruguay, central and southern Argentina, Tierra del Fuego, Falklands and other islands.

Characteristic vegetation: coniferous (*Araucaria* and other genera), deciduous and evergreen (*Nothofagus*) forests, sclerophyll shrubs, cushion heath, dry grassy places, cold boggy sites, and alpine meadow formations.

Ranunculaceae: 7 genera, 50 species (186, 188, 210, 212).

North Chilean and Middle Chilean Provinces

Location: territory of Chile.

Ranunculaceae: 8 genera, about 30 species.

Related floras: Andean (5/10), Pampean (3/5, e.g., *Caltha sagittata*, *Ranunculus biternatus*) and Magellanian (3/5, e.g., *Caltha sagittata*, *Ranunculus biternatus*).

Observations: 10 endemic species (e.g., *Anemone rigida*, *Ranunculus chilensis*). There are some species of two endemic genera, *Barneoudia* (e.g., *B. chilensis*, *B. major*) and *Hamadryas* (e.g., *H. argentea*).

Pampean Province

Location: southern Brazil, partly Argentina and Uruguay.

Ranunculaceae: 3 genera, about 10 species.

Related floras: Chilean (3/5).

Observations: few endemic species (e.g., *Anemone decapetala*, *Clematis bonariensis*).

Patagonian Province

Location: southern Argentina.

Ranunculaceae: 3 genera, 5 species (e.g., *Ranunculus patagonicus*, *Myosurus patagonicus*).

Magellanian Province

Location: Magellanian and adjacent islands.

Ranunculaceae: 3 genera, about 15 species.

Related flora: Chilean (3/5).

Observations: 10 endemic species (e.g., *Hamadryas magellanica*, *Caltha appendiculata*, *C. dioneifolia*).

Fernandesian Region

Location: Juan-Fernández and Desventuradas islands.

Ranunculaceae: absent.

South Subantarctic Islands Region

Location: Tristan d'Acunha, Kerguelen, and adjacent islands.

Ranunculaceae: 1 genus, 5 species (e.g., endemic *Ranunculus carolii*).

Neozeylandic Region

Location: New Zealand and adjacent islands.

Ranunculaceae: 5 genera, 60 species (5, 45, 80, 111, 196, 336).

Related flora: Chile-Patagonian (5/2, e.g., *Ranunculus acaulis*, *R. biternatus*).

Observations: about 55 endemic species (e.g., *Caltha obtusa*, *Clematis australis*, *Myosurus novae-zelandiae*, *Ranunculus gracilipes*). Most species occur in the South Island only, while some (e.g., *Ranunculus insignis*, *Caltha novae-zelandiae*) are distributed in North Island and South Island. The majority of species are high-mountain plants, and a few (e.g., *Clematis afoliata*, *Ranunculus rivularis*) occur in low-mountain zones or plains.

Our analysis showed that within the Holantarctic Kingdom the Ranunculaceae are distributed mainly in the temperate highlands or in very cold plains. Two endemic oligotypic genera, *Barneoudia* and *Hamadryas*, were formed in the Chile-Patagonian Region, while in the high zones of mountains of extreme southern South America and New Zealand some groups of the Ranunculaceae (mainly *Ranunculus*) developed, evidently from common

ancestors. Fisher (80) noted the predominance of polyploids within the New Zealand species of *Ranunculus* and listed 10 pairs of alpine species with one member in New Zealand and the other member a similar South American species (e.g., *R. haastii–R. semiverticillatus* and *R. nivicolus–R. caprarum*). Consequently, Fisher supposed that high-elevation New Zealand *Ranunculus* was derived from the South American one, not from Malesian species.

Mountain ridges in New Zealand formed in the Late Pliocene (248), along with the rise of the mountains in Australia and New Guinea. According to Raven (248) and Wardle (334) the initial species of *Anemone*, *Clematis*, and *Ranunculus* arrived in New Zealand from South America in the Late Pliocene or later, while species of *Caltha* already spread there in the Paleogene.

AUSTRALIAN KINGDOM

Location: Australian continent.

Ranunculaceae: 5 genera, about 50 species.

This kingdom includes the Southwest, East, and Central Australian regions.

East Australian Region

Location: Queensland, New South Wales, Victoria, and Tasmania.

Characteristic vegetation: high-mountain forest and ericoid formations.

Ranunculaceae: 5 genera, about 45 species (24, 37, 38, 52).

Related floras: Neozeylandic (2/5, e.g., *Clematis foetida*, *Ranunculus rivularis*) and Chile-Patagonian (2/3, e.g., *Ranunculus acaulis*, *R. biternatus*).

Observations: about 30 endemic species (e.g., *Anemone crassifolia*, *Caltha introloba*, *Clematis aristata*, *C. gentianoides*, *Ranunculus gunnianus*), and most of them are endemics of Tasmania only (e.g., *Ranunculus muelleri*, *R. scapigeri*).

Southwest Australian Region

Location: southwestern Australia.

Characteristic vegetation: dry and rainy sclerophyllous forests of *Casuarina* and *Eucalyptus*, also scrub.

Ranunculaceae: 2 genera, 5 species (e.g., *Clematis microphylla*, *Ranunculus lappaceus*).

Central Australian Region

Location: North Territory, Great Sandy Desert, Victoria and Gibson deserts, and other areas.

Characteristic vegetation: tropical desert and dry savanna formations.

Ranunculaceae: absent.

The Ranunculaceae in Australia are related to those in the Holantarctic floras. Thus, *Caltha introloba*, like other species of *Caltha* in the Southern Hemisphere, belongs to sect. *Psychrophila*; *Anemone crassifolia* belongs to sect. *Rivulariadium*; and Australian species of *Ranunculus* are related to South American species. Our conclusion is similar to that of Raven (248) who supposed that most high-mountain plants, including species of *Anemone* and *Ranunculus*, migrated to Australia and New Zealand from South America in the Late Pliocene or later. Raven suggested that a northern migratory route for plants into Australia through Malesia was geologically impossible because the alpine flora of New Guinea is younger than the Australian one (334). Moreover, Melville (201) included the Ranunculaceae with a group of five families that invaded in Australia from the north.

Conclusions

The peculiarities of the role of the Ranunculaceae in the floras of regions and provinces worldwide reflect the peculiarities of origin, differentiation, and distribution of this family, including the relationships of tropical, temperate, mountain, and lowland floras, and including the relationships of the floras of the Northern and Southern hemispheres.

According to paleobotanical literature (22, 60–63, 93, 253–255), there are no fossil remnants of the Ranunculaceae in the Cretaceous. The earliest such fossils, fruits of some species of *Clematis* and *Ranunculus*, are Oligocene and come from Eurasia (e.g., England, Ukraine, the Urals). Ranunculaceae are represented in Miocene deposits by remnants of few species of *Clematis*, *Ranunculus*, and *Thalictrum*. Pliocene ranunculaceous remnants belong to *Aquilegia*, *Anemone*, *Clematis*, *Ranunculus*, and *Thalictrum*, about 40 temperate species altogether. They were found in many places within the vast territories of Eurasia, North America, and South America.

These paleobotanical phenomena reflect the considerable differentiation of the Ranunculaceae and their radiation throughout the world during the Neogene. The sharp increase of the development and dispersion of the Ranunculaceae was associated with the Upper Eocene general fall of temperature and replacement of tropical and subtropical floras with temperate ones across Eurasia and North America (78, 229, 307).

There are two different opinions about the origin of the Ranunculaceae. Scharfetter (263) placed the origin within the Early Tertiary tropical flora, while Popov (235) claimed that the Ranunculaceae originated within the Neogene warm-temperate flora of Eurasia, similar to 50 other derivative angiospermous families.

We disagree with both these propositions and claim an Early Cretaceous origin and differentiation of the Ranunculaceae. This is based partly on the peculiarities of the disjunctive areas of such genera as *Caltha*, *Anemone*, *Clematis*, *Ranunculus*, and *Thalictrum*. The origin and primary differentiation of the family must have taken place after the breakup of the supercontinent Pangaea (or one like it). Our data are consistent with the horizontal drift of the continents (138, 201, 250, and others).

Development of the distinctive Holarctic and Holantarctic groups of *Caltha* (sects. *Caltha* and *Psychrophila*) occurred in temperate parts of Gondwana and Eurasia and seems likely to reflect the Middle Cretaceous differentiation of the northern and southern temperate floras. In this point we agree with Tolmachev (310) and Moore (211) who considered *Caltha* as one of the most ancient temperate Angiosperm genera.

The above-mentioned *Anemone*, *Clematis*, *Ranunculus*, and *Thalictrum* are temperate genera that occur fairly continuously throughout the montane Palaeotropics and Neotropics and suggest the routes by which their migrations could have taken place. Notably, *Anemone rivularis* and *Clematis ranunculoides* with archaic morphological features are tropical-mountain forest elements of the flora of Southeastern Asia. Boughey (27) regarded the mountain forest flora in Africa and Asia as very old and maintained that its survival to the present as an insular flora scattered discontinuously over huge land masses implies a connection with continental drift, land-bridges, and long periods of time.

Our analysis showed that the majority of species of all genera occur in mountains and that, moreover, species of more than half of the genera, including all endemics, are restricted chiefly to mountain locations. Moreover, the most numerous groups of species of large genera such as *Aconitum*, *Delphinium*, *Anemone*, *Clematis*, *Ranunculus*, and *Thalictrum* are distributed mainly in mountains. Our data confirm Rau (243) who considered the Ranunculaceae to be an important member of the high-mountain ecosystems and is the basis for supposing its origin in mountain locations.

Within temperate montane floras of the temperate regions the Ranunculaceae take fourth to seventh place, while in tropical montane habitats, the Ranunculaceae fall to 15th–17th place (70, 140).

Comparison of the ranunculaceous representatives in the modern floras of the Northern and Southern hemispheres (the former contains 51 genera and about 2,200 species of all 14 tribes, the latter is home to 11 genera and about 250 species of 5 tribes) and comparison of their endemic genera (17 genera of 10 tribes vs. 4 genera of 2 tribes, respectively) indicates that primary differentiation of the Ranunculaceae took place in the Northern Hemisphere.

From our geographical analysis together with data on comparative morphology, we propose that the ancestors of the tribes Cimicifugeae, Anemoneae, Clematideae, Aquilegieae, Asteropyreae, and Kingdonieae initially developed within the ancient floras of eastern Asia, while the tribes Coptideae (at least *Xanthorhiza*) and Hydrastideae were formed in North America. It was impossible to pinpoint the place of the development of the ancestors of the tribes Trollieae, Helleboreae, Delphinieae, Isopyreae, Ranunculeae, and Thalictreae, because some of their genera (e.g., *Beesia*, *Calathodes*, *Trollius*, *Aconitum*, *Eranthis*, *Aquilegia*, *Semiaquilegia*, *Urophysa*, and *Dichocarpum*) originated in eastern Asia, while other genera (e.g., *Helleborus*, *Nigella*, *Consolida*, *Leptopyrum*, and *Aconitella*) differentiated in the Ancient Mediterranean Subkingdom or North America (*Enemion* and *Anemonella*). Some associated in their origin and distribution with the temperate palearctic flora (*Delphinium*, *Callianthemum*, *Adonis*, *Trautvetteria*, *Isopyrum*, *Paraquilegia*, and *Paropyrum*).

In conclusion, we regard the Ranunculaceae as an ancient temperate family that originated in Cretaceous time within montane temperate floras of the Northern Hemisphere.

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A REVISION OF THE NEW WORLD SPECIES OF *EHRETIA* (BORAGINACEAE)[1]

James S. Miller[2]

Abstract

Ehretia is a pantropical genus of about 50 species with centers of diversity in eastern Africa and tropical Asia. Although as many as 12 species of *Ehretia* have been recognized in the New World, field and herbarium studies suggest that the patterns of variation in the New World are best treated as three species. Most recent authors have recognized *Ehretia anacua* and *E. tinifolia* as distinct species and have distinguished several species with serrate leaf margins. Field studies suggest that characters used to differentiate species with serrate leaf margins often vary within populations or on a single individual. Thus *Ehretia latifolia* is treated in a broad sense, including all segregate species with serrate leaves.

The largest genus of the subfamily Ehretioideae, *Ehretia*, contains about 50 species (Airy-Shaw, 1973) distributed tropically and subtropically in both hemispheres. The genus is primarily Old World in distribution with more species in Africa than in Asia; Baker & Wright (1905) recognized 23 African species, mostly in eastern Africa, Johnston (1951) recognized 12 species in eastern Asia, and perhaps several more occur in the Malay archipelago and Australia. The genus is poorly represented in the New World where it ranges from Texas to Panama and the Greater Antilles. The last complete treatment of the New World species was that of Miers (1869) who recognized eight species. An additional six species were published by various authors after his work. Standley (1924) recognized seven species in Mexico and one more in Costa Rica (Standley, 1938) based on relatively few collections of the species with serrate leaf margins. With the great increase of collections available since Standley's work, initial studies suggested that the characters he used to separate the species were of questionable validity, and delimitation of the species became problematic. The present revision combines a study of herbarium specimens with extensive field study of the variation of leaf and indument characters to resolve these problems. The work is supplemented with surveys of leaf architecture and pollen morphology throughout the Ehretioideae to be published later; only results directly relevant to the New World species of *Ehretia* are included here.

In addition to problems with delimitation of species of *Ehretia* in the New World, there have been questions regarding definition of the genus. An additional aspect of this study was an examination of generic limits in the arborescent genera of Ehretioideae. Selected species of *Bourreria*, *Carmona*, *Rochefortia*, *Rotula*, and Old World species of *Ehretia* were examined.

Taxonomic History and Generic Delimitation

Patrick Browne (1756) named *Ehretia* after Georg Dionysius Ehret, the illustrator of Browne's

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Ann. Missouri Bot. Gard. 76: 1050–1076. 1989.

Civil and Natural History of Jamaica. Linnaeus (1759) later validated the genus with the binomial *Ehretia tinifolia*. De Candolle (1845) significantly enlarged the concept of the genus by treating 58 species, many of which are now referred to the segregate genera *Bourreria*, *Carmona*, *Rochefortia*, and *Rotula*. De Candolle recognized four sections within *Ehretia*. All of the species of his sect. *Ehretia* are still referred to the genus but his sect. *Bourreria* was a diverse group of species now assigned to *Bourreria* and *Ehretia*. The two species that he treated in sect. *Carmona* have been considered conspecific and treated as *Carmona retusa* (Vahl) Masamune (Thulin, 1987). His fourth section, sect. *Xeroderma*, was another diverse group containing species now distributed in *Bourreria*, *Ehretia*, *Rochefortia*, and *Rotula*. Several species of sects. *Bourreria* and *Xeroderma* have since been excluded from Boraginaceae (see excluded species).

John Miers published a series of papers on the Boraginaceae shortly after De Candolle's work and treated *Ehretia* (Miers, 1869) in a more restricted sense. Miers segregated the genus *Rotula* (as *Rhabdia*) and allied it with *Ehretia* and *Cortesia* (a small genus endemic to saline areas in northern Argentina). Miers also sorted the species that most recent authors have included in *Bourreria* into *Bourreria* and *Crematomia*. *Crematomia* was characterized by having fruits with four pyrenes, each retaining an apical attachment to the stigma at maturity. Recent authors (Schulz, 1911; Nowicke, 1969; Gibson, 1970; Miller, 1988) have not accepted this as sufficient for generic recognition and have included these "*Crematomia*" species in *Bourreria*. Miers pointed out that *Bourreria* was distinct in its fleshy calyx with five marginally tomentose, valvate lobes; fleshy, rotate corollas; and fruits that at maturity divide into four angular pyrenes, each with a ridged endocarp and spongiose mesocarp.

Bentham & Hooker (1876) recognized three sections of *Ehretia*, one of which, *Carmona*, has been treated as a segregate genus by most recent authors (Johnston, 1951; Nowicke & Miller, in press). Johnston (1951) recognized their other two sections, *Euehretia* and *Bourrerioides*, in his treatment of the eastern Asian species. Although Johnston devoted most of his research career to Boraginaceae, he published little on *Ehretia* or *Bourreria*. He did recognize *Carmona* and *Rotula* as distinct from *Ehretia* (Johnston, 1951). In his treatment of the Boraginaceae of the southern West Indies (Johnston, 1949) he also considered *Bourreria* and *Rochefortia* as distinct from *Ehretia*. Hence, although Johnston never treated *Ehretia*, it appears that his generic concept was similar to that of most recent authors.

As currently defined, the Ehretioideae consist of eleven genera that segregate into four probably monophyletic groups, but the relationships among them remain obscure. Richardson (1976, 1977) separated *Tiquilia* from *Coldenia* and these two genera of prostrate plants with dry nutlets form a distinct lineage within the Ehretioideae. *Lepidocordia*, including *Antrophora* (Miller & Nowicke, in prep.), is also quite distinct from any of the other genera of the Ehretioideae, and Johnston (1950) considered the genus intermediate between the Ehretioideae and Heliotropioideae. The Argentinian endemic *Cortesia* and the Australian endemic *Halgania* comprise a questionable third group of shrubby plants of xeric regions with often trifid or unevenly toothed sclerophyllous leaves. Whether these two genera are closely related or simply share a similar appearance because of convergence in similar habitats is unclear. *Halgania* is unique in the Ehretioideae in its stamens connate around the style.

The remaining genera of Ehretioideae, *Bourreria*, *Carmona*, *Ehretia*, *Pteleocarpa*, *Rochefortia*, and *Rotula*, seem to form a rather close group. Of these only *Pteleocarpa* seems to stand apart in its unusual winged fruits. Although recent pollen studies (Nowicke & Miller, in prep.) supported recognition of *Bourreria*, *Carmona*, *Rochefortia*, and *Rotula* as distinct from *Ehretia*, they still appear closely related and form a distinct group within the subfamily. (See Table 1 for comparison.)

Thulin (1987) transferred five African species of *Ehretia* to *Bourreria*, a genus previously considered to be restricted to the Neotropics. These species seem to form a monophyletic group distinct from *Ehretia* in their valvate calyces, campanulate to urceolate corollas, and ridged endocarps. *Ehretia* is a more natural genus without these species, but they are probably distantly related to the New World species of *Bourreria*, which are characterized by rotate corollas and pollen grains with thickened ridges on each side of the colpi (Nowicke & Miller, unpublished). The characteristics of the genera closely allied to *Ehretia* are compared in Table 1 and a key to the genera of the Ehretioideae is provided below. Although Johnston (1935) included *Saccellium* in the Ehretioideae, recent pollen studies (Nowicke & Miller, in prep.) indicate that it is more closely related to the genera of the Cordioideae where Tahktajan (1987) placed it.

KEY TO THE GENERA OF THE EHRETIOIDEAE

1a. Procumbent shrubs or annual herbs; inflorescences crowded or few-flowered; fruits dry, of 4 nutlets.
  2a. Annuals with adventitious roots; leaves asymmetrical; flowers tetramerous, Old World ..... *Coldenia*
  2b. Perennials without adventitious roots; leaves symmetrical; flowers pentamerous, New World ..... *Tiquilia*
1b. Trees or erect or arching shrubs; inflorescences cymose or paniculate; fruits fleshy at least when young, but not of 4 nutlets.
  3a. Leaves sclerophyllous; low shrubs.
    4a. Anthers connate in a cone surrounding the style; Australia ..... *Halgania*
    4b. Anthers free; Argentina ..... *Cortesia*
  3b. Leaves coriaceous to membranaceous; erect shrubs or trees.
    5a. Flowers unisexual, the plants dioecious.
      6a. Plants with spines; endocarp dividing into four parts at maturity ..... *Rochefortia*
      6b. Plants lacking spines; endocarps remaining entire at maturity ..... *Lepidocordia*
    5b. Flowers all bisexual.
      7a. Style 1, entire or divided only to the middle.
        8a. Calyx valvate; fruits with a spongiose mesocarp, the endocarps with a ridged outer surface and often retaining an apical attachment with the style ..... *Bourreria*
        8b. Calyx imbricate; fruits with a fleshy to mucilaginous mesocarp, the endocarps usually not ridged and never retaining an apical attachment with the style.
          9a. Rheophytic shrubs with flexuous branches; style simple and obscurely bilobed ..... *Rotula*
          9b. Trees or shrubs; style usually divided with 2 distinct stigmas ..... *Ehretia*
      7b. Styles 2, free to the base.
        10a. Fruits compressed, with broad, reticulately winged margins; leaves entire ..... *Pteleocarpa*
        10b. Fruits drupaceous, not compressed; leaves toothed at the apex ..... *Carmona*

The New World Species of *Ehretia*

Only three of the New World species that DeCandolle (1845) included in *Ehretia* still belong to the genus. These are *Ehretia anacua* (Teran & Berl.) I. M. Johnston (as *E. elliptica* DC.), *E. latifolia* DC., and *E. tinifolia* L. Miers (1869) adopted a very narrow species concept, recognizing seven species with entire leaf margins, where only two have been recognized by recent authors (Standley, 1924; Nash & Moreno, 1981). Various authors described six New World species of *Ehretia* with serrate leaves between 1891 and 1938. Standley (1924) recognized five species with serrate leaves in Mexico and an additional one from Costa Rica (Standley, 1938). They differed in leaf shape and indument, although field studies reveal these characters are extremely variable. The present study recognizes three species of *Ehretia* in the New World. This differs from recent treatments by grouping all populations with distinctly serrate leaf margins as a single, variable species. This variation in leaf morphology of *Ehretia latifolia* is discussed in detail under that species.

The determination of the natural ranges of the three New World species is complicated by the fact that all are cultivated. *Ehretia tinifolia* is the most widely grown, often significantly outside its natural range, and the other two species are frequently planted near houses in areas where they occur naturally. These trees seem to be valued mostly for shade because of their dense crowns, and they are attractive when in flower and fruit. *Ehretia latifolia* is apparently not used for wood by local people.

Almost everyone questioned in Mexico had a different common name for the local species of *Ehretia* and because of this no common names are reported in this study.

Morphology

Habit

All species of *Ehretia* are trees or shrubs (Fig. 1). Although New World species are trees, *E. anacua* is frequently multistemmed. Habit is much more variable among the Old World species, which range from trees, like *E. acuminata* R. Br., to desert shrubs, such as *E. rigida* (Thunb.) Druce. The genus *Rotula* differs from *Ehretia* in its arching, flexuous branches associated with its rheophytic habitat. The trunk of *E. latifolia* is usually fluted, at least on mature plants (Fig. 2).

Leaves

All species of *Ehretia* have simple, alternate, nearly lanceolate to nearly round leaves. A few Old World species are extreme, for example *Ehretia saligna* R. Br. of Australia has elongate, straplike leaves. Leaf shape is variable within species, a single individual often showing a significant diversity of leaf shapes on a single branch (see *E. latifolia*).

Ehretia tinifolia and *E. anacua* have entire-

FIGURES 1, 2. Habit of *Ehretia latifolia*. — 1. Tree 8 m tall, near Guelatao, Oaxaca, Mexico. Note the dense crown. These trees are often left as shade trees after other species have been cut. — 2. Fluted trunk of the same individual. (Both vouchered by *Miller & Myers 2802* MO.)

margined leaves. In some specimens of *Ehretia anacua*, however, a few leaves exhibit short teeth along the margin. *Ehretia latifolia* is unique among the New World species in its evenly serrate leaf margins. Only rarely are the teeth short and uneven.

Leaf architecture can be valuable in delimitation of higher taxa (Hickey & Wolfe, 1975; Lorence, 1985; Levin, 1986a, b, c) and has been used within genera (Rury & Dickison, 1977). Leaves of 36 species of 10 genera of Ehretioideae were examined for leaf architectural features. Eleven species of *Ehretia* were selected, including the three New World species. Leaves were removed from herbarium collections, cleared, stained, and mounted according to methods of Dilcher (1974), and architectural features were analyzed following the system of Hickey (1973, 1977, 1979). A complete survey of the genera of the Ehretioideae will be published separately, but results are reported here for the New World species of *Ehretia* and several other taxa for comparison. Voucher specimens for the leaves examined are cited in the figure captions.

Leaves of *Ehretia* appear to be primitively brochidodromous, this being the condition in nearly all of the species, and in the closely related genera *Bourreria*, *Rochefortia*, and *Rotula*. Craspedodromous venation is restricted to the few species with serrate leaf margins. Of the New World species, *E. tinifolia* has brochidodromous venation (Fig. 4). *Ehretia latifolia* is the only New World species consistently with craspedodromous venation (Fig. 3). Although this might appear to be a conservative character, it is variable in *E. anacua*, which generally has brochidodromous venation (Fig. 7) but occasional individuals and leaves on juvenile shoots have serrate margins and semicraspedodromous venation (Fig. 6). Even in *E. acuminata*, an Old World species with serrate leaves (Fig. 5), leaves are brochidodromous with veins that arise secondarily from outer loops beyond the secondaries and extend into the teeth.

The patterns of tertiary and higher-order venation vary only slightly among the species of *Ehretia*. Generally, five or six orders are visible in most species. *Ehretia anacua* (Fig. 8) and *E. tinifolia* have randomly reticulate tertiary veins that anastomose and form a weak, composite intersecondary vein. The higher orders of venation vary from random to orthogonal reticulate. The ultimate marginal venation is looped in both of these species.

Ehretia latifolia (Fig. 9) and *E. acuminata* (Fig. 10) have randomly reticulate to weakly percurrent tertiary veins. Intersecondary veins are weak and restricted to the apical portion of the leaf, or are completely absent. Ultimate marginal venation is incomplete in *E. latifolia* but looped in *E. acuminata*.

The New World species of *Ehretia* are essentially evergreen. *Ehretia anacua* is partly deciduous only at the northern extreme of its range in Texas. *Ehretia latifolia* appears to produce most of its leaves during the onset of spring rains and hold them for about two years. Only in the population near Monte Alban, Oaxaca, in Mexico did I observe a plant that seemed to shed all of its leaves during the dry season. New leaves were emerging even as the last few old leaves dropped.

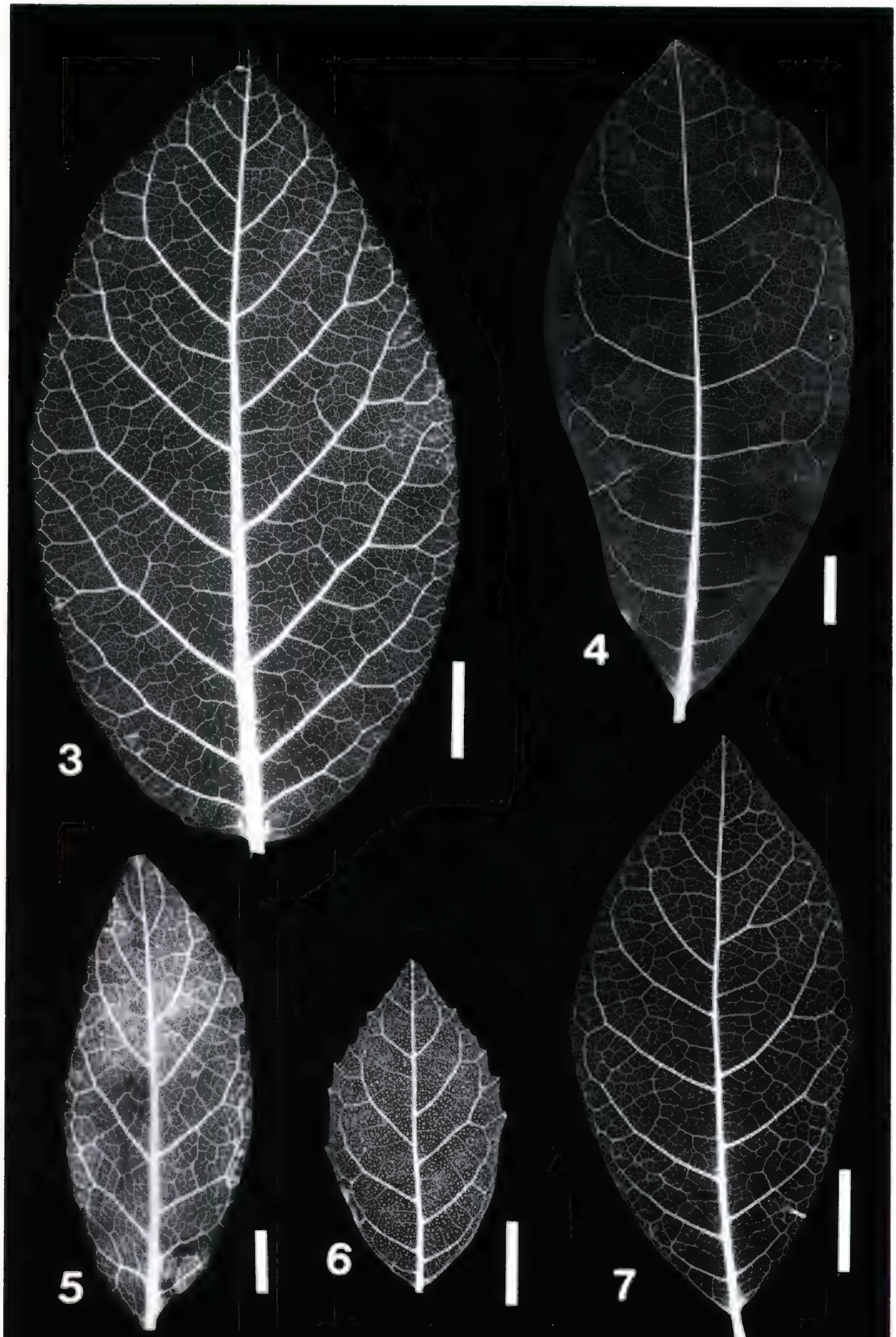
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TABLE 1. Comparison of the major morphological characters of *Bourreria* (New World), *Bourreria* (African, sensu Thulin, 1987), *Carmona*, *Ehretia*, *Rochefortia*, and *Rotula*.

Characters	*Bourreria* New World	*Bourreria* African sensu Thulin	*Carmona*	*Ehretia*	*Rochefortia*	*Rotula*
Habit	trees and shrubs	trees and shrubs	shrub	trees and shrubs	trees and shrubs	rheophytic shrubs with arching branches
Leaves	entire	entire	apically retuse or trifid	entire or serrate	entire	entire
Calyx aestivation	valvate	valvate	quincuncial	quincuncial	imbricate	quincuncial
Corolla form	rotate	urceolate to campanulate	tubular	tubular to campanulate	shortly tubular	tubular
Corolla texture	leathery	thin	thin	thin	thin	thin
Fruit, number of parts	4	4	1	1, 2, or 4	4	4
Endocarp	ridged	ridged	lightly rugulose	rugulose to smooth	striate	reticulate
Mesocarp	spongiose	spongiose	fleshy	fleshy	fleshy	fleshy

INDUMENT

Standley (1924) differentiated New World species of *Ehretia* using density and thickness of hairs and presence or absence of glandular hairs. Field observations indicate that neither of these are significant in the sense that Standley used them. The widely scattered geographic pattern of plants with glandular hairs is not indicative of a monophyletic group, but rather probably a character that is expressed only rarely.

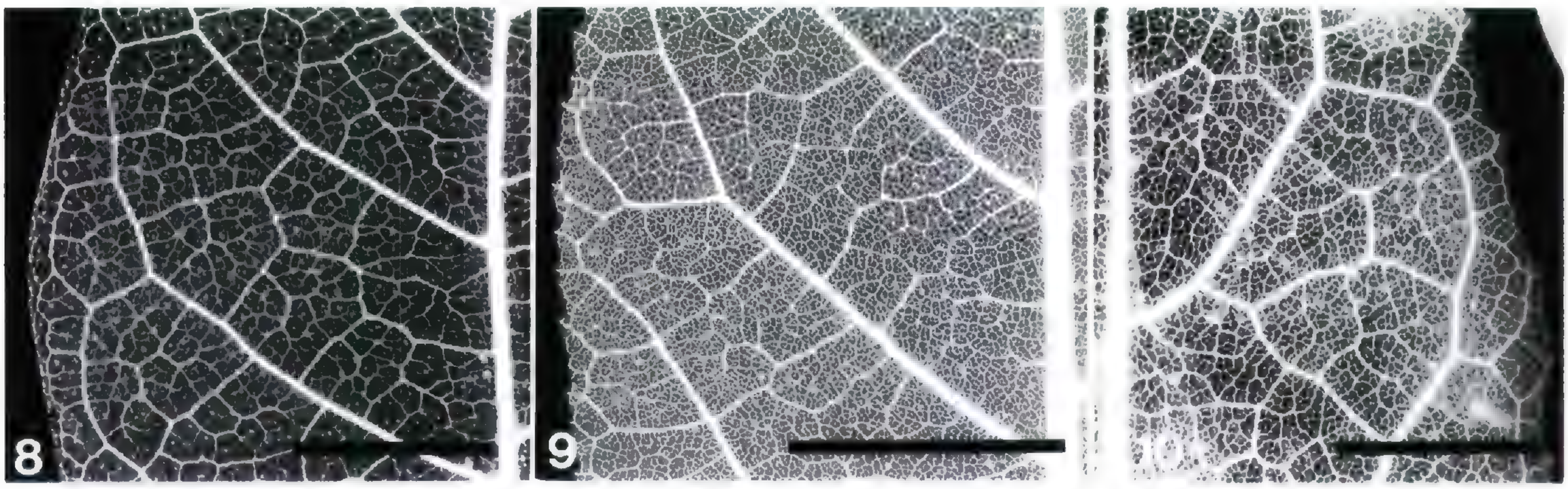
Collections of *Ehretia anacua* and *E. latifolia* show considerable variability in leaf indument, much of which can be explained as a temporal phenomenon. Young leaves of *E. latifolia* are densely and softly pubescent. Expansion of the leaf blade decreases the density of hairs, and young, fully expanded leaves are less densely pubescent with long-shafted, simple hairs from a multiple-celled, basal cystolith. During the life of an individual leaf, the majority of the brittle shafts of the hairs are often broken off and the leaf may appear nearly glabrous without magnification. As the leaf reaches senescence, the cells of the basal cystolith continue to expand and harden. The basal cystoliths with the remaining portions of the hair shafts often make up what appears to be a scabrous indument. Thus an individual leaf may pass through stages from velutinous, to sparsely pubescent, to nearly glabrous, and finally to scabrous. In the southern portion of the range of *Ehretia latifolia* the dry season is less severe. Here leaves are somewhat larger, and seldom do herbarium collections contain leaves old enough to have reached the last, seemingly scabrous, stage. These field observations suggest that indument is not a reliable character for the delimitation of segregate species from *E. latifolia*.

INFLORESCENCES

All species of *Ehretia* have many-flowered inflorescences that are cymose or are paniculate with the individual branches of the panicles cymose.

←

FIGURES 3–7. Cleared leaves of *Ehretia* species.—3. *E. latifolia* (*Miller et al. 2690* MO, Mexico). 4. *E. tinifolia* (*Miller & Téllez 3194* MO, Mexico).—5. *E. acuminata* (*Pételot 6382* MO, Vietnam). 6, 7. *E. anacua*.—6. Juvenile leaf (*E. J. Palmer 10809* MO, Texas).—7. Mature leaf (*Duke 3690* MO, Mexico). Scale bars equal 1 cm.



FIGURES 8–10. Cleared leaves of *Ehretia* species.—8. *E. anacua* (*Duke 3690* MO, Mexico).—9. *E. latifolia* (*Miller et al. 2690* MO, Mexico).—10. *E. acuminata* (*Pételot 6382* MO, Vietnam). Scale bars equal 1 cm.

The inflorescences of *Ehretia tinifolia* and *E. latifolia* have a distinct central rachis and are basically paniculate with cymose individual branches. *Ehretia anacua* has a short-pedunculate, cymose inflorescence without a central leader. This type of cymose inflorescence is widespread in the Ehretioideae and Cordioideae and is probably the primitive character state in the two subfamilies.

FLOWERS

The floral morphologies of the New World species of *Ehretia* are quite similar. *Ehretia anacua* has hairs on the corolla that are not present in *E. latifolia* or *E. tinifolia*, but other differences are small. Floral features that vary among the New World species are compared in Table 2. The Old World species are quite different and vary in numerous floral characters, including features of the calyx and size, color, and form of the corolla.

The diversity of breeding systems in the Boraginaceae is well documented (Bawa & Beach, 1981; Ganders, 1979; Vuilleumier, 1967) and second only to Rubiaceae in the number of distylous species. *Ehretia* has monomorphic, bisexual flowers with the stamens exserted and exceeding the style. This is the most common breeding system in the Ehretioideae; the only genera that differ are *Lepidocordia* (Miller & Nowicke, in prep.) and *Rochefortia* (Lefor, 1968), both dioecious. Corollas are small and white in the New World species and are visited by a wide variety of small generalistic Diptera, Hymenoptera, and Lepidoptera. The plants I observed of *Ehretia latifolia* were visited by many small insects, mostly dipterans.

POLLEN

Pollen is particularly useful in generic delimitation in the Boraginaceae (Avetissian, 1956; Nowicke & Ridgway, 1973; Nowicke & Skvarla, 1974; Nowicke & Miller, in press). Pollen of *Ehretia* is more or less prolate and three-colporate (Nowicke & Miller, in prep.). Three pseudocolpi or pseudocolpoid depressions alternate with the colpi. The apertures have elongate colpi with a bridge of ektexine over the endoaperture. The tectum is more or less complete and faintly rugulose, slightly granular, or psilate.

Ehretia is homogeneous and distinct from other genera of the Ehretioideae in its pollen morphology (Nowicke & Miller, in prep.). Evidence from pollen does not support earlier sectional divisions of the genus (see Bentham & Hooker, 1876; Johnston, 1951).

FRUITS

The fruits of *Ehretia* are drupaceous with a thin to leathery exocarp, fleshy to mucilaginous mesocarp, and bony endocarp. They vary from white, as in *E. latifolia*, through yellow and orange, as in *E. anacua*, to red, as in *E. longiflora* Champ. (Johnston, 1951). The calyx generally persists basally but is not at all accrescent. Although the stigma is usually lost, the base of the style often persists at the apex of fruits.

Fruit morphology has been important for generic delimitation in the Ehretioideae. *Bourreria*, *Carmona*, *Ehretia*, *Rochefortia*, and *Rotula* have essentially drupaceous fruits, varying in the texture of the mesocarp, number of parts into which the endocarp divides at maturity, and surface sculpturing of the endocarp. The mesocarp of these genera except for *Bourreria* is fleshy to mucilaginous. That of *Bourreria* is spongiose, being fleshy only when fruits are immature, becoming somewhat fibrous with large open air pockets.

The structure of endocarps was examined by

TABLE 2. Comparison of floral features of the New World species of *Ehretia*.

	Ehretia anacua	*E. latifolia*	*E. tinifolia*
Calyx length	2.7–3.5 mm	1.6–2.6 mm	1.5–2 mm
Calyx lobe shape	narrowly triangular	deltate to triangular	ovate
Calyx indument	pubescent to densely strigillose	glabrous to strigillose	glabrous
Corolla shape	tubular-campanulate	campanulate	campanulate
Corolla length	6–7.8 mm	3.2–6 mm	4–4.6 mm
Corolla indument	strigillose to puberulent	glabrous	glabrous
Corolla lobe shape	obovate	broadly ovate	widely oblong to oblong-ovate
Corolla lobe length	2.8–3.4 mm	1.8–2 mm	2.5–5 mm
Staminal filament length	4–6.3 mm	4–4.5 mm	3–4.5 mm
Style length	2.7–5 mm	3–4 mm	2–3.4 mm

removing mature fruits from herbarium specimens, soaking in 5% NaOH for 1–5 days to soften the exocarp and mesocarp, washing in running water until clear of all outer material, and then drying. They were then examined with an Hitachi S450 scanning electron microscope. Fruits of 54 species of ten genera of Ehretioideae were examined. *Coldenia* and *Tiquilia* stand apart in having fruits of four dry nutlets. The fruits of *Halgania*, *Lepidocordia*, and *Rotula* all differ in having a thin-walled endocarp. *Bourreria*, *Carmona*, *Ehretia*, and *Rochefortia*, however, all have somewhat similar fruits.

Fruits of *Ehretia* vary in the number of parts into which the endocarp divides. Of the species examined, *Ehretia latifolia* is the only species whose endocarp remains entire at maturity. *Ehretia acuminata*, *E. anacua*, *E. dicksonii*, and *E. tinifolia* have fruits with two separate two-seeded pyrenes at maturity. *Ehretia amoena*, *E. coerula*, *E. cymosa*, *E. laevis*, *E. obtusifolia*, and *E. rigida* have fruits with four separate single-seeded pyrenes. Of related genera, *Carmona* has an endocarp that remains entire. *Rotula* has a two-parted endocarp and *Bourreria* and *Rochefortia* have four-parted endocarps.

The surfaces of the endocarps of *Ehretia* species have distinct sculptural patterns. Two major types occur in *Ehretia*, and several others turn up in related genera. Verrucose endocarps are found in *Ehretia acuminata* (Fig. 15), *E. dicksonii*, *E. latifolia* (Fig. 13), and *E. tinifolia* (Fig. 12). *Ehretia dicksonii* is unusual among these species in having an evenly puberulent endocarp with numerous short hairs on the outer surface. Areolate endocarps, with angular depressed areas, characterize most of the Old World species with four-parted endocarps, including *E. rigida* (Fig. 14). *Ehretia anacua*, of the New World (Fig. 11), also has an areolate endocarp but differs in being less regularly areolate and in only dividing into two parts at maturity.

The endocarps of the most closely related genera are quite different in sculpturing pattern. *Carmona retusa* has an entire endocarp with few, low, broad ridges but is otherwise nearly smooth (Fig. 16). *Rochefortia* has endocarps with broad, thick, rounded ridges as exemplified by *R. spinosa* (Jacq.) Urb. (Fig. 19). *Bourreria* has ridged endocarps varying from erect, as in *B. rubra* Lott & Miller (Fig. 18), to overlapping, as in *B. nemoralis* (Gurke) Thulin (Fig. 17).

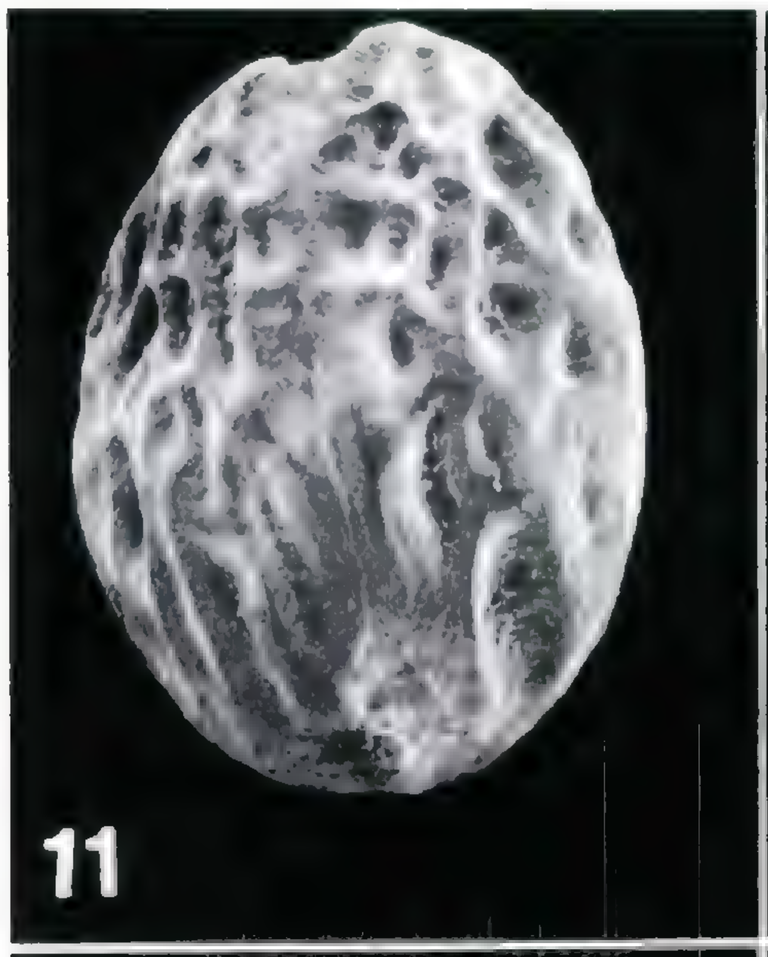
Fruit structure suggests that *Ehretia* consists of two groups. One has one- or two-parted endocarps with a verrucose surface and is found in the New World and Asia. The second has four-parted endocarps with an areolate surface and is widespread in the Old World. *Ehretia anacua* is the only New World species in the latter group but differs in having a two-parted endocarp.

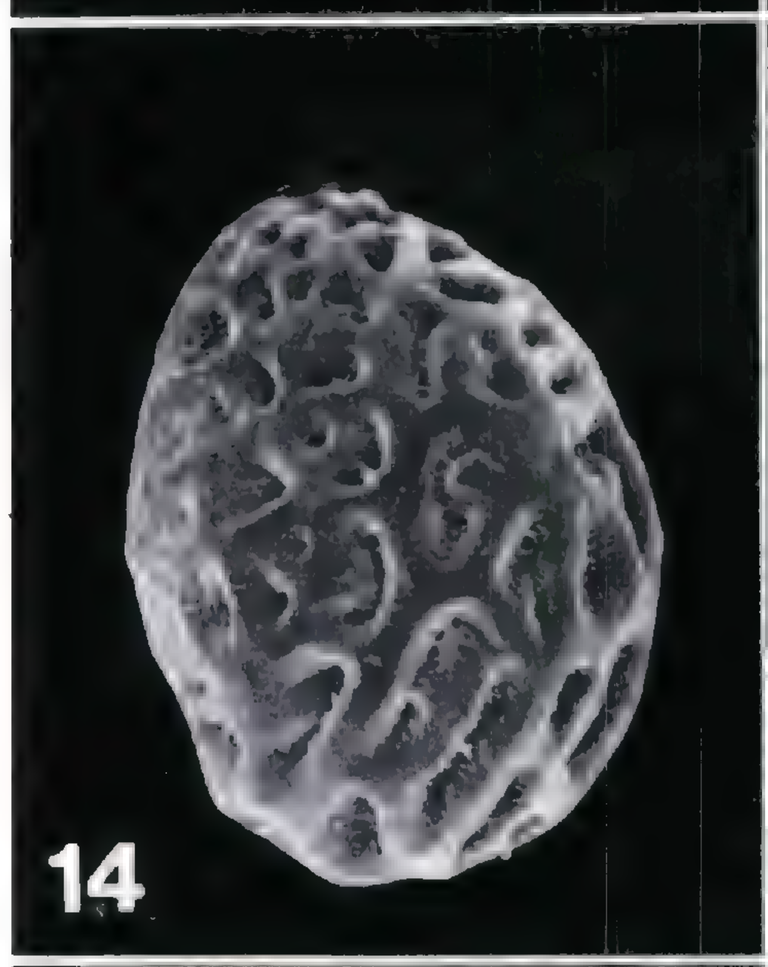
SYSTEMATIC TREATMENT

Ehretia P. Browne, Civ. Nat. Hist., Jamaica 168. 1756. TYPE: *Ehretia tinifolia* L., Syst. Nat. ed. 10. 936. 1759.

Gaza Terán & Berlandier, Mem. Comis. Limites 5. 1832. TYPE: *Gaza anacua* Terán & Berlandier, Mem. Comis. Limites 5. 1832.

Pubescent or glabrous, trees or shrubs. Leaves alternate, petiolate, the margin entire or serrate, the venation pinnate, brochidodromous or less commonly semicraspedodromous or craspedodromous. Inflorescences terminal, cymose to paniculate. Flowers bisexual; sepals 5, imbricate or open in bud; corolla white in the New World species (blue in *E. coerula* and *E. rigida*, Africa), tubular with 5 spreading to reflexed lobes or urceolate; stamens





FIGURES 11–19. Endocarps of species of Ehretioideae. 11–15. *Ehretia*.—11. *E. anacua* (*Hansen & Nee 7489* MO, Mexico). 12. *E. tinifolia* (*Miller & Myers 2824* MO, Mexico).—13. *E. latifolia* (*Purpus 5820* MO, Mexico).—14. *E. rigida* (*Armitage 305/59* MO, S Rhodesia).—15. *E. acuminata* (*Wilson 74* MO, China).—16. *Carmona retusa* (*Merrill: Species Blancoanae 3* MO, Philippines). 17, 18. *Bourreria*.—17. *B. nemoralis* (Gurke) Thulin (*Frazier 2267* MO, Kenya).—18. *B. rubra* Lott & Miller (*Lott 683* MO, Mexico).—19. *Rochefortia spinosa* Jacq. (*Liesner & Gonzalez 12160* MO, Venezuela). Scale bar equals 5 mm.

5, usually exserted, the anthers oblong to ellipsoid; ovary ovoid, 2- or 4-locular, the style 1, terminal, bifid, the stigmas 2, clavate to capitate. Fruits drupaceous, ovoid to nearly spherical, the endocarp separating into 2, 2-seeded pyrenes or into 4, 1-seeded pyrenes, or rarely remaining entire.

KEY TO THE SPECIES OF *EHRETIA* IN THE NEW WORLD

1a. Leaf margin distinctly serrate; endocarp remaining entire ..... *E. latifolia*
1b. Leaf margin entire or nearly so; endocarp dividing into 2 parts at maturity.
  2a. Upper leaf surface glabrous; inflorescence paniculate; corolla glabrous ..... *E. tinifolia*
  2b. Upper leaf surface scabrous; inflorescence cymose; corolla strigillose to puberulent ..... *E. anacua*

Ehretia anacua (Terán & Berlandier) I. M. Johnston, Contr. Gray Herb. 70: 89. 1924. *Gaza anacua* Terán & Berlandier, Mem. Comis. Limites 5. 1832. TYPE: Mexico. Tamaulipas: prope Matamoros ubi vulgo adpellatur Anacua, *Berlandier 2369* (lectotype, G, here designated; isolectotypes, BM, G, K, P).

Ehretia elliptica DC., Prodr. 9: 503. 1845. TYPE: Mexico: *Berlandier 2330* (holotype, G-DC, not seen; microfiche, MO; isotypes, BM, G, GH, K, LE, MO, NY—2 sheets, P).

Ehretia scabra Kunth & Bouché, Sp. Nov. Hort. Berol. 12. 1847. "Crescit in Mexico," no type seen.

Ehretia ciliata Miers, Ann. & Mag. Nat. Hist. Ser. IV. 3: 111. 1869. TYPE: U.S.A. Texas: *Lindheimer 665* (holotype, K; isotypes, BM, F, GH—2 sheets, K, MO—2 sheets, NY, P, US).

Ehretia exasperata Miers, Ann. & Mag. Nat. Hist. Ser. IV. 3: 112. 1869. TYPE: U.S.A. Texas: *M. Drummond 296* (holotype, K; isotypes, BM—2 sheets, GH, K, NY—2 sheets).

Ehretia lancifolia Sessé & Mociño, Fl. Mex. 51. 1894; ed. 2. 47. 1894; I. M. Johnston, J. Arnold Arbor. 30: 106. 1949. TYPE: Mexico. *Sessé et al. 5250* (lectotype, MA, here designated, photo, MO, fragment, F).

Tree 3–10(–15) m tall, often with multiple trunks, the twigs puberulent, the older wood with thick furrowed bark separating into thin gray or reddish scales. Leaves persistent or partially deciduous at northern edge of range; petioles 2–6(–11) mm long, puberulent, canaliculate adaxially; leaf blade elliptic to less commonly ovate, (1.9–) 2.3–5(–9.2) cm long, (1.2–)1.6–3.8(–5) cm wide, the apex obtuse or rarely acute to slightly acuminate, the base obtuse to rounded, rarely slightly cordate, the margin entire or sometimes unevenly serrate on some of the leaves, often somewhat revolute, the upper surface scabrous, the lower surface scabrous to puberulent, the lateral veins 4–7. Inflorescence terminal, cymose, 2.5–6 cm long, the peduncle puberulent. Flowers bisexual, fragrant; sepals 5, narrowly triangular, sometimes slightly connate basally, 2.7–3.5 mm long, 0.8–1.1 mm wide basally, pubescent to strigillose, the hairs 0.3–0.4 mm long; corolla white, 6–7.8 mm long, strigillose to puberulent on the exterior surface, 5-merous, the lobes obovate, 2.8–3.4 mm long, 1.8–2.6 mm wide, the tube 2.8–4.2 mm long; stamens 5, the filaments 4–6.3 mm long, the upper 1.8–3 mm of these free, glabrous, the anthers ellipsoid, 1.2–1.4 mm long; ovary ovoid-conical, 1.3–1.8 mm long, 0.9–1.2 mm broad, glabrous; disc not evident; style 2.7–5 mm long, the stylar branches 0.7–1.7 mm long, the stigma lobes capitate to terete. Fruits drupaceous, yellow to orange when mature, glabrous, globose, 5–8 mm diam., the endocarp dividing into 2, 2-locular pyrenes, these randomly reticulate-rugulose on the outer surface.

Distribution. *Ehretia anacua* occurs in southern Texas and northeastern Mexico from sea level to 1,300(–2,200) m in dry forests (Fig. 20). Collections from Guanajuato, Oaxaca, and Queretaro are outside the natural range of the species and are not included in the distribution map.

This common species was known as *Ehretia elliptica* DC. until Johnston (1924) discovered the older epithet published in *Gaza* Terán & Berlandier. The description of *E. scabra* indicates that it is synonymous although the brief citation of "crescit in Mexico" does not indicate a type collection. The names *E. ciliata* and *E. exasperata* are clearly synonymous; *E. ciliata* differs from *E. anacua* in no discernible characters, and the type of *E. exasperata* is merely a juvenile shoot with serrate-margined leaves. Likewise, the type of *E. lancifolia* does not differ significantly in any character from *E. anacua*. Although most type material for the names lacks adequate locality information, it seems likely that all were collected in northeastern Mexico or Texas, a region in which no other species of *Ehretia* occur.

In addition to its distinct geographic range, *E. anacua* is easily distinguished from the other New World species of *Ehretia* by its scabrous upper leaf surface, cymose inflorescence, strigillose corolla tube, and usually entire leaf margins. It is quite distinct in the genus with no apparent close relatives.

Ehretia anacua is valued for its showy flowering display and its shade. The specific epithet is derived from the common name "anacua" (Nuevo León,

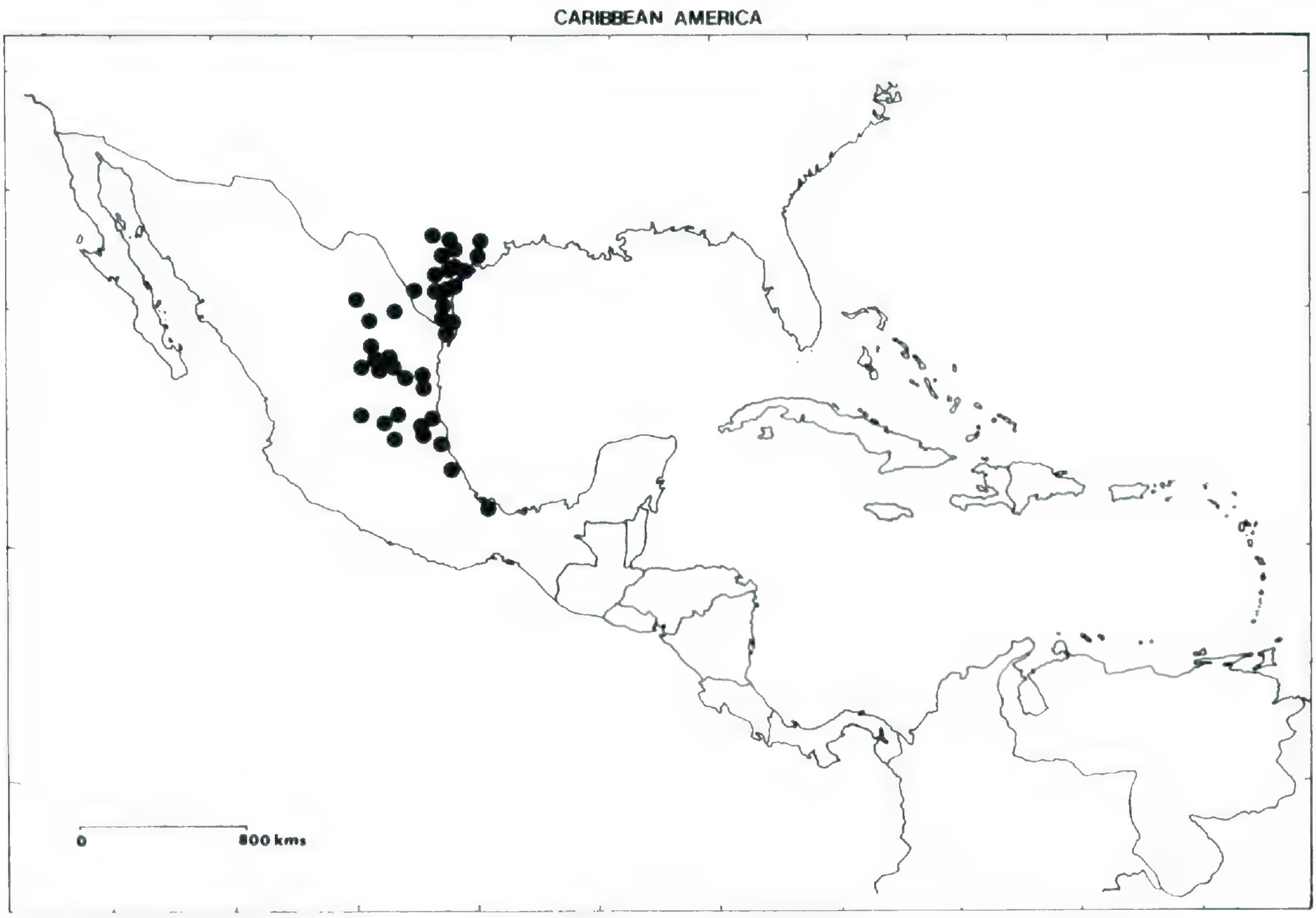


FIGURE 20. Distribution of *Ehretia anacua*.

Tamaulipas, Texas). Standley (1924) reported the wood to be used for wheel spokes, axes, tool handles, and yokes.

Representative specimens examined. U.S.A. TEXAS: Esperanzo Ranch, Brownsville, *Barber 26* (LL, US); Los Borregos, 18 mi. NE of Brownsville, *Barber 26a* (US); Odum, cultivated, *Bauml et al. 74-350* (TEX); Webb Co., Laredo, *Benavides 81* (TEX); Corpus Christi, *Benke 5407* (A, F), *5429* (A, F); without definite locality, *Berlandier 900* (K), *939* (GH); Live Oak Co., 1 mi. SW of Three Rivers, *Bluhm s.n.* (TEX); Webb Co., Laredo, *Botello & Ayala 51* (TEX); Cuiro, *Bray 152* (TEX, US); Hays Co., back of Speck Hall, *Chesser s.n.* (TEX); Hidalgo Co., transplanted from the Rio Grande wooded area, *Clover 896* (MICH); Las Palmas Plantation, about 4 mi. SW of Brownsville, in palm grove, *Correll 14869* (A, GH, LL, TEX, UC, US); Gonzalez Co., Palmetto State Park, Ottine, *Correll & Schweinfurth 15533* (A, LL); Hidalgo Co., Santa Ana Wildlife Refuge, *Correll & Schweinfurth 15636* (LL); along levee of the Rio Grande, 1 2 mi. SE of Southmost, *Correll & Johnston 17922* (A, GH, LL, TEX); Hidalgo Co., about West Pond, Santa Ana Wildlife Refuge, *Correll & Johnston 18032* (A, LL); Refugio Co., in field along route #77, just N of intersection of route #13, *Correll & Correll 18998A* (LL, MO); Calhoun Co., Indianola, *Cory 11626* (GH); Cameron Co., Brownsville, *Cory 28361* (GH), *36616* (GH); Aransas Co., Aransas Refuge, *Cory 45876* (TEX), *49033* (A, NY), *51160* (MICH, NY); Aransas Co., 6.5 mi. NE of Rockport, *Cory 51230* (GH, MICH, NY); Cameron Co., Rabb Palm Grove, 5.5 airline mi. SE of Brownsville, *Cory 51436* (GH, MICH, NY, UC, US); Goliad Co., 13⅓ mi. N of Goliad, *Cory 54619* (LL); Victoria Co., cultivated, Cory 55111 (US); Hidalgo Co., E of Mercedes, *Crockett 8026* (LL); Austin Co., bank of Brazos River, Stephen F. Austin State Park, *Crutchfield 2501* (LL, NY); Cameron Co., *Davis s.n.* (TEX); 9 mi. NW of Brownsville, *Davis 46* (TEX); Refugio Co., Mission River at Refugio, *Dixon 424* (UC); Jackson Co., *Druskel 9601* (GH); Jackson Co., Cordele, *Druskel 9976* (GH); Aransas Co., along Aransas Bay about 7 mi. N of Rockport, *Duncan & Duncan 29248* (G); Victoria Co., hedges in Victoria, *Eggert s.n.* (MO); Welder Wildlife Refuge, Javelina Bend, Aransas River, *Fosberg 44654* (US); Hidalgo Co., Weslaco, *Friend s.n.* (GH); Hidalgo Co., city of Mission, cultivated, *Gereau 940* (MO, NY); Webb Co., Laredo, *Guajardo 14* (GH, LL); Duval Co., Benavides, *Guevara s.n.* (US); Bensten–Rio Grande Valley State Park, Rio Grande Valley, 10 mi. (by air) W of McAllen, 100 ft., *Hansen et al. 3766* (LL, MICH, US, WIS); Brownsville, *Hansen 436* (NY, US); Hidalgo Co., in yard beside Motel Matador, in McAllen, *Harriman & Jansen 12394* (MICH); New Braunfels, *Harvard s.n.* (US 2 sheets); Neuces Co., Corpus Christi, *Heller 1502* (A, BH, BM, F, G, GH, LE, MICH, MO, NY—2 sheets, P, UC—2 sheets, US—3 sheets); Goliad Co., SE side of highway 59, 2.6 mi. SW of the San Antonio River, McNamara Ranch, *Hill 8234* (NY); Hays Co., San Marcos Lake, San Marcos, *Innes 816* (GH, TEX); roadside 4 mi. E of Choate, *Johnson 1180* (TEX); Laredo, *Jones 29240* (MO—2 sheets, UC); without definite locality, *Lindheimer s.n.* (NY—2 sheets, US); *Lindheimer 416* (GH); Comanche Springs, New Braunfels,

Lindheimer 1015 (BM, F, G, GH, LE, MEXU—2 sheets, MO—2 sheets, NY, P, TEX, UC, US), *1016* (BM, F, G, GH, LE, MEXU, MO—2 sheets, NY, TEX, UC, US—2 sheets), *1017* (BM, F, GH, MO, NY, P, TEX, UC, US); Gonzalez Co., levee of San Marcos River, Palmetto State Park, *Loucks s.n.* (LL, WIS); Cameron Co., Brownsville, *Lundell & Lundell 8709* (LL, MICH); Cameron Co., in Palm Grove, S of Brownsville, *Lundell & Lundell 10028* (GH, LL, MICH, US); Cameron Co., Brownsville, *Lundell 10839* (GH, LL, MICH, NY, US); Hidalgo Co., in Park, McAllen, *Lundell & Lundell 12771* (LL); Kennedy Co., King Ranch, Norias Division, on grounds at lodge, headquarters, *Lundell & Correll 15221* (A, F, LL, MO, NY, UC); Comanche Springs, New Braunfels, *Mohr 85* (A); Corpus Christi, *Nealy 4* (US); Hidalgo Co., between Weslaco and Mercedes, *Nogle 9* (F); Neuces Co., Corpus Christi Bay, *Palmer 870* (A, GH, K, MO, NY, US—2 sheets); Jackson Co., low woods, Navidad River, Ganado, *Palmer 9235* (A, K, MO, US); Jackson Co., Vanderbilt, *Palmer 9730* (A, MO, US); Wilson Co., river banks, Sutherland Springs, *Palmer 10809* (A, F, MO); Hayes Co., San Marcos, *Palmer 11558* (A, F, MO, TEX); Uvalde Co., Montell, *Palmer 12322* (K); Hays Co., San Marcos, along rocky bluffs of San Marcos river, *Palmer 33886* (A, MO, NY, P); Texas Co., San Antonio, *Parks RX001* (TEX), *1849* (TEX); chiefly in the valley of the Rio Grande, below Donna, *Parry et al. s.n.* (US); Webb Co., Laredo Junior College, Laredo, *Perez 86* (LL, TEX); Hays Co., SWTSC campus, San Marcos, *Peterson 126* (TEX); Webb Co., Laredo, *Ramos 32* (WIS); Corpus Christi, *Reverchon s.n.* (A); Brownsville, tropical nursery, *Richardson 1408* (TEX); DeWitt Co., Western, *Riedel s.n.* (GH, TEX); Willacy Co., farm road 186, 5 mi. W of Raymondville, *Rios & Cavazos 274* (LL); Webb Co., Laredo, *Rodriguez 78* (TEX); Brownsville, *Rose & Russell 24278* (NY, US); Hays Co., San Marcos Lake, San Marcos, *Rose-Innes & Warnock 816* (F); Brownsville, *Runyon 3226* (TEX), *3227* (TEX), *5175* (TEX), *5176* (TEX), *5177* (TEX); throughout the lower Rio Grande Valley, Brownsville, *Runyon 6053* (GH, LL, UC); Cameron Co., Cavazos tract dove preserve, Cavazos, *Sanderson 56* (NY); San Antonio, *Sargent s.n.* (A 2 sheets); Corpus Christi, *Sargent s.n.* (A); Victoria, *Sargent s.n.* (A); Cameron Co., Brownsville, *Schiller 1013* (MEXU); Kingsville, *Sinclair s.n.* (TEX); Santa Ana National Wildlife Refuge, *Solomon 2689* (MO); Mercertown, *Swarz s.n.* (US); San Marcos, *Tharp s.n.* (MO); Gonzalez Co., *Tharp s.n.* (TEX—2 sheets); San Marcos, *Tharp s.n.* (GH, MO, TEX, UC); near Braunfels, *Tharp 1369* (TEX, US); Jackson Co., river flood plain, *Tharp 8629* (GH, MO, NY, TEX, UC, US); Gonzalez Co., Saefje Bog, *Tharp 49-1247* (TEX); Karnes Co., 1.5 mi S of Karnes City, *Thompson & Turner 7* (TEX); Corpus Christi, *Tracy 9209* (BH, BM, F, G, GH, MO, NY, TEX, US, WIS); Cameron Co., Southmost at edge of Palm Grove, ca. 1.4 mi. S from end of highway 1419, 20 ft., *Traverse 1111* (F, GH, LL, MO, TEX, US); San Patricio Co., Welder Wildlife Foundation, N of Sinton Hackberry Mott, 2 mi. from place where S loop of river road bends west, ca. 6 m above and 40 m back from Aransas River, *Traverse 1271* (F, GH, MO, TEX, US); Hidalgo Co., Santa Ana National Wildlife Refuge, ½ mi. S of main gate, on main N S road, 80 ft., *Traverse 1828* (LL, TEX); Harris Co., Houston, Lowrey's Nursery, *Traverse 1959* (LL); Webb Co., Laredo Junior College Campus, *Trevino 48* (TEX); Cameron Co., Santa Maria, *Tucker s.n.* (US—2 sheets); Gonzalez Co., Palmetto State Park, *Warnock 169* (TEX); Comal Co., Comal Spring, Lande Park, New Braunfels, *Warnock 46503* (TEX); Cameron Co., near Southmost, grove of *Sabal texana*, *Celtis zanthoxylum*, *Tournefortia volubilis*, et al., on raised ground above level of cotton field, *Webster & Wilbur 3033* (GH, MICH, NY); Green Lake, *Whitehouse s.n.* (GH, MICH, MO, NY, TEX); Palm Grove, Brownsville, *Whitehouse s.n.* (TEX); Hidalgo Co., Santa Ana Wildlife Refuge, S of Alamo on Rio Grande River, *Whitehouse 19838* (MICH, NY, US); Cameron Co., E of Brownsville, *Wiegand 1915* (BH); Goliad Co., Goliad, *Williams 82* (TEX); San Patricio Co., sandy clay on Dr. Wright's place, NW of Sinton, *Williges 393* (TEX); without definite locality, *Wislizenus s.n.* (MO); without definite locality, *Wright s.n.* (GH 2 sheets, NY); bank of Colorado River, north of Austin, *Young 103* (MO, UC). MEXICO. COAHUILA: Saltillo, 1,650 m, *Arsene 3385* (US); Paila, 1,200 m, *Aguirre & Reko 123* (NY); near road just W of Ocampo, road from Ocampo W over the mountains to Puertecito (via Cuesta de Zozaya), *Johnston 8890* (GH); Muzquiz, *Marsh 1072* (F, GH, TEX); Monclova, Gloria Mountains, *Marsh 1977* (F, TEX). GUANAJUATO: jardín du College, *Duges s.n.* (GH); without definite locality, *Duges 153B* (GH, US). NUEVO LEÓN; Highway 60, 18 mi. W of Linares, *Ahshapanek 319* (TEX); Cañon de Valle Alto, 2,000 ft., *Bowen 42* (TEX); Ojo de Agua, Sabinas Hidalgo, 610 ft., *Chase 7024* (F, GH, MICH); Monterrey–Mexico road, *Crockett 8075* (LL); Monterrey, *Dodge 101* (MO, NY, US); base of Mt. Chapinqui, Monterrey, *Druskel 9693* (GH); Monterrey, *Eaton & Edwards 70* (K); *Edwards 70* (K, NY); near Monterrey, *Gregg 769* (MO, NY); 10 mi. S of Linares, *Kenoyer & Crum 3271* (GH); Juarez, *López-Portillo 2* (F); Monterrey, Sierra Madre Mountains, *Mueller & Mueller 167* (F, GH, TEX); Sierra Madre Oriental, Diente Canyon about 12 mi. S of Monterrey, *Mueller & Mueller 1302* (A, F, LE, MEXU, MICH, TEX); Monterrey, *Palmer 871* (A, GH, K, NY, P, US 2 sheets); about 4 mi. SE of Monterrey on Mex. 85 and W to Diente Canyon and Río Elisonda, *Parker 430* (LL); Cañon de Huajuco, *Pequeña et al. 16M 628* (F, TEX); Villa de Santiago, *Perkins & Hall 3561* (BH); valley near Monterrey, 1,800 ft., *Pringle 10171* (BH, BM, F, G, GH, L—2 sheets, LE, MEXU, MO, NY, P, UC, US); hills near Monterrey, 1,800 ft., *Pringle 11640* (BH, F, GH, L—2 sheets, MEXU, MICH); *Pringle 11650* (MEXU, MO); Horsetail Falls, ca. 35 km SSE of Monterrey, 600–700 m, *Sanders & Harborne 76077* (TEX); 40 mi. S of Monterrey on clayish loam, *Smith & Barkley 17M164* (F—2 sheets, MEXU, MICH, NY, TEX, WIS); Florida Motel at Montemorelos, *Spessard 112* (TEX); Sierra Madre Oriental, limestone slopes of Chipinque Mesa SW of Monterrey, 2,200–4,100 ft., *Webster et al. 11187* (MEXU); on the campus of I.T.E.S.M., 1,700 ft., *Wettinger 73* (TEX); Cerro de la Silla, near Monterrey, 1,700 ft., *White 1419* (GH, MICH, US); Hacienda Vista Hermosa, 35 mi. S of Monterrey, 2,200 ft., *White 1602* (GH, MICH); 2 mi. N of Monterrey on highway 85, *Wilson 10847* (TEX, WIS); Monterrey, *Wislizenus s.n.* (MO); Rinconada, near Monterrey, *Wislizenus 322* (MO). OAXACA: Ravín de Mextilán, *Ghiesbreght 30* (GH). QUERETARO: "Los Panales," a 4 km al S de El Trapiche, Mpio. de Arroyo Seco, *Tenorio & Hernández 288* (MEXU). SAN LUIS POTOSÍ: La Mirall, Mpio. San Antonio, *Alcorn 2581* (MEXU, TEX); Tzineja, Mpio. Huehuetlán, *Alcorn 2871* (TEX); Tanjasnec, Mpio. San Antonio, *Alcorn 3121* (TEX); Río Verde, *Palmer 46* (F, GH, MO, NY, US); in the region of San Luis Potosí, 6,000–8,000 ft., *Parry & Palmer*

591 1/2 (GH, MO, NY); Tamasopo Canyon, *Pringle 3709* (A, BM, F, G, GH, K, LE, MEXU—2 sheets, MICH, MO, NY—2 sheets, P, UC—2 sheets, US—2 sheets); minas de San Rafael, *Purpus 5323'* (BM, F, GH, MO, NY—2 sheets, US); Rascon, Río de las Gallinas, *Purpus 5323* (F, GH, MEXU, MO, UC, US); 4 km al W de El Naranjo, Mpio. de Ciudad de Maíz, 400 m, *Rzedowski 7378* (MEXU, MICH), *7405* (MEXU, MICH, TEX); 4 km al NE de Ciudad del Maíz, 1,300 m, *Rzedowski 10240* (US, WIS); entre Guascama y Minas de San Rafael, Mpio. de Villa Juarez, 1,200 m, *Takaki 1686* (MEXU). TAMAULIPAS: vicinity of San José, 2,000 ft., *Bartlett 10008* (F, GH, MEXU, MICH); alrededores del municipio de San Carlos, 500 m, *Jiménez 290* (MO); Morales, *LeSueur 572* (F, GH, TEX, US); S of Matamoros, *LeSueur 634* (F, TEX); a 3 km al SE de la Caseta Fiscal, en la entrada a Rancho Nuevo y a 1 km al E de Rancho El Gachupin, 200 m, *Martínez 80* (MEXU—2 sheets, MO); a 5 km al E de San Rafael (Sierra de San José de la Rusias), Mpio. Soto La Marina, 140 m, *Martínez 131* (MEXU, MO, NY); 2 km al N de San Carlos en el camino a Marmolejo, 600 m, *Martínez 952* (MO); road to Juamave, 6 mi. SW of Ciudad Victoria, *McVaugh 10540* (BM, G, GH, MEXU, MICH, NY, TEX, US); Ciudad Guerrero, *Montemayer 34* (TEX); San Fernando to Jimenez, *Nelson 6613* (GH, US); vicinity of Victoria, 320 m, *Palmer 7* (F, GH, MO, NY, UC, US); vicinity of Tampico, 15 m, *Palmer 23* (BM, CAS, F, G, GH, MO, NY, US); vicinity of Victoria, 320 m, *Palmer 132* (F, GH, MO, NY, UC, US), *Palmer 573* (F, GH, MO, NY, UC, US); Hacienda Buena Vista, *Wooten s.n.* (US); cañon al W de Ciudad Victoria atras de la Sierra Gorda, sea level, *Yanez 786* (MO); camino a Cerro el Oriente de San Carlos, 700 m, *Yanez 812* (MO). VERACRUZ: Silosuchil, Mpio. Tantoyuca, *Alcorn 1889* (TEX); El Hijo, *Alcorn 2652B* (TEX); en el poblado de Santa Clara, Misantla, 40 m, *Calzada 4730* (F); El Mirador, Presa Paso de Piedra, 40 m, *Calzada et al. 6162* (F); en la Ciudad de Tuxpan, antes de cruzar el Puente del Río Tuxpan, 50 m, *Calzada et al. 6336* (F); camino paralelo a la carretera Panuco–Tuxpan, a 12 km de Panuco, 20 m, *Chiang 288* (GH, MEXU); along road from Baños de Carrizal to Emiliano Zapata (= Carrizal), 2–6 km SE of Emiliano Zapata, Mpio. Apazapan, 250–400 m, *Hansen & Nee 7489* (F, MO); vicinity of Panuco, *Palmer 365* (CAS, F, G, GH, K, MO, NY, US); Río Grande, 3.2 km al S de Santiago Tuxtla, 200 m, *Sousa 2448* (MEXU); plan del Río, Mpio. Dos Ríos, 350 m, *Ventura 8022* (MICH, MO); 250 m, *Ventura 8552* (MEXU). STATE UNKNOWN: without definite locality, *Sessé et al. 773* (F), *774* (F), *775* (F), *5247* (F).

Ehretia latifolia DC., Prodr. 9: 503. 1845. TYPE: herb. amat. (holotype, G-DC, not seen; microfiche, MO).

Ehretia mexicana S. Watson, Proc. Amer. Acad. 26: 144. 1891. TYPE: Mexico. Jalisco: base of mountains near Lake Chapala, *C. G. Pringle 3085* (lectotype, GH, here designated; isolectotypes, BH, BM, F, G, GH, K, L, LE, MO, NY—2 sheets, UC, US—2 sheets). There are two collections at GH, neither annotated as holotype by Watson.

Ehretia luxiana J. D. Smith, Bot. Gaz. 18: 5. 1893. TYPE: Guatemala. Quiche: San Miguel Uspanlán, 6,000 ft., Apr. 1892, *Heyde & Lux 3065* (holotype, US 944452; isotypes, F, G, GH, K, MO, NY, P).

Ehretia cordifolia Robinson, Proc. Amer. Acad. Arts 29: 319. 1894; Pringle in Gard. and Forest 8: 153. 1894. TYPE: Mexico. Jalisco: valley, Zapotlán, 19 May 1893, *C. G. Pringle 4382* (holotype, F 106011; isotypes, A, BM, G, GH, K, LE, MO, NY, P, UC, US—2 sheets).

Ehretia viscosa Fernald, in Sargent, Trees and Shrubs 1: 25, pl. 13. 1902. TYPE: Mexico. Morelos: near Cuernavaca, 29 May 1899, *C. G. Pringle 7777* (lectotype, F 120287, here designated; isolectotypes, BH, GH, K, MEXU—2 sheets, MO, NY, UC). In describing this species, Fernald cited three collections. The order in which these are cited and his mention of them in his discussion indicates that he felt that the first one was the type collection.

Ehretia tehuacana Greenman, Publ. Field Mus. Nat. Hist. Chicago, Bot. 2: 339. 1912. TYPE: Mexico. Puebla: Las Mohoneras, Tehuacán, 2,200 m, *C. Conzatti 2220* (holotype, F 235156; isotype, GH).

Ehretia austinsmithii Standley, Publ. Field Mus. Nat. Hist., Chicago, Bot. Ser., 18: 984. 1938. TYPE: Costa Rica. Alajuela: Zarcero, 1,850 m, *Austin-Smith H528* (holotype, F 919653; isotypes, F, MO).

Tree to 15(–25) m tall, the trunk fluted, the twigs pubescent or shortly hirsute to nearly glabrous. Leaves persistent; petioles (3–)6–20(–31) mm long, puberulent or strigillose to nearly glabrous, narrowly canaliculate adaxially; leaf blades ovate to lanceolate or elliptic, (5.5–)7–12(–17) cm long, (2–)3–6(–9.5) cm wide, the apex acute to acuminate, rarely obtuse, the base obtuse or less commonly acute or slightly cordate, the margin serrate, rarely minutely so, adaxially scabrous to strigillose, abaxially coarsely to minutely puberulent or strigillose, occasionally nearly glabrous with only a few hairs on the major veins, the lateral veins 5–7. Inflorescence terminal or subterminal, a dense panicle, 4.5–7 cm long, (2–)3–5 cm broad, the branches puberulent to nearly glabrous. Flowers bisexual, monomorphic, sessile or short-pedicellate; calyx 1.6–2.6 mm long, glabrous to strigillose on the outer surface, sparsely to evenly ciliate along the interior margin, the 5 lobes deltate to triangular, 0.7–1 mm long; corolla white, 3.2–6 mm long, tubular with 5 reflexed, broadly ovate lobes 1.8–2 mm long and 1.6–2 mm wide, the tube 2.5–3 mm long; stamens 5, the filaments 4–4.5 mm long, the upper 2.5–3.2 mm free, glabrous, anthers ellipsoid, 1–1.5 mm long; ovary ovoid, 1.3–1.5 mm tall, 1 mm broad, disc not evident, style 3–4 mm long, faintly bilobed, the stigmas capitate. Fruits drupaceous, white, glabrous, broadly ellipsoid, 7–10 mm long, 6–9 mm wide, the endocarp remaining entire, 4-locular, only lightly ridged on the outer surface.

Distribution. *Ehretia latifolia* occurs from

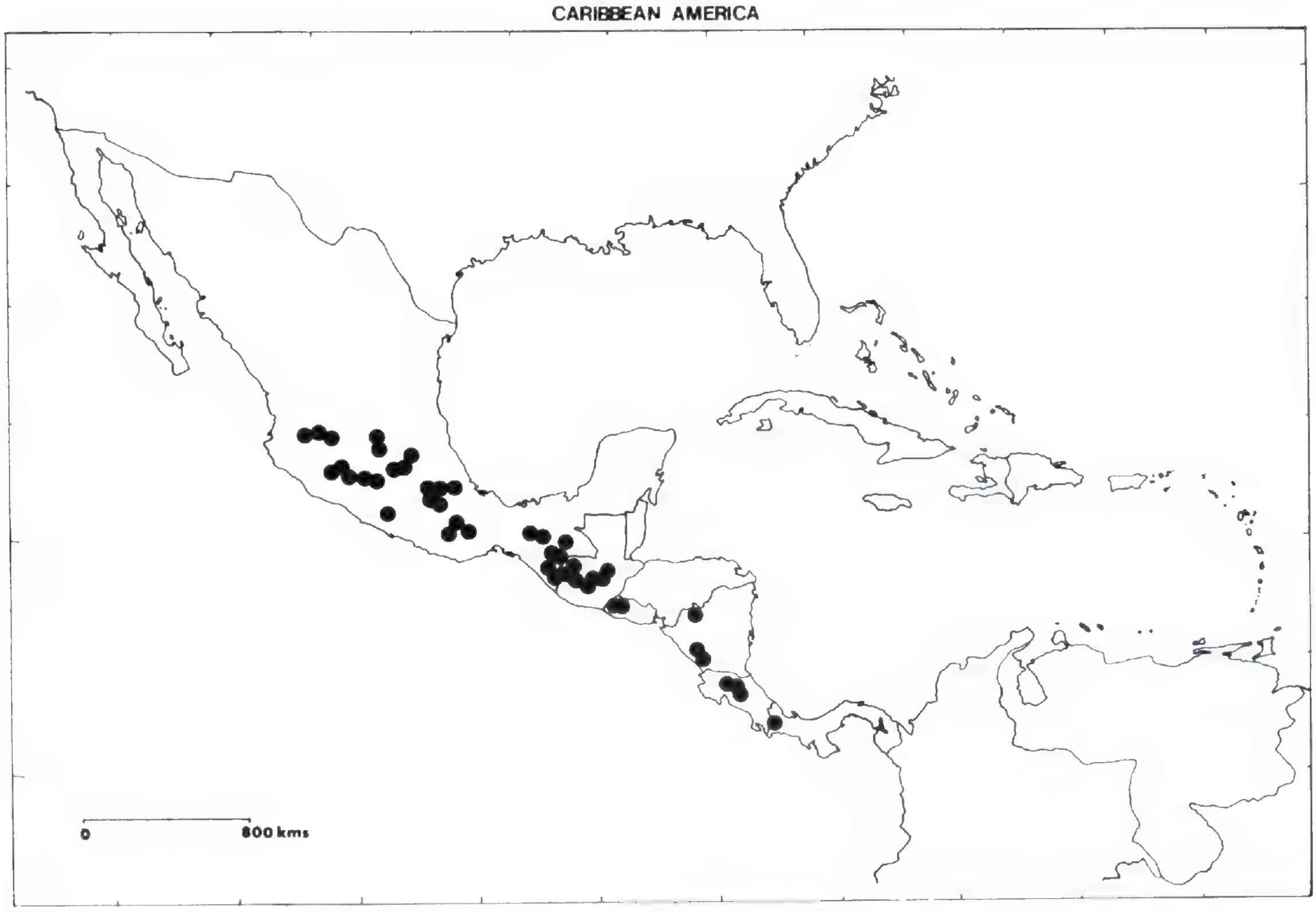


FIGURE 21. Distribution of *Ehretia latifolia*.

Jalisco in western Mexico through Central America to Chiriquí Province in Panama in cloud forests and dry montane forests at (1,500–)1,800–2,300 m (Fig. 21).

Ehretia latifolia exhibits extreme variability in leaf shape and indument, which has bred confusion. Standley (1924, 1938) recognized six species with serrate leaves in the New World. With the exception of *E. tehuacana*, all were based on characters of leaf shape and indument. When Watson (1891) published *E. mexicana*, he made no mention of how it differed from *E. latifolia*. The types of the two are nearly identical, and Standley (1924) reduced *E. mexicana* to synonymy. Smith (1893) published *E. luxiana* based on a collection from Guatemala with broader leaves that was almost glabrous abaxially and supposedly had larger flowers. The populations from the southern portion of the range do have slightly broader leaves that more often tend toward abaxial glabrousness, but there are many exceptions and there is no clear geographic discontinuity. At the time that Robinson (1894) published *E. cordifolia* it appeared distinct in having cordate leaf bases. However, field studies (discussed below) indicate that this is not a valid character since it varies on single individuals as well as within populations.

The problem with *Ehretia viscosa*, a species supposedly distinct in having glandular hairs, is slightly more complex. The few collections of it differ only in the possession of glandular hairs and in all other respects are identical to *E. latifolia*. Further, they come from localities scattered throughout the Mexican range of *E. latifolia*. Glandular hairs thus appear to be an infrequently expressed trait rather than a monophyletic group that should be recognized as a species.

Standley (1924) differentiated *Ehretia tehuacana* by its corollas about 10 mm long (supposedly more than 3 mm longer than the other species he recognized). None of the corollas on the type collection exceed 6 mm (Standley must have based his distinction on Greenman's original description) and are within the normal range of variation for *E. latifolia*. At the time that Standley (1938) described *E. austinsmithii*, it appeared to be geographically disjunct with the nearest population to the north in Guatemala. As currently defined, *E. latifolia* has a relatively continuous distribution in Central America, being unknown only in Honduras. The Central American populations are quite uni-

TABLE 3. Populations of *Ehretia latifolia* sampled for variation in leaf shape and indument.

Population	State	Voucher numbers	Elevations	Numbers of individuals sampled
Volcan Tacaná	Chiapas	2667–2670	2,300 m	4
Benito Juarez	Chiapas	2690–2695	2,100 m	5
Union Juarez	Chiapas	2721	2,010 m	1
San Cristóbal	Chiapas	2793–2795	1,800 m	3
Zinacantán	Chiapas	2799–2800	2,190 m	2
Gueletao	Oaxaca	2801–2805	2,200 m	5
Chicomezuchil	Oaxaca	2806–2810	2,200 m	5
Monte Albán	Oaxaca	2817–2823	1,800 m	5
Acatzingo	Puebla	2957	1,960 m	1
Chapulco	Puebla	2960–2962	2,000 m	3
Ciudad Mendoza	Veracruz	2971–2975	2,000 m	5
Ixthuatlancillo	Veracruz	2992–2993	1,500 m	2
Tepoztlán	Morelos	2996–2998	1,700 m	3
Campo Morado	Guerrero	2888–2892	1,400 m	5
Querendaro	Michoacan	3059–3063	1,870 m	5
Tiripitio	Michoacan	3064–3068	2,040 m	5

form while most of the significant variation appears in Mexico.

FIELD STUDIES OF VARIATION OF LEAF MORPHOLOGY

The numerous synonyms of *Ehretia latifolia* seem to have arisen via a paucity of collections and a failure to understand how leaf shape and indument vary on individual plants, within populations, and between populations. Herbarium specimens are only limited samples of individual trees and seldom provide an adequate representation of variation of leaf morphology. In order to assess how leaf morphology varied on a single individual, within populations, between populations, and over the developmental life span of individual leaves, collections were made over the range of *E. latifolia* in Mexico.

Some variation emerges during the ontogeny of an individual leaf (discussed earlier under leaf morphology) and a small portion correlates with geography, but most variation appears random and often can be found within a single population.

Two characters seem to vary geographically. Plants from Central America and part of adjacent Chiapas tend toward slightly broad, abaxially nearly glabrous leaves, while plants from populations further north have narrower, abaxially pubescent leaves. However, other collections from Central America have leaves puberulent below, and such leaves are found over a long geographic distance with no clear discontinuity. Trends of this sort occur in other woody Boraginaceae, for example, *Cordia curassavica* (Jacq.) Roemer & Schultes (Miller, 1985), and are perhaps a result of a more pronounced dry season than occurs to the north in parts of Mexico. In *Cordia curassavica* much of the variation disappears in plants raised in the greenhouse (Miller, 1985).

The second geographically correlated variation is that plants from the Tehuacán Valley in Puebla, Mexico, have leaves with smaller than usual serrations on the margin. This extreme of variation is not even consistent within Puebla and is not considered worthy of taxonomic recognition.

Most variation in leaf morphology appears random, varying in form and indument on individuals and within populations. Five leaves from five individuals (in some cases five individuals could not be found) in each population from various parts of the distributional range in Mexico were measured for length, width, length/width ratio, broadest point (calculated as distance from broadest point of the leaf to the base divided by total leaf length), apical angle, and basal angle (Tables 3, 4). In addition the indument on the adaxial and abaxial leaf surfaces was noted. The leaves selected were at least three nodes below the apex of the shoot to avoid immature leaves and never adjacent to a branch, as these are often quite different in form.

Field studies reveal considerable variation in leaf shape on a single tree, with leaf bases often varying from acute to obtuse and sometimes even cordate

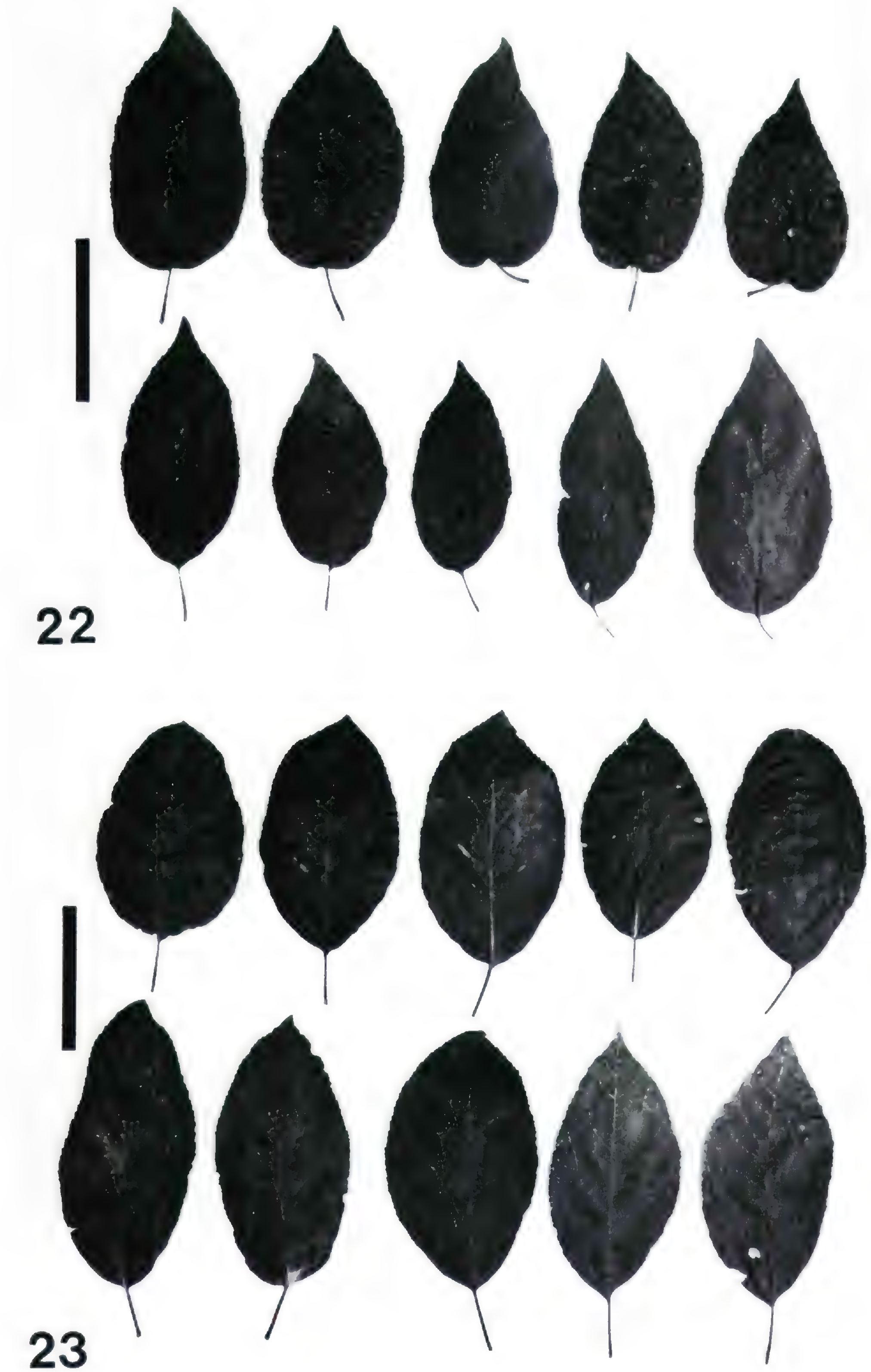
TABLE 4. Variation in leaf shape among Mexican populations of *Ehretia latifolia*. Upper figures are means and lower figures are standard deviations.

Population	Leaf length/ width ratio	Broadest point of leaf	Apical angle	Basal angle
Volcán Tacaná	2.13	0.44	73.75	109.25
	0.33	0.059	18.50	32.14
Benito Juarez	1.60	0.45	96.80	140.40
	0.24	0.068	20.24	27.20
Union Juarez	1.95	0.47	83.00	124.00
	0.16	0.049	16.91	13.56
San Cristóbal	2.37	0.44	68.33	89.33
	0.27	0.049	18.32	18.96
Zinacantán	2.69	0.50	51.00	66.00
	0.43	0.047	9.95	10.20
Gueletao	1.81	0.43	70.80	137.20
	0.46	0.043	14.95	36.85
Chicomezuchil	2.23	0.46	62.00	113.60
	0.32	0.054	13.27	20.91
Monte Albán	2.10	0.41	67.80	131.60
	0.45	0.044	15.37	30.22
Acatzingo	2.17	0.45	70.00	95.00
	0.20	0.029	10.49	13.04
Chapulco	1.88	0.44	80.00	134.67
	0.22	0.040	17.22	27.41
Ciudad Mendoza	2.46	0.44	57.80	109.60
	0.46	0.045	18.44	33.52
Ixthuatlancillo	1.97	0.44	71.50	105.00
	0.25	0.060	14.67	28.28
Tepoztlán	2.08	0.46	66.67	97.67
	0.22	0.078	8.88	15.37
Campo Morado	1.97	0.43	75.80	119.40
	0.29	0.054	21.10	28.12
Querendaro	1.93	0.39	67.40	143.40
	0.25	0.041	15.24	18.91
Tiripitio	2.07	0.39	56.20	162.00
	0.31	0.055	8.40	33.88

from one branch to another. Shape of the leaf base was the character used to distinguish *Ehretia cordifolia*, but examination of leaves from different branches of a single tree collected near Guelatao, Oaxaco, Mexico (Fig. 22) shows this character to vary on a single individual. The same type of variation in shape of leaf apices often occurs on single individuals, as exemplified by leaves from different branches of an individual collected near Motozintla, Chiapas, Mexico (Fig. 23).

Most of the Mexican populations examined were relatively constant in terms of leaf indument, although occasional plants were more or less pubescent than surrounding individuals. There did appear to be, however, a significant amount of variation in leaf shape among individuals from a single population. Leaves from the population at Monte Alban (Fig. 24) ranged from 1.5 to 3.2 in leaf length/width ratio and 45° to 100° in apical angle. The sampled population near Ciudad Mendoza (Fig. 25) had leaf length/width ratios of 1.7 to 3.4 and a range of 60° to 240° in basal angle. If this degree of variation can be found in a single population, leaf apex, blade, and base shape are not reliable characters for delimiting species.

Mean values and standard deviation are given for characters of leaves from Mexican populations of *Ehretia latifolia* in Table 4. Leaf length/width ratio, broadest point, apical angle, and basal angle appear to be the best measures of overall leaf shape.



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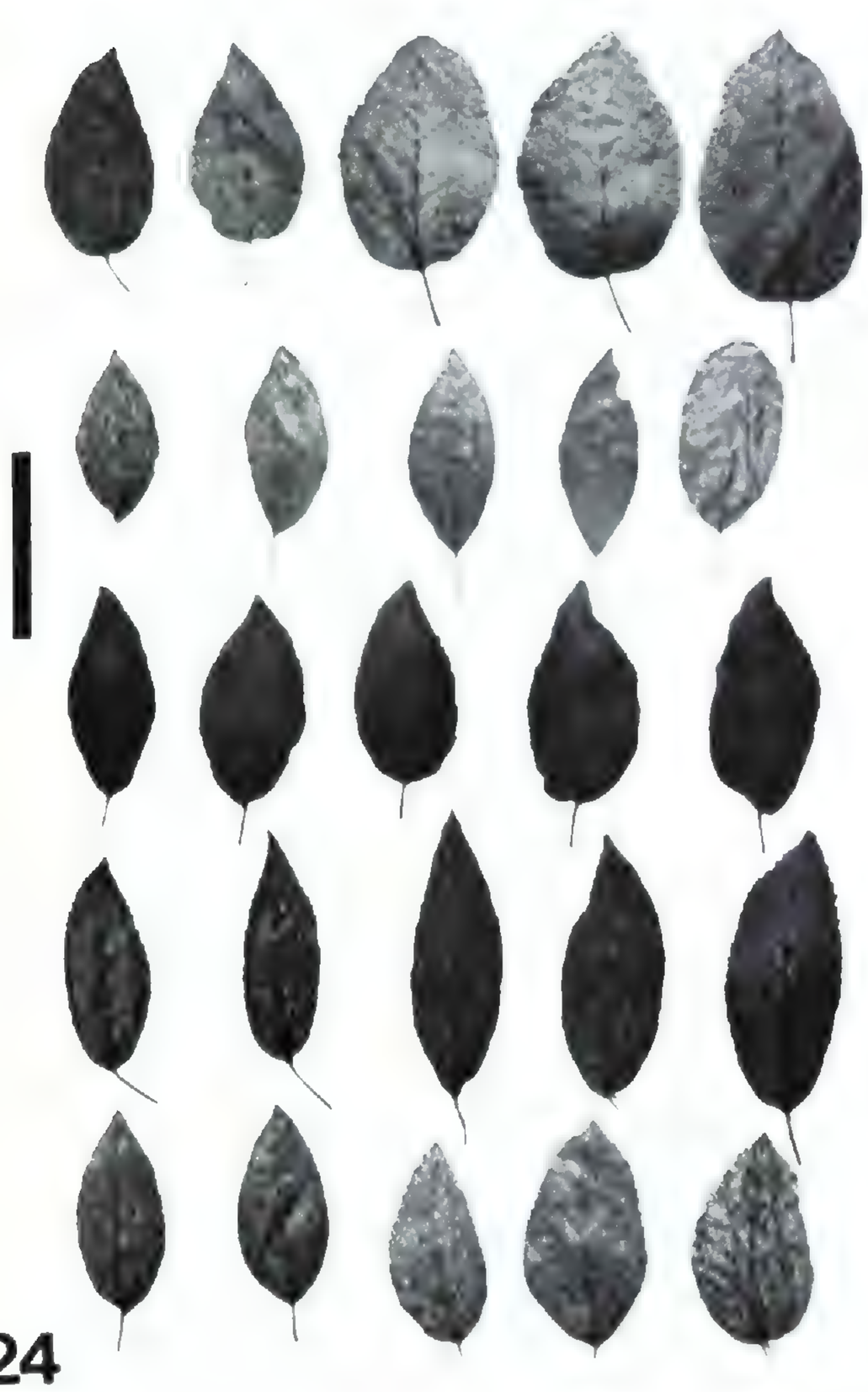

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FIGURES 24, 25. Variation in leaf shape among five individuals from single populations of *Ehretia latifolia*. Each row consists of five leaves from a single individual.—24. From top to bottom, *Miller & Myers 2817–2821* (MO).—25. From top to bottom, *Miller & Torres 2971–2975* (MO). Scale bars equal 5 cm.

Variation in leaf morphology among populations is overlapping in range, and no clear geographic patterns appear.

Representative specimens examined. MEXICO. CHIAPAS: slope with *Quercus* and *Pinus* in the barrio of Chihk Ha', paraje of Yashanal, Mpio. of Tenejapa, 6,000 ft., *Breedlove 9396* (F, NY); slope with *Quercus* and *Pinus* in the paraje of Kulak'tik, Mpio. of Tenejapa, 6,000 ft., *Breedlove 10947* (DS, F); steep slope along the river of Chihk Ha', barrio of Yashanal, paraje of Matsab, Mpio. of Tenejapa, 5,500 ft., *Breedlove 11110* (DS); in the barrio of Tuk, paraje of Matsab, Mpio. of Tenejapa, 7,500 ft., *Breedlove 12567* (DS, F, MICH); slope with *Quercus* and *Pinus*, paraje of Kulak'tik, Mpio. of Tenejapa, 5,500 ft., *Breedlove 12856* (DS, F, LL, US); 45–50 km NW of Huiztla along road to Motozintla, Mpio. of Motozintla de Mendoza, 1,900 m, *Breedlove & Thorne 31080* (DS); SW side of Cerro Mozotal, 11 km NW of the junction of the road to Motozintla along the road to El Porvenir and Siltepec, Mpio. de Motozintla de Mendoza, 2,100 m, *Breedlove 31108* (DS, MO); second growth slopes paraje Chikinibalvo, Mpio. of Zinacantán, 1,200 m, *Breedlove 39606* (DS, MEXU); slope with *Pinus* and *Quercus*, 6 10 km NNE of La Soledad along logging road from Las Margaritas to Campo Alegre, Mpio. of La Independencia, 1,600 m, *Breedlove 51268* (CAS, MEXU, MO, TEX); a 6 km al N de Oxchuc, sobre el camino a Ococingo, *Cabrera & Cabrera 6146* (MEXU—2 sheets, MO); steep slopes with *Quercus* near the paraje of Yal'ichen on the road to Chenalo, Mpio. of Chamula, 6,000 ft., *Laughlin 691* (DS, US); slope with *Quercus* and *Pinus* in the paraje 'Apas, Mpio. of Zinacantán, 5,500 ft., *Laughlin 1197* (DS, NY); slope with *Quercus* and *Pinus* in the paraje of Sek'emtik, Mpio. of Zinacantán, 6,000 ft., *Laughlin 1222A* (DS, LL, US); slope with *Quercus* on trail from Zinacantán, center to Ixtapa near Paraje Bo'pits, Mpio. of Zinacantán, 4,500 ft., *Laughlin 2441* (DS, US); Mt. Ovando, *Matuda 495* (F, MICH, US); hills E of Unión Juárez, lower slopes of Volcán Tacaná, 1,700–2,300 m, *Miller et al. 2667* (MEXU, MO), *2668* (MEXU, MO),

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FIGURES 22, 23. Variation in leaf shape on individual trees of *Ehretia latifolia*.—22. *Miller & Myers 2802* (MO). Note variation in leaf base.—23. *Miller et al. 2690* (MO). Note variation in leaf apex. Scale bars equal 5 cm.

2669 (MEXU, MO), *2670* (MEXU, MO); along the dirt road to Ejido Benito Juarez and Siltepec, 4–6 km from the turnoff from Mexican highway 190, S of Motozintla, ca. 2,100 m, *Miller et al. 2690* (MEXU, MO), *2691* (MEXU, MO), *2692* (MEXU, MO), *2693* (MEXU, MO), *2694* (MEXU, MO), *2695* (MEXU, MO); along the incomplete dirt road to Motozintla, hills above Unión Juárez, lower slopes of Volcán Tacaná, 1,900–2,010 m, *Miller & Myers 2721* (MEXU, MO); along Mexican highway 190 between San Cristóbal de las Casas and Tuxtla Gutierrez et km 52, 1,800 m, *Miller et al. 2793* (MEXU, MO), *2794* (MEXU, MO), *2795* (MEXU, MO); along the dirt road 4 km SW of Zinacantán, 2,190 m, *Miller et al. 2799* (MEXU, MO), *2800* (MEXU, MO); sumidero adelante La Coyota, *Miranda 7752* (US); 3 km NW of Pueblo Nuevo Solistahuacán, 4,500 ft., *Thorne & Lathrop 41515* (DS); paraje of Kulak'tik, Mpio. of Tenejapa, 5,800 ft., *Ton 369* (F). GUERRERO: Campo Morado and hills above town, ca. 1,400 m, *Miller & Campos 2888* (MEXU, MO), *2889* (MEXU, MO), *2890* (MEXU, MO), *2891* (MEXU, MO), *2892* (MEXU, MO). HIDALGO: Cerro de San Isidro, Mpio. de Tlalnalapa, 2,600 m, *Ventura 414* (MEXU). GUANAJUATO: cerca del Río, 1,900 m, *Arguelles 25* (MEXU); El Batán, 2,000 m, *Arguelles 1095* (CAS, MEXU), *Arguelles 1223* (MEXU, MO); pres de Guanajuato, *Duges 153* (GH); shore of saline, alkaline crater lake La Piscina de Yuriria, 1,730 m, *Perrott 44a* (BM); carretera Silao–Guanajuato, Cerro Culiacán, *Villareal de Puga 275* (WIS). JALISCO: vicinity of Guadelajara, 1,500 m, *Diquet s.n.* (MICH—2 sheets, NY, P, US); E of La Barca, *Gregg 841* (MO—2 sheets); Chiquilistlan, *Jones 78* (F, MO, US); vicinity of San Juan Cosalá, mountainsides above (N of) Lake Chapala, 1,500–2,200 m, *Puga s.n.* (MICH); along the highway near Ciudad Guzmán, *Puga s.n.* (MICH); Calabazas, *Reko 4875* (US). MÉXICO: dist. Temascaltepec, Cumbre Tejupilco, 1,500 m, *Hinton 2837* (A, G, GH, K, NY); dist. Temascaltepec, Nanchititla, *Hinton 3419* (A, BM, G, GH, NY, US); Mpio. Tezcoco, San Nicolás Tlaminca, ca. 7 km al E de Tezcoco, 2,600 m, *Koch 821* (CAS, F, MICH, MO, NY, TEX, WIS); Tlatlaya y cercanías, *Matuda et al. 30007* (MEXU, MO); Tlapacoyan, Mpio. de Chalco, 2,250 m, *Rzedowski 26798* (CAS, LL, MICH); *Urbing s.n.* (MEXU); San Nicolás Tlamincas, Mpio. Texcoco, 2,300 m, *Ventura 354* (CAS, NY, WIS); 2,400 m, *Ventura 793* (MEXU). MICHOACAN: Morelia, 2,100 m, *Arsène s.n.* (G); Tócuaro, Mpio. Erongaricuaro, 2,000 m, *Bello 86* (MEXU); W of Morelia, *Gregg 778* (MO); Patzcuaro, 1,850 m, *Hinton 18199* (TEX); 25 mi. W of Lake Patzcuaro, 6,900 ft., *Hitchcock & Stanford 7179* (CAS, GH, UC, US); Tiripetío, Mpio. Morelia, 1,950 m, *Madrigal 2852* (MEXU); Tócuaro, Mpio. Erongaricuaro, 2,000 m, *Madrigal 3148* (MEXU); along Mexican highway between Morelia and El Oro, 3 km E of Querendaro at km 132, 1,870 m, *Miller & Telléz 3059* (MEXU, MO), *3060* (MEXU, MO), *3061* (MEXU, MO), *3062* (MEXU, MO), *3063* (MEXU, MO); just S of Tiripitío along Mexican highway between Morelia and Patzcuaro at km 27, 2,040 m, *Miller & Telléz 3064* (MEXU, MO), *3065* (MEXU, MO), *3066* (MEXU, MO), *3067* (MEXU, MO), *3068* (MEXU, MO); en la desviación a Capula, 21 km al SW de Morelia, carretera a Guadalajara, 2,140 m, *Soto 2382* (CAS, MEXU); a 15 km de Ciudad Hidalgo, rumbo a Zitcuaro, 1,830 m, *Soto 6273* (CAS, MEXU, MO). MORELOS: Zona Arquelógica Tepoztlán, in the Cerro Tepozteca above Tepoztlán, ca. 30 km SE of Cuernavaca, 1,700 m, *Miller & Torres 2996* (MEXU, MO), *2997* (MEXU, MO), *2998* (MEXU, MO); Chapultepec Springs near Cuernavaca, 5,000 ft., *Pringle 8748* (A, BH, BM, F, G, GH 2—sheets, K, L—2 sheets, MEXU—2 sheets, MO, NY, P, UC, US), *10261* (BH, BM, CAS, F, G, GH, L—2 sheets, MEXU—2 sheets, MICH, MO, NY, P, UC—2 sheets, US); near Cuernavaca, *Rose & Hough 4371* (US); *Rose & Painter 6880* (NY, US). OAXACA: Oaxaca de Juárez, *Bailey 540* (BH, MICH); near Monte Albán, *Camp & Conzatti 2781* (NY); Dist. de Ixtlán, ruta 175 Tuxtepec a Oaxaca, Guelatao de Juárez, 2,200 m, *Cedillo & Lorence 643* (MEXU, MO); al 500 m al SW de la desviación a La Ascunción, carretera a San Agustín Atenango, dist. de Silacayoapán, 1,980 m, *Cedillo & Torres 1449* (MEXU); Río el Molino, 4.5 km al N de Ixtlán, camino a Calpulalpán de Méndez, 2,000 m, *Cedillo & Lorence 2324* (MEXU); *Cedillo & Lorence 2330* (MEXU); a 12 km al SE de Dominguillo, por la carretera a Oaxaca, *Chiang et al. 157* (MO); Monte Albán, 1,800 m, *Conzatti 146* (GH); Cerro de San Felipe, 1,800 m, *Conzatti 210* (GH, K); Monte Albán, 1,700 m, *Conzatti 4848* (MICH); *Conzatti 4918* (CAS); 1,380 m, *Conzatti 5245* (MICH, NY); ruins at Monte Albán, *Croat 935* (MO); Dorantes Plateau, 5,500 ft., *Galeotti 3099* (K); 1 km al SE de Tamazulapán, camino a San Jerónimo, Dist. de Teposcolula Mixteca Alta, 2,000 m, *García 937* (MEXU); without definite locality, *Kenoyer A660* (F); Monte Albán, *Kenoyer 1541* (GH); Oaxaca, *Liebmann 12722* (F, UC); Dist. de Ixtlán, Sierra de Juárez, camino de Ixtlán a Xiacui, 2,050 m, *Lorence et al. 3573* (BM, MEXU, MO); Monte Albán, 6,000 ft., *Messer 153* (MICH); along Mexican highway 175 at km 159 just SW of Guelatao, 2,200 m, *Miller & Myers 2801* (MEXU, MO), *2802* (MEXU, MO), *2803* (MEXU, MO), *2804* (MEXU, MO), *2805* (MEXU, MO); along the dirt road to Chicomezuchil, 1 km SE of Mexican highway 175, 4 km W of Chicomezuchil, ca. 2,200 m, *Miller & Myers 2806* (MEXU, MO), *2807* (MEXU, MO), *2808* (MEXU, MO), *2809* (MEXU, MO), *2810* (MEXU, MO); Monte Albán, short deciduous forest surrounding the ruins and adjacent roadsides, 1,800 m, *Miller & Myers 2817* (MEXU, MO), *2818* (MEXU, MO), *2819* (MEXU, MO), *2820* (MEXU, MO), *2821* (MEXU, MO), *2822* (MEXU, MO), *2823* (MEXU, MO); Monte Albán, 5,800 ft., *Pringle 6138* (A, BH, BM, G, GH—2 sheets, L, MO, NY, P, UC, US—3 sheets), *6138a* (A, BH, BM, G, GH, K, MO, NY, P, UC, US—2 sheets); 6,200 ft., *Smith 146* (GH), *1194* (IJ, MO, NY 2 sheets, UC, US); Cerro San Felipe, 1,800 m, *Urbing et al. s.n.* (MEXU); cerca del Puente de Río Grande, Mpio. de San Juan Chicomezuchil, 1,400 m, *Ventura 16098* (MEXU, NY). PUEBLA: aprox. 12 km al NW de Tehuacán, rumbo a Orizaba, *Chiang et al. F-280* (MEXU, MO); San Nicolás, Tehuacán, 2,000 m, *Conzatti 2221* (F, GH—2 sheets); Tehuacán, *Liebmann 15166* (F); 5 km al E de Santa Catarina Tehuixtla, aprox. 5 km al SE de Tepoztitlán, 1,820 m, *Medrano et al. F-1377* (MEXU); along Mexican highway 150 between Tepeaca and Tecamachalco at the turnoff to Acatzingo, km 234, 1,960 m, *Miller & Torres 2957* (MEXU, MO); along the road in between Tecamachalco and Cañada Morelos, at Chapulco, 16 km from Cañada Morelos, 2,000 m, *Miller & Torres 2960* (MEXU, MO), *2961* (MEXU, MO), *2962* (MEXU, MO); vicinity of San Luis Tultitlanapa, *Purpus s.n.* (BM), *2716* (BM, F, G, GH, MO, UC—2 sheets, US), *3082* (BM—2 sheets, F, GH, MO, NY, UC—2 sheets, US); Tlaucuislaltepec, *Purpus 3976* (L, UC); cerros near San Luis Tultitlanapa, Sierra Mixteca, *Purpus 4215* (L); near

Oaxaca, in the vicinity of San Luis Tultitlanapa, *Purpus 4249* (DS, F, G, GH, L, P, UC, US), *4251* (BM, F, GH, MO, UC, US), *4252* (BM, F, GH, MO, P, UC, US); El Riego, near Tehuacán, *Purpus 5818* (BM, UC); Tehuacán, *Purpus 5820* (BM, F, GH, MO, NY, UC, US); road Puebla–Tehuacán, *Reko 10* (F); Nacozcalco and San Antonio Cañada, along the Barranca de los Mangos, 1,000–1,800 m, *Smith 4087* (F, G); Azumbilla, *Smith & Tejeda 4530* (US); Chapulco, *J. E. Smith F-9* (MICH); aprox. 9 km al NE de Tecamachalco, por la carretera a Cañada Morelos, *Villaseñor et al. 143* (MEXU). VERACRUZ: Orizaba, *Botteri 1022* (BM, G), *1322* (P); *Bourgeau s.n.* (GH, K, P); steep slopes of high valley above route 150, 4 km W of Acultzingo, 5,500 ft., *Long & Burch 3300* (F); Acultzingo, *Matuda 1106* (LL, MEXU, MICH); along Mexican highway 150 at the turnoff to Puente Colorado, hills above Ciudad Mendoza, ca. 2,000 m, *Miller & Torres 2971* (MEXU, MO), *2972* (MEXU, MO), *2973* (MEXU, MO), *2974* (MEXU, MO), *2975* (MEXU, MO); Ixhuatlancillo and vicinity, ca. 10 km N of Orizaba, ca. 1,500 m, *Miller & Torres 2992* (MEXU, MO), *2993* (MEXU, MO); Orizaba, *Muller s.n.* (NY, US), *502* (L). STATE UNKNOWN: without definite locality, *Gregg 778* (MO); *Sessé et al. 767* (F), *772* (F), *5246* (F), *5248* (F). GUATEMALA. ALTA VERAPAZ: 3 km de Villa Hermosa 1,400 m, *Molina & Molina 12356* (F, NY). AMATITLAN: San Vicente Pacaya, 1,400 m, *Tonduz 472* (G, MO, US). BAJA VERAPAZ: Chilasco, *Contreras 10978* (LL, S); along dirt road 4 mi. NE of Purulhá, 1,500 m, *Croat 41360* (MO); Mpio. Rabinal, at summit of Sierra de Chuacús, at border of Mpio. Rabinal and Mpio. El Chol, along road between slopes at summit, 1,800 m, *Croat & Hannon 63635* (MO), *63656* (MO); 6–8 km S of Rabinal, *Harmon & Dwyer 3178* (MICH, MO). EL QUICHE: below falls of Río de las Violetas, ca. 3 mi. N of Nebaj, 5,300–5,500 ft., *Proctor 25547* (IJ, LL—2 sheets). GUATEMALA: without definite locality, *Aguilar 717* (F); vicinity of San Andrecillo, 1,700 m, *Molina & Molina 27570* (F, MICH). QUEZALTENANGO: region of Las Nubes, S of San Martín Chile Verde, 2,250 m, *Standley 85162* (F); Montaña Chicharro, on lower southeast facing slopes of Volcán Santa María, 2–4 km S of Santa María de Jesús, 1,400–1,500 m, *Steyermark 34279* (F, NY). SACATEPEQUEZ: near Antigua, 6,500 ft., *Kellerman 7426* (F, MICH, NY, US); nacimiento del Cangrajal, Cuesta de Las Cañas, 1,650 m, *Molina 15468* (F, GH); near Pastores, 1,560–1,650 m, *Standley 59911* (F); barranca above Dueñas, 1,590 1,800 m, *Standley 63268* (F); near Barranca Hondo, SE of Alotenango, 1,000–1,260 m, *Standley 64959* (F). SAN MARCOS: barrancas 6 mi. S and W of town of Tajumulco, northwestern slopes of Volcán Tajumulco, 2,300–2,800 m, *Steyermark 36607* (F); above Finca El Porvenir, between "Todos Santos Chiquitos" and "Loma de la Paloma," south-facing slopes of Volcán Tajumulco, 1,400 1,700 m, *Steyermark 37277* (F, GH); Finca El Porvenir, on Potrero Matasano along Río Cabús, Volcán Tajumulco, 1,000 1,300 m, *Steyermark 37631* (F); Potrero Matasano, Finca El Porvenir, slopes of Volcán Tajumulco, 1,200 m, *Steyermark 52124a* (F, GH). STATE UNKNOWN: without definite locality, *Heyde 572* (US). EL SALVADOR. LA LIBERTAD: Santa Tecla, *Calderón 1418* (GH, NY, US); vicinity of Santa Tecla, 790–950 m, *Standley 23081* (GH, NY, US). SAN SALVADOR: Cerro de San Jacinto, *Calderón 2246* (F, GH, NY, US—2 sheets); *Calderón 2247* (GH, US); Santiago de María, *Calderón 2254* (US); Cerro de San Jacinto, near San Salvador, 800–1,171 m, *Standley 20630* (GH, NY, US). SONSONATE: highway to Cerro Verde, area S of Lake Coatepeque, 3,500 ft., *Allen 7072* (F, G, GH, LL, NY—2 sheets, US). STATE UNKNOWN: Berlín, *Calderón 2144* (US); without definite locality, *Renson 332* (US—2 sheets); Volcán de San Salvador, 1,000–1,800 m, *Standley 22884* (US). NICARAGUA. GRANADA: Volcán Mombacho, 1,100 m, *Moreno 24363* (MO). JINOTEGA: vicinity of Jinotega, 1,030–1,300 m, *Standley 9689* (F); region of La Montañanita and Las Mesitas, in Sierra W of Jinotega, about 1,100–1,400 m, *Standley 10403* (F). MANAGUA: Sabana Grande, Managua, 90–100 m, *Suárez 99* (MO). COSTA RICA. ALAJUELA: Bella Vista de Zarcero, 1,800 m, *Austin-Smith 139* (F, GH—2 sheets, NY); Zarcero, 5,500 ft., *Austin-Smith A384* (F—2 sheets); Zarcero, Alfaro Ruiz, 1,800 m, *Austin-Smith P2500* (GH, UC); Zarcero, *Austin-Smith 2702* (F); Zarcero, Alfaro Ruiz, 1,900 m, *Austin-Smith 10048* (F, GH). CARTAGO: La Carpintera, *Echeverria 402* (CR, F, UC); cerca del quebrador Ochomogo, *Poveda 459* (CR); Cerro de la Carpintera, 1,500–1,850 m, *Standley 34518* (US); Cerro del Aguacate, La Carpintera, 1,500 m, *Williams 11578* (CR, F); on open slopes of Cerro Carpintera above Tres Ríos, 1,500 m, *Williams 16156* (BM, F, MO, US); Cerro del Aguacate, La Carpintera, 1,500 m, *Williams 16578* (F). HEREDIA: along road N of Gethsemini de Heredia, 1,500–1,700 m, *Hartshorn 1208* (CR, F, MO); en depresión al Oeste del Monte de la Cruz, San Rafael, 1,700 m, *Jiménez 2513* (F). PUNTARENAS: Monteverde, lower community, 1,450 m, *Haber 203* (CR, MO); Santa Elena, 5 km W of Santa Elena on road to highway, *Haber 1775* (MO); Monte Verde, along Río Guacimal below Lechería, 1,500 m, *Hammel & Trainer 13837* (MO). SAN JOSÉ: Tres Ríos, *Córdoba 317* (CR); vicinity of Santa María de Dota, 1,500–1,800 m, *Standley & Valerio 44145* (US). PANAMA. CHIRIQUÍ: a lo largo del camino que va de Bambito a los llanos de lava, 6,000 ft., *Correa & Lazor 1410* (F, MO); at opening to canyon to Bambito, 5,000 ft., *Tyson 5870* (MO—2 sheets); Río Chiriquí Viejo valley, near Bambito, *P. White 220* (F, GH, MO).

Ehretia tinifolia L., Syst. Nat. ed. 10. 2: 936. 1759. TYPE: from Patrick Browne's Jamaican herbarium purchased by Linnaeus in 1758 (lectotype, here designated, LINN (Savage Catalog number 254.1); microfiche, MO; photo, F; isolectotype, BM).

Ehretia longifolia Miers, Ann. & Mag. Nat. Hist. Ser. IV. 3: 110. 1869. SYNTYPES & ISOSYNTYPES: In Antillis et Mexico, Jamaica, *in herb. Hook., Lane* (BM); Jamaica, *Macfadyen* (BM, K); Mexico, Oaxaca, Ravins a 3,000 ft., *Galeotti 7194* (G, K).

Ehretia sulcata Miers, Ann. & Mag. Nat. Hist. Ser. IV. 3: 109. 1869. SYNTYPES & ISOSYNTYPES: in Antillis, *herb. Mus. Brit.* (not identified); Jamaica, *herb. Sloan. Vol. vii. Fol. 5* (not identified); in hort. Kew. cult., Jamaica, *Houston* (BM); in herb. Hook., Jamaica, *Purdie* (BM); Cuba, *La Sagra* (K, LE); Cuba, Havana, *Greene* (BM, K).

Tree to 15(–25) m tall, the twigs essentially glabrous. Leaves persistent; petioles (3–)5–10(–14) mm long, glabrous canaliculate adaxially; leaf blades elliptic, (5–)6.5–12(–16.5) cm long, (2.5–)3–6(–8) cm wide, the apex obtuse to rounded, the base

obtuse to acute, the margin entire, adaxially glabrous and lustrous, abaxially glabrous, the lateral veins 6–7. Inflorescence terminal, paniculate, 7–15 cm long, the branches glabrous. Flowers bisexual, sessile or short-pedicellate; calyx campanulate, 1.5–2 mm long, the 5 lobes ovate, 1.5–2 mm long, 0.7–0.9 mm wide, glabrous externally, ciliate along the interior margin; corolla white, tubular-campanulate with 5 reflexed lobes, 4–4.6 mm long, glabrous on the exterior surface, the lobes widely oblong to oblong-ovate, 2.5–5 mm long, 1.3–1.7 mm wide, the tube 1.3–2.1 mm long; stamens 5, the filaments flattened, 3–4.5 mm long, the upper 2–3 mm free, glabrous, the anthers ellipsoid, 1–1.3 mm long; ovary ovoid to broadly ovoid, 1–1.2 mm long, 1 mm broad; style 2–3.4 mm long, divided for 0.5–0.7 mm, the stigmas truncate. Fruits drupaceous, yellow-orange, glabrous, broadly ellipsoid, 5–7 mm long, 4–6 mm broad, the endocarp dividing into 2, 2-locular pyrenes, these ridged-reticulate on the outer surface.

Distribution. *Ehretia tinifolia* occurs from southeastern Mexico to Honduras and on Cuba, Hispaniola, Jamaica, and the Cayman Islands in lowland, moist to wet forests from sea level to 600(–1,500) m (Fig. 26). Collections cited from Guerrero, Michoacán, Nayarit, San Luis Potosí, and Sinaloa are not included in the distribution map as they are presumed to be out of the natural range of the species and are probably from cultivated plants.

Ehretia tinifolia is distinguished from the other New World species by its glabrous, lustrous, entire-margined leaves and elongate, paniculate inflorescence. It is widely cultivated, even outside of its natural range for its attractive flowering and fruiting display and as a shade tree.

The two species described by Miers, *Ehretia longifolia* and *E. sulcata*, are both clearly synonymous from Miers's description and their West Indian distributions. Unfortunately, Miers cited specimens with little information and these collections remain difficult to identify. For this reason, these names have not been lectotypified, and syntypes are cited here.

Representative specimens examined. MEXICO. CAMPECHE: a 3 km al sur de la carretera Champotón–Campeche, sobre el camino a El Zapote, *Cabrera & Cabrera 2389* (MEXU, MO); sobre el camino a Pixoyal, a 30 km al norte de Escarcega, *Cabrera & Cabrera 2410* (MEXU); 5 km al sur de Constitución, a 70 km al este de Escarcega, *Cabrera & Canul 5063* (MEXU, MO); Rancho-Guadalupano, Mpio. Campeche, 12 m, *Chan & Flores 478* (F); Yohaltum, Mpio. Champoton, 12 m, *Flores & Chan 8715* (F); environs de Campeche, *Linden 107* (K); Campo Experimental, Escarcega, 100 m, *Marroquín 294* (WIS); 45 km al NE de Campeche, camino a Merida, 30 m, *Martínez et al. 3011* (BM, CAS, MEXU); cultivated in garden, *Seler 4016* (F); near Xujil, 300–400 m, *Shepherd 93* (LL, MICH—2 sheets, WIS—2 sheets); Hecelchakan, *Stewart 52* (GH). CHIAPAS: in the sitios or along the streets of Ocozocuautla, Mpio. of Ocozocoautla, 580 m, *Breedlove & McClintock 23514* (DS, MEXU, MO); along the streets or in the sitios of Tonala, Mpio. Tonala, *Breedlove & Thorne 30658* (B, DS, F, LL, MEXU, MICH, MO, NY); cultivated, dry open slope with tropical deciduous forest, 32 km NNW of Soyalo, along the road to Copainala above Chicoasen, Mpio. of Chicoasen, 450 m, *Breedlove 34039* (DS, MEXU, MO); Mpio. of Cintalapa, 23 km W of Las Cruces along the road to La Mina microwave station, 870 m, *Breedlove & Davidse 54141* (CAS, MO, NY); Chiapa de Corzo, Mpio.. of Chiapa de Corzo, *Laughlin 794* (DS, F, LL); Margaritas, Comitán, 1,530 m, *Matuda 5783* (LL, MEXU, MICH, MO), *15783* (F); Escuintla, cultivated, *Matuda 16607* (F, MEXU); Paderón, Tonala, *Matuda 16951* (F—2 sheets, MEXU); Encañana, arriba Chancona, N Tuxtla Gutierrez, *Miranda 5263* (MEXU, US); on plaza at Chiapa, *Souviron & Erlanson 103* (US). GUERRERO: Iguala, highway 95, La Cabaña Motel, cultivated, *Freeland & Spetzman 33* (MEXU—2 sheets); Motel "Costa Azul," cultivated, *Lorence & Lorence 3511* (CAS, MEXU, MO); along Mexican highway 95 at Tierra Colorado, ca. 800 m, *Miller & Campos 2954* (MEXU, MO); Jardín Botánico, Chilpancingo, 1,300 m, cultivated, *Toledo & Blanco 50* (MEXU). MICHOACAN: 1 km S of Nueva Italia along Mexican highway 37, cultivated at gas company, ca. 200 m, *Miller & Téllez 3079* (MEXU, MO). MORELOS: Colonia López Mateos, Mpio. Tepalzingo, 1,100 m, *Guerrero et al. 1477* (MEXU); Barranca Honda, Mpio. Tlaltizapan, 1,050 m, *Gutiérrez M. 254* (MEXU); Yautepec, alrededores del poblado Ignacio Bastidas, 1,520 m, *Muskus 40* (MICH); Cuernavaca, carretera a Acapulco, *Palacios s.n.* (DS, MICH, WIS); Villa de Ayala, 1,260 m, *Palacios s.n.* (MEXU); Mpio. Yautepec, Ignacio Bastidas, 1,520 m, *Valdez 43* (CAS). NAYARIT: Acaponeta, *Martínez 7* (F); Las Isletas, 5 km E of San Blas on the road to Miramar, sea level, *Miller & Téllez 3194* (MEXU, MO). OAXACA: Union Hidalgo, *Bailey 572* (BH, MICH); Puerto Escondido, *Boege 2642* (GH, MEXU); Pinotepa Nacional, *Boege 2660* (MEXU); Cuicatlán, *Conzatti & Gonzalez 38* (MEXU); along highway 125 between Pinotepa Nacional and Tlaxiaco between the towns of Coxcatitlán and San Sebastian Ixcapa, 280 m, *Croat 45768* (MO, WIS); Oaxaca, *Davis & Johnston s.n.* (TEX); Cuicatlán, 1,600 ft., *González 38* (GH); El Carrizal, a 2 km al SW del Morro de Mazatlán, o sea a 35 km al SW de Salina Cruz, sobre la carretera a Pochutla, Mpio. de Tehuantepec, *González 473* (MEXU, TEX); Ixtalpec, *Mell 2145* (NY, US); Oaxaca, park in town, 1,600 m, cultivated, *Miller & Myers 2824* (MEXU, MO); cerca y a S de Cuicatlán, *Miranda 4544* (MEXU—3 sheets); Tlacolula, 1,600 m, *Palacios s.n.* (DS); Cuicatlán, 2,000 ft., *Pringle 5790* (GH, MEXU, US); Pochutla, 100 m, *Reko 3305* (US); Huatulco, 150 m, *Reko 6004* (F); Cuicatlán, *Rusby 74* (NY—2 sheets, US); Cacahuatepec, cultivated in Panla, *Sousa et al. 5216* (CAS, US); Salina Cruz, 0–300 m, *Williams 9736* (F, GH). QUINTANA ROO: en la brecha de Divorciados a la Pantera, por la via corta a Mérida, *Cabrera & Alvarez 1678* (BM, MEXU—2 sheets); a 1 km al W de Ciudad Vallarta, sobre el camino a Leona Vicario, *Cabrera et al. 2577* (MO); a 14 km al NW de

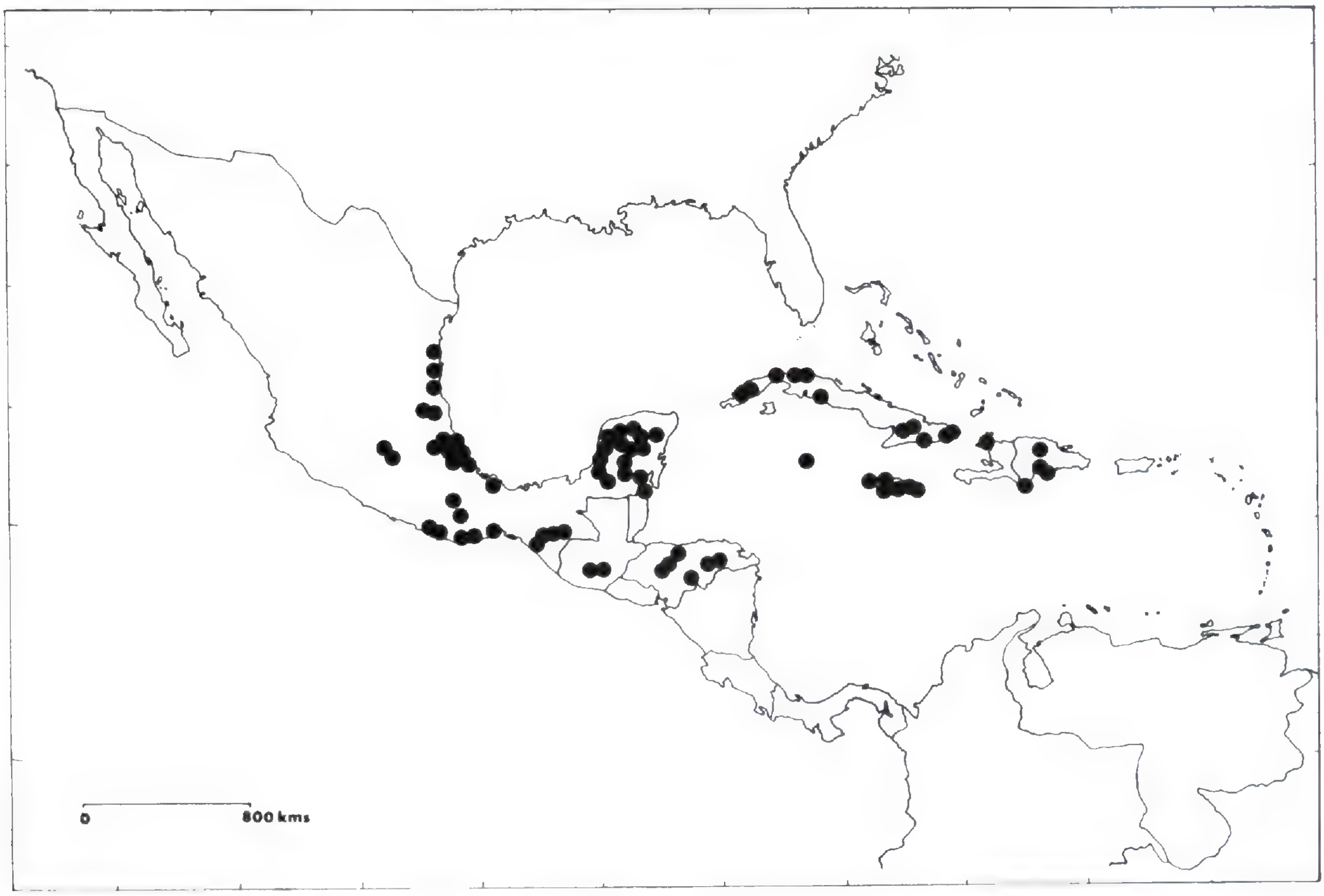

FIGURE 26. Distribution of *Ehretia tinifolia* L.

Calderitas, sobre el camino a Laguna Guerrero, *Cabrera & Cabrera 3223* (MO); a 5 km al W de La Pantera, sobre el camino a Margarita Maza, sobre la carretera via corta a Mérida, *Cabrera & Cabrera 3326* (MO); a 12 km al norte de San Felipe Bacalar, *Cabrera 4527* (MEXU—2 sheets); Laguna de Chichankanab, Mpio. José M. Morelos, 5 m, *Chan & Burhos 1361* (F); Cobá, *Lundell & Lundell 7696* (LL, MICH, US); *Téllez 1903* (BM, MEXU, MO, NY); Ruinas de Cobá, *Téllez 2349* (MEXU, MO); *Téllez & Cabrera 2365a* (BM, MO); Balneario Alvaro Obregón, a 25 km al sur de Ucum, *Téllez 2375* (MEXU, MO). SAN LUIS POTOSÍ: cultivated, Ciudad Valles, *Hansen & Nee 7357* (F, MO). TAMAULIPAS: Ejido Noche Buena, margen sur del Río Soto La Marina, 50 m, *González-Medrano 2627* (MEXU), *2628* (MEXU); 33 km al E de Soto La Marina, cerca del Rancho Carricitas, Mpio. Soto La Marina, 30 m, *González-Medrano 2635* (MEXU); 6 km al NW de El Porvenir, Mpio. de Soto La Marina, 100 m, *Martínez 1* (MEXU); 7 km al NW de Cachimba (El Moron), Mpio. de Aldama, 50 m, *Martínez 220* (MEXU—2 sheets, MO); vicinity of Tampico, 15 m, *Palmer 323* (BM, CAS, F, GH, MO, NY, US), *518* (BM, CAS, GH, K, MO, NY, US); Chamal, *Wooten s.n.* (US). SINALOA: Culiacán, cultivated, *Clarke et al. 1328-1* (MICH). VERACRUZ: Tierra Caliente, camino Zampoala, Actopán, *Aporte et al. 241* (F); Zapotal no. 1, 5 m, *Calderón 1301* (CAS, F—3 sheets, MEXU, MICH); San Andres Tuxtla, parque central, *Calzada 833* (F); carretera Tuxpan–Panuco, 5 km antes de Tantoyuca, *Chiang 3* (CAS, GH, MEXU); a 38 km de Tepetzintla, hacia Tantoyuca, *Chiang 380* (CAS, F—2 sheets, GH, MEXU); Puente Nacional, carretera Xalapa–Veracruz, Emiliano Zapata, 250 m, *Dorantes 549* (F, MEXU); ladera norte del Cerro de Los Metates, 60 m, *Dorantes et al. 982* (F, MEXU); Actopán, 450 m, *Gandara & Dorantes 40* (CAS, F. MEXU, NY—2 sheets); Baños de Carrizal, 7 km SE of Emiliano Zapata (= Carrizal), Mpio. Apazapan, 250 m, *Hansen & Nee 7492* (F, MO); Mirador, *Liebmann 15* (US); Ruta 140, ca. 2 km NW of San Andres Tuxtla, orilla de la carretera, probablamente cultivado, *Lorence & Cedillo 3136* (MEXU); La Bandera, 10 km al SE de Actopán, *Márquez & Dorantes 149* (F, MEXU, MO); Platón Sánchez, *Medillín s.n.* (MEXU—2 sheets); in the city of Veracruz, *Nee & Taylor 19625* (NY); Jalapa, Mpio. Jalapa, 1,308 m, cultivated in the city, *Nee 26575* (F, G, LL, NY); Baños de Carrizal, 5 km SE of Emiliano Zapata, Mpio. Puente Nacional, 220 m, *Nee & Taylor 26610* (F, LL, NY); norte de La Boca de Laguna de la Mancha (1 km) Actopan, sea level, *Novelo 402* (MEXU); Playa Paraiso, 2 km al N de La Boca de La Laguna de La Mancha, Actopán, sea level, *Novelo 421* (MEXU); km 43 carretera La Concha–Actopán, Actopán, 190 m, *Ortega 232* (F, MEXU, MO, NY—2 sheets); La Concepción, Jilotepec, 1,000 m, *Ortega 324* (BM, F, G, MEXU, MO); vicinity of Pueblo Viejo, 2 km S of Tampico, *Palmer 431* (BM, CAS, F, G, GH, MO, NY, US), *446* (GH, MO, NY, US); Remuladero, *Purpus 8753* (GH, MO, NY, UC); shore of Río los Pescados, near Puente Nacional, *Purpus 11168* (BM, DS, F, GH, MICH, MO, NY—2 sheets, UC, US); plan del Río, 350 m, *Rosas 633* (F); camino Atoyac Tepatlaxco, Tepatlaxco, 800 m, *Velázquez 285* (F,

MEXU, MO); Plan del Río, Mpio. Dos Ríos, 265 m, *Ventura 3738* (CR, DS, MICH, US, WIS); El Aguaje, Mpio. Dos Ríos, 200 m, *Ventura 8505* (MEXU); Las Trancas, Mpio. de Dos Ríos, 1,100 m, *Ventura 10264* (MEXU); La Bocana de Actopán, con la carretera Xalapa, Mpio. de Dos Ríos, 200 m, *Ventura 11021* (MEXU); Puente Nacional, Mpio. de Puente Nacional, 100 m, *Ventura 12623* (MEXU); La Ceiba, Mpio. de Puente Nacional, 200 m, *Ventura 17238* (MEXU—2 sheets, MO); plan del Río, Mpio. Emiliano Zapata, 300 m, *Villanueva 116* (NY, WIS), *123* (NY, WIS); La Orduna, carretera Xalapa–Coatepec, Coatepec, 1,100 m, *Zola et al. 344* (F, MEXU—2 sheets, NY); La Concepción, 1,000 m, *Zola 534* (F, MEXU—3 sheets, NY). YUCATÁN: Chichén Itzá, *Bequaert 52* (F, GH, US); *Bruff 1465* (MEXU); ruins of Ake 30 km SE of Mérida, *Butterwick 141* (F, LL); 3 km al N de Tikal, por la carretera a Mérida, *Cabrera & Cabrera 2376* (MEXU—2 sheets, MO); Peto, *Castillo s.n.* (MEXU—2 sheets); ruinas de Labna, al sur del Mirador, Takax, 80 m, *Chan et al. 256* (MO); 2 km N of the border between Yucatán and Campeche, on highway 180 between Mérida and Hopelchén, 80 m, *Davidse et al. 20603* (MO); Tunkas, *Enríquez 538* (MEXU); Mérida, 8 m, *Flores 8108* (MEXU, MO); Izamal, *Gaumer s.n.* (F, K); without definite locality, *Gaumer 381* (CAS, DS, F, GH, LE, MICH, MO, NY—2 sheets, UC, US), *464* (A, BM, F, GH, MO, NY, US, WIS); Chichankanab, *Gaumer 1721* (A, B, BM, F, GH, LE, MO, US); SE Kancabonot, *Gaumer et al. 23868* (DS, F, G, GH, MO, US); Chichén Itzá, *Lundell 7386* (DS, F, GH, MICH, NY, TEX, US); Camino Colonia Yucatán–Tizimin, 100 m, *Pennington & Sarukhan 9402* (A, MEXU, NY); Labna, sur del Arco mas o menos a 30 m, Mpio. Tekax, *Puch et al. 273* (F); Mérida, *Roble 29* (WIS); *Schott 139* (BM), *800* (BM, F); *Seler 3848* (F, GH); Terul, *Seler 3866* (F); Mérida, *Souza-Novelo 254* (US); Chichén Itzá, near Hacienda de Chichén, *Steere 1468* (MICH); without definite locality, *Steggerada 32B* (F); Cenote de X-Kikil, Mpio. X-Kikil, 10 m, *Ucan & Burgos 1195* (F); without definite locality, *Valdez 42* (B, BM, F, GH, LL—2 sheets, MICH, MO, NY—2 sheets, US); Tixcacaltuyub, Mpio. Yaxcaba, 25 m, *Vargas & Sima 421* (F); Ruinas de Labná, 28 km al SW de Oxkutzcab, Mpio. Oxkutzcab, *Xelhuantzi 5436* (MEXU). BELIZE. COROZAL: without definite locality, *Gentle 40* (F), *4793* (F, GH, MICH, NY). ORANGE WALK: Maya ruin, Indian Church, *Arnason & Lambert 17026* (MO). GUATEMALA: GUATEMALA: Guatemala, *Aguilar 530* (F); Parques de Guatemala, *Salas 739* (US); cultivated in Guatemala City, *Steyermark 48083a* (F). PETÉN: shoreline of Lakè Yaxha at mile 70, *Croat 24614* (CAS, CR, F, GH, L, LL, MO, NY, WIS); *Gentry 8289* (F, MO, NY); *Harmon & Dwyer 2766* (MO, NY, US). SACATEPEQUEZ: near Antigua, 6,500 ft., *Kellerman 7426* (NY, US). HONDURAS. COMAYAGUA: La Libertad, *Caballero 155* (NY); Valle Comayagua, orillas del Río Humuya, 700 m, *Molina 6771* (F, G, GH, NY, US); a la salida de Comayagua, carretera a Siguatepeque, 400 m, *Molina 13695* (F, LL, NY, US); El Banco, 640 m, *Rodríguez 2340* (F); El Banco, 640 m, *Rodríguez 2586* (F—2 sheets, MEXU); vicinity of Comayagua, 600 m, *Standley & Chacón 5212* (F, GH, NY); El Banco, *Valerio 2586* (GH). EL PARAISO: llanos de Valle Jamastrán entre Río Los Almendros y Chichicaste, 600 m, *Molina 11393* (BM, F, G, LL, NY, US); Vegas y matorrales de Río Los Almendros, Valle Jamastrán, 400 m, *Molina 13769* (F, LL, NY, US). OLANCHO: orillas de Santa María de Real, Valle de Catacamas, 500 m, *Molina 8416* (F, MO); vicinity of Juticalpa, 380 480 m, *Standley 17604* (F); vicinity of Catacamas, 400–500 m, *Standley 18380* (A, F, US). SWAN ISLANDS: Little Swan, *Clough 12* (IJ); Great Swan Island, *Proctor 32495* (BM, F, GH, IJ, LL); Swan Island, *Chandler s.n.* (GH). YORO: Ciudad de Yoro y alrededores, 640 m, *Nelson & Martínez 2037* (MO). CUBA. HAVANA: roadsides near Havana, *Curtiss 724* (A, BH, BM, F, G, GH, MO, NY, P, US); Cabaña, *Ekman 280* (F, G, S, US); Havana, below Cabañas Fortress, *Jack 4005* (A); Cacahual, *Alain 4247* (GH, US); near Tapaste, E of Habana, *Morton 10718* (US); Buena Vista, *Schafer 243* (GH, NY); Santiago de las Vegas, *Van Hermann 781* (NY); Fortaleza de la Cabaña, *Van Hermann 1951* (NY); El Morro to Cojimar, *Wilson 9131* (NY). ISLA DE PINOS: Vivijagua, *Britton & Wilson 15610* (NY). LAS VILLAS: Farallones de Guajimico, on the coast E of Cienfuegos, *Morton 10471* (US), *10481* (US), *10491* (US). MATANZAS: dry thickets, Cardenas, *Britton & Wilson 160* (NY); Canasí to Boca de Canasí, *Morton 10233* (US); ad montes supra Matanzas, *Rugel 326* (F, LE, NY—2 sheets). ORIENTE: vicinity of Guantanamo, *Britton 2277* (NY); vicinity of Santiago, *Britton et al. 12914* (MO, NY); Enseñada de Mora, *Britton et al. 12921* (NY, US); thickets, Ciudamar, Santiago, *Clemente 5331* (GH, US); coastal thickets, Sardinero, *Clemente 5937* (GH—2 sheets, US); Jiguaní, *Clemente 6064* (GH); coastal thickets, Sardinero, Santiago, *Clemente 6106* (GH, US); Santiago, *Ekman 1434* (MICH, S); Baracoa, Finca Plazuela, in forest on the coral reef, *Ekman 4501* (F, MICH, S); Bayate, Monte Oscuro, *Ekman 4607* (MICH, S, US); Bayate, Cayo del Rey, *Ekman 4676* (S); Bayate, in forest, *Ekman 6225* (F, S); Bañas, *Ekman 6572* (S); roadsides near La Cienaga, Santiago, *Ekman H13235* (LL); potreros de la Finca "La Nena" Laguna Blanca, cercanias de Bayamo, *López 648* (US); carretera de Punta Gorda, Bahia de Santiago de Cuba, *López 914* (US); Río Yao, *Marie-Victorin 60017* (GH); Holguin to Myabe, *Shafer 1415* (F, NY, US); Holguin to Cacocum, *Shafer 1526* (F, NY, US). PINAR DEL RÍO: San Diego de los Baños, along stream, *Britton et al. 6656* (F, NY); on limestone rocks, Mogote de José María, Viñales, *Alain 2928* (GH, US); in mountains near El Guama, *Palmer & Riley 412* (US); limestone hills between Río Cayaguete and Sierra Guane, *Shafer 10471* (NY); Sierra Caliente, S of Sumidero, *Shafer 13734* (A, US). SANTA CLARA: vicinity of Cienfuegos, *Britton & Wilson 56009* (NY); district of Cienfuegos, *Combs 176* (F, GH, MO, NY); Gavilán, *Howard 4945* (GH, NY); Dolores pasture, *Howard 5410* (GH, NY); open fields at Gavilán, *Howard 6311* (GH, NY); Soledad, Cienfuegos, *Jack 4991* (A); Belmonte, Soledad, Cienfuegos, *Jack 5106* (A, US); Soledad, Cienfuegos, *Jack 5180* (A, DS, UC); Limones, Soledad, Cienfuegos, *Jack 6005* (A, G, K, P), *6029* (A, LE, US); Belmonte, Soledad, Cienfuegos, *Jack 7153* (A, US); Gavilán, *Jack 7815* (A, BH, F, S); Soledad, Cienfuegos, 25 m, *Salvoza 727* (A). STATE UNKNOWN: Vedado, *Baleer 1431* (A, NY, US—2 sheets); without definite locality, *Bush 24* (BM, L), *31* (BM); *Cook s.n.* (NY); Ingenio Capitolio, *Day 60* (NY); Potrero Redondo ad Ronulie, *Eggers 4863* (A, F, K, P, US); Trinidad Mountains, San Blas Buenos Aires, *Howard 5274* (GH); without definite locality, *La Sagre s.n.* (B, K, P); *Linden 1983* (BM 2 sheets, G, K—2 sheets, P); *Rugel 326* (BM, L); Atalaya, Camaguey, *Shafer 986* (NY); without definite locality, *Wright 561* (S); prope villam Monte Verde, *Wright 1366* (G, GH, K, MO), *1370* (BM, G, GH—2 sheets,

K, LE, MO, NY—3 sheets, P, S, UC, US). CAYMAN ISLANDS. GRAND CAYMAN: in coppice, West Bay Village area, *Correll & Correll 51037* (NY); edge of coppice along roadway near Hell, West Bay Village area, *Correll & Correll 51047* (F, IJ, MO, NY); N end of Grand Sound Road, *Proctor 15044* (BM, GH, IJ); NW of Boddentown, *Proctor 31038* (BM, IJ, LL). JAMAICA. HANOVER: 5 mi. W of Lucea, near sea level, *Proctor 28561* (IJ); interior of Hanover, *Purdie s.n.* (K). KINGSTON: Kingston, *Alexander 6563* (NY); Kingston, Tower Street, *Barry s.n.* (IJ); corner of Church St. and North St., *Proctor 8173* (IJ, NY, US); along East Race Course, *Proctor 23605* (LL, MICH, NY, US). MANCHESTER: Spur Tree Hill near Ellington, 1,600–2,000 ft., *Proctor 28751* (BM, F, IJ, LL, NY); Montpelier District, below Spur Tree, 1,000–1,250 ft., *Proctor 30018* (IJ). ST. ANDREW: Gordon Town, 1,200 ft., *Barry s.n.* (IJ); Hope, 600 ft., *Barry s.n.* (IJ); Wolmer's Boys School, *Bengry s.n.* (IJ); Green Valley, 600 m, *Harris 6073* (A, BM, F, NY); W slope of Long Mountain, *Scudamore s.n.* (IJ); Long Mountain, along road to Wareika, 750–1,250 ft., *Webster 4987* (A, IJ); roadside below Irish Town, ca. 2,000 ft., *Webster et al. 8060* (BM, G, IJ, S); in waste area adjacent to U.C.W.I. campus, 550 ft., *Yuncker 17721* (F, MICH, S). ST. ANN: vicinity of Green Grotto Caves, 2.5 mi. W of Runaway Bay, 5–50 ft., *Proctor 36485* (IJ). ST. CATHERINE: Caymanas, 30 ft., *Adams & Carrington 11513* (BM). ST. ELIZABETH: Lititz Savana, 300–900 ft., *Harris 11726* (BM, F, MO, NY, US); limestone hillsides near new buildings, Kaiser mine area S of Gutters, *Howard & Proctor 13858* (A, IJ); Kaiser mine area at Comfort, 500 ft., *Howard & Proctor 14448* (IJ); 2–4 mi. SW of Lacovia, *Howard & Proctor 14522* (A, BM, IJ); Parotte, sea level, *Proctor 28836* (IJ); Giddy Hall, *Sangster s.n.* (A, BM). ST. JAMES: Rose Hall, *G. S. Miller 1419* (US); Greenwood estate, 5 mi. ESE of Little River P.O., *Stearn 614* (A, BM—2 sheets). ST. THOMAS: Yallahs, 30 m, *Araque-Molina & Barkley 225438* (BM, IJ—3 sheets); Yallahs Valley–Green Valley, *Harris 6838* (F, NY—2 sheets); Grant's Pen, near sea level, *Proctor 28801* (BM, IJ). WESTMORELAND: 0.5 mi. SE of Mt. Airy school, 250 ft., *Proctor 36729* (IJ). PARISH UNKNOWN: Thicket Pepper, *Britton 1077* (NY); near camp, 67 m, *Campbell 5690* (F, NY, US); asylum grounds, *Fawcett s.n.* (BM); Malvern to Mountain side, *Harris 9755* (BM, F, NY, US); road from Hall-way Tree to Spanish Town Road, *Harris 10381* (A, BM, F, NY, US); without definite locality, *Macfadyen s.n* (K); *Molle s.n.* (GH); *Herb. Montinii* (S): *Swartz s.n.* (S); *Waters s.n.* (K); Trelawny, roadside near Duncans, *Whitefoord 1464* (BM, IJ). HAITI: Fond Parisien, *Bailey 175* (BH, US); Massif du Nord, Port-de-Paix, Bassin Bleu, 150 m, *Ekman H3992* (IJ, LL, NY, US); vicinity of Fond Parisien, Etang Saumatre, *Leonard 4173* (NY, US—2 sheets); vicinity of Port de Paix, ridge W of La Coup River, *Leonard & Leonard 11142* (US); vicinity of Bassin Bleu, 630–1,500 m, *Leonard 14709* (US—2 sheets). DOMINICAN REPUBLIC: Monte Cristi, Guayubín, 100 m or less, *Abbott 990* (GH, US); Santiago, Mao, 100–300 m, *Abbott 1069* (NY, US); Santiago, Navarrete, 100–300 m, *Abbott 1077* (US); in sylvestribus ad Río Gurabito, 200 m, *Eggers 1971a* (K); Santo Domingo, near Santiago, *Eggers 1990* (BM, G); Santo Domingo, Valle del Cibao, Prov. Santiago, Santiago, roadsides, near La Cienago, *Ekman H13235* (S, US); Barahona, Baum, *Fuertes 296* (BM, F, G, GH—2 sheets, LE, MO, NY, P, S, US); Santiago, along banks of the Río Yaque near Santiago, *Howard & Howard 9689* (A, B, BM, NY, US); Hotel Yaque, near Santiago City, *Jiménez 5688* (NY); Pedernales, near Las Mercedes from Cabo Rojo to Aceitillar, 400 m, *Liogier 16688* (NY); Santo Domingo, En Manigua, Pedernales, *Liogier 19691* (NY); a orilla de la carretera 100 entre Bani y Azua a nivel del mar, *Liogier 24871* (NY); Valverde, at stream crossing Autopista Duarte in center of town of Laguna Salada, 60 m, *Megía & Zanoni 6516* (NY); Azua, Santo Domingo, *Rose et al. 4005* (NY, US); Santo Domingo, Trujillo City, *Schiffino 150* (GH), *162* (GH).

EXCLUDED SPECIES

The majority of names published in *Ehretia* for the Neotropics are now considered synonyms of *Bourreria* and *Rochefortia*. In the following list, types have been examined when possible, but many of the names can be excluded from *Ehretia* based on the published descriptions. In placing the names I have relied heavily on the revisions of *Bourreria* (Miers, 1869; Schulz, 1911) and *Rochefortia* (Lefor, 1968) supplemented with notes from Johnston's extensive series of papers on the Boraginaceae. When *Ehretia* names are assigned to species of *Bourreria*, they should be considered cautiously as the best name available from the literature since *Bourreria* is probably the most nomenclaturally confused genus of Ehretioideae.

Ehretia acanthophora DC., Prodr. 9: 510. 1845. TYPE: Dominican Republic, Santo Domingo: *Bertero s.n.* (holotype, G-DC, not seen; microfiche, MO; isotypes, MO, P). = *Rochefortia acanthophora* (DC.) Griseb., Fl. British West Indies 482. 1864; O. Schulz in Urban, Symb. Antill. 7: 70. 1911; León & Alain, Fl. Cuba 4: 265. 1957; Lefor, 30. 1968.

Ehretia andrieuxii DC., Prodr. 9: 510. 1845. TYPE: Mexico. Puebla: May, *Andrieux 200* (holotype, G-DC, not seen; microfiche, MO). = *Bourreria andrieuxii* (DC.) Hemsley, Biol. Cent.-Amer., Bot. 2: 369. 1882; Miers, Contr. Bot. 2: 254. 1869; Gibson, Fieldiana Bot. 24, pt. 9: 113. 1970; Miller, Fl. Nicaragua (in press).

Ehretia bogotensis Spreng., Syst. Veg. 1: 648. 1825. = *Aegiphila bogotensis* (Sprengel) Moldenke, Repert. Spec. Nov. Regni Veg. Beih. 33: 114. 1933.

Ehretia bourreria Desf. (non L.), Ann. Mus. 1: 279. = *Bourreria recurva* Miers, Ann. & Mag. Nat. Hist. Ser. 4, 3: 203. 1869.

Ehretia bourreria L., Sp. Pl. 2 ed. 1: 275. 1762. = *Bourreria succulenta* Jacq., Enum. Syst. Pl. Carib. 14. 1760; O. Schulz in Urban, Symb. Antill. 7: 55, 56, and 62; León & Alain, Fl. Cuba 4: 269. 1957.

Ehretia calophylla A. Rich. in Sagra, Fl. Cuba 2: 112, t. 61. 1853. = *Bourreria rotata* (DC.) I. M. Johnston, J. Arnold Arbor. 30: 107. 1949; León & Alain, Fl. Cuba 4: 268. 1957.

Ehretia cassinifolia A. Rich. in A. Sagra, Fl. Cuba 2: 113. 1850. = *Bourreria cassinifolia* (A. Rich.) Griseb., Pl. Wright. Cub. 528; O. Schulz in Urban, Symb. Antill. 7: 67. 1911; León & Alain, Fl. Cuba 4: 270. 1957.

Ehretia cirrhosa Lam. = *Maripa scandens* Aublet; DC., Prodr. 9: 511. 1845.

Ehretia cumanensis DC., Prodr. 9: 511. 1845. = *Tournefortia hirsutissima* L., Sp. Pl. 140. 1753. O. Schulz (in Urban, Symb. Antill. 7: 50. 1911) treated this name as applicable to *Tournefortia*, not *Ehretia* or *Bourreria*. The name *Bourreria cumanensis* (Loefl.) O. Schulz is based on *Rhamnus cumanensis* Loefl., Iter Hispan. 182. 1758.

Ehretia cuneifolia Sessé & Mociño, Fl. Mexic. 51. 1894; ed. 2. 47. 1894. = *Bourreria spathulata* (Miers) Hemsley, Biol. Cent.-Amer., Bot. 2: 370. 1882; I. M. Johnston, J. Arnold Arbor. 30: 107. 1949.

Ehretia cymosa Willd. ex Roemer & Schultes (non Thonn). = *Tournefortia hirsutissima* L., Sp. Pl. 140. 1753; O. Schulz in Urban, Symb. Antill. 7: 50. 1911.

Ehretia divaricata A. Rich. (non DC.) in Sagra, Hist. Fis. Cuba, Bot. 11: 113. 1850. = *Bourreria succulenta* var. *revoluta* (Kunth in Humb., Bonpl. & Kunth) O. Schulz in Urban, Symb. Antill. 7: 59. 1911.

Ehretia divaricata DC., Cat. Hort. Monspel. 108. 1813; Prodr. 9: 506. 1845. = *Bourreria divaricata* (DC.) G. Don, Gen. Hist. 4: 389. 1838; O. Schulz in Urban, Symb. Antill. 7: 69. 1911; León & Alain, Fl. Cuba 4: 271. 1957.

Ehretia domingensis DC., Prodr. 9: 508. 1845. = *Bourreria domingensis* (DC.) Griseb., Fl. Brit. W.I. 482. 1861; Miers, Ann. & Mag. Nat. Hist. Ser. 4, 3: 202. 1869; O. Schulz in Urban, Symb. Antill. 7: 64. 1911.

Ehretia dubia Jacq., Obs. 1, 19. 1764; O. Schulz in Urban, Symb. Antill. 7: 71. 1911. = *Cordia* sp. probably *C. collococca* L. or *C. nitida* Vahl.

Ehretia exsucca Bert. ex Griseb. (non L.), Fl. Brit. W.I. 482. 1861. = *Bourreria domingensis* (DC.) Griseb., Fl. Brit. W.I. 482. 1861; O. Schulz in Urban, Symb. Antill. 7: 64. 1911.

Ehretia exsucca L., Sp. Pl. ed. 2. 1: 275. 1762. = *Bourreria cumanensis* (Loefl.) O. Schulz in Urban, Symb. Antill. 7: 49. 1911.

Ehretia fasciculata Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 66. 1818. TYPE: *Humboldt s.n.* (holotype, P-HBK, not seen; microfiche, MO). = *Rochefortia spinosa* (Jacq.) Urb. in Fedde, Repert. Spec. Nov. 13: 472. 1915; Lefor, 1968.

Ehretia formosa DC., Prodr. 9: 510. 1845. = *Bourreria huanita* (Llave & Lex.) Hemsley, Biol. Cent.-Amer., Bot. 2: 369. 1882; O. Schulz in Urban, Symb. Antill. 7: 51. 1911; Standley, Contr. U.S. Natl. Herb. 28: 1225. 1924; Gibson, Fieldiana Bot. 24, pt. 9: 114. 1970.

Ehretia formosa var. *oaxacana* DC., Prodr. 9: 510. 1845. TYPE: Mexico. Oaxaca: Tehuantepec, *Andrieux 201* (photo, GH). = *Bourreria huanita* (Llave & Lex.) Hemsley, Biol. Cent.-Amer., Bot. 2: 369. 1882; O. Schulz in Urban, Symb. Antill. 7: 51. 1911; Standley, Contr. U.S. Natl. Herb. 28: 1225. 1924.

Ehretia grandiflora Poir., Encycl. Suppl. 2: 3. 1811. = *Bourreria wrightii* Alain, Contrib. Ocas. Mus. Hist. Nat. Coleg. "De La Salle" 15: 9. 1956, a new name for *Bourreria grandiflora* Griseb., non Bertol., O. Schulz in Urban Symb. Antill. 7: 52. 1911; León & Alain, Fl. Cuba 4: 268. 1957.

Ehretia grisebachii Maza, Periant. 256. 1890. = *Bourreria microphylla* Griseb., Cat. Pl. Cuba 210. 1866; O. Schulz in Urban, Symb. Antill. 7: 69. 1911; León & Alain, Fl. Cuba 4: 271. 1957.

Ehretia guatemalensis DC., Prodr. 9: 507. 1845. = *Bourreria huanita* (Llave & Lex.) Hemsley, Biol. Cent.-Amer., Bot. 2: 370. 1882; O. Schulz in Urban, Symb. Antill. 7: 51. 1911; León & Alain, Fl. Cuba 4: 268. 1957.

Ehretia havanensis Willd. ex Roemer & Schultes, Syst. Veg. 4: 805. 1819. = *Bourreria succulenta* var. *revoluta* (Kunth in Humb., Bonpl. & Kunth) O. Schulz in Urban, Symb. Antill. 7: 59. 1911; León & Alain, Fl. Cuba 4: 269. 1957.

Ehretia laevis Roxb. var. *cymosa* Roemer & Schultes, Syst. Veg. 4: 805. 1819. = *Tournefortia hirsutissima* L., Sp. Pl. 140. 1753. Although *Ehretia laevis* is an Old World species, Roemer & Schultes published this variety from the New World; it was excluded by O. Schulz (in Urban, Symb. Antill. 7: 50. 1911) as a species of *Tournefortia*.

Ehretia lanceolata Vell., Fl. Flum. 79. 1829. In Prodr. 9: 511. 1845, De Candolle listed this as unknown in his list of excluded species, indicating a distribution in Brazil, where *Eh-*

retia does not occur. This is sufficient to exclude it from the genus.

Ehretia microphylla Lam., Tab. Encycl. 1: 425. 1791. = *Carmona retusa* (Vahl) Masamune, Trans. Nat. Hist. Soc. Formosa 30: 61. 1940; Thulin, Nord. J. Bot. 7: 413. 1987. Although this species is native in the Old World, it is known from cultivated collections from Honduras and Cuba.

Ehretia montana Griseb., Pl. Wright. 528. 1862. = *Bourreria divaricata* Don, Dict. 4: 389; Griseb., Pl. Wright. 528. 1862; Cat. Pl. Cuba 210. 1866.

Ehretia montevidensis Sprengel, Syst. 1: 647. 1825. = *Citharexylum montevidense* (Sprengel) Moldenke, Phytologia 1: 17. 1933.

Ehretia radula Chapman (non Poir.), Fl. South. U.S. 329. 1872. = *Bourreria succulenta* var. *revoluta* (Kunth in Humb., Bonpl. & Kunth) O. Schulz in Urban, Symb. Antill. 7: 59. 1911.

Ehretia radula Poir., Encycl. Suppl. 2: 2. 1811; DC., Prodr. 9: 506. 1845. = *Bourreria tomentosa* (Lam.) G. Don, Gen. Hist. 4: 390. 1838; O. Schulz in Urban, Symb. Antill. 7: 54. 1911.

Ehretia radula Sprengel (non Poir. or Chapman), Syst. Veg. 1: 648. 1825. = *Bourreria divaricata* (DC.) G. Don, Gen. Hist. 4: 389. 1838; O. Schulz in Urban, Symb. Antill. 7: 70. 1911.

Ehretia revoluta DC., Prodr. 9: 507. 1845. = *Bourreria succulenta* var. *revoluta* (Kunth in Humb., Bonpl. & Kunth) O. Schulz in Urban, Symb. Antill. 7: 60. 1911.

Ehretia rupestris Salisb., Prodr. 112. = *Bourreria succulenta* (Jacq.) Urban.

Ehretia scandens Poir., Encycl. Suppl. 3: 590. 1806. = *Maripa scandens* Aublet; DC., Prodr. 9: 511. 1845).

Ehretia spinifex DC., Prodr. 9: 506. 1845. = *Bourreria divaricata* (DC.) G. Don, Gen. Hist. 4: 389. 1838. O. Schulz (1911) treated *Ehretia spinifex* DC., a name De Candolle attributed to Roemer & Schultes, as a synonym of *Bourreria divaricata* but excluded *Ehretia spinifex* Roemer & Schultes as a synonym of *Basanacantha spinifex* (Roemer & Schultes) Urban of the Rubiaceae. León & Alain (1957) listed *Ehretia spinifex* Griseb. as a synonym of *Bourreria divaricata* but made no mention of the other names. The proper application of De Candolle's and Roemer & Schultes's names will require further study, but they certainly can be excluded from *Ehretia* based on their descriptions.

Ehretia spinifex Griseb. (non Roemer & Schultes) Pl. Wright. Cuba 528. = *Bourreria divaricata* Don, Dict. 4: 389; Griseb., Pl. Wright. Cuba 528; Cat. Pl. Cuba 210.

Ehretia spinifex Maza, Periant. 255. 1890. = *Bourreria cassinifolia* (A. Rich.) Griseb., Cat. Pl. Cuba 210. 1866; O. Schulz in Urban, Symb. Antill. 7: 67. 1911; León & Alain, Fl. Cuba 4: 270. 1957.

Ehretia spinosa Jacq., Enum. Syst. Pl. 14. 1760. = *Rochefortia spinosa* (Jacq.) Urban in Fedde, Repert. Spec. Nov. 13: 472. 1915; O. Schulz in Urban, Symb. Antill. 7: 71. 1911; León & Alain, Fl. Cuba 4: 266. 1957; Lefor, 1968.

Ehretia spinosa Spreng. ex DC. (non Jacq.), Prodr. 9: 510. 1845. = *Rochefortia acanthophora* (DC.) Griseb., Fl. Brit. W.I. 482. 1862; Lefor, 1968.

Ehretia ternifolia Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 66. 1818. TYPE: Colombia (holotype, P-HBK; photo, GH). = *Aegiphila ternifolia* (Kunth in Humb., Bonpl. & Kunth) Moldenke, Repert. Spec. Nov. Regni Veg. Beih. 33: 141. 1933.

Ehretia tomentosa Lam., Tab. Encycl. 1: 425. 1793; DC., Prodr. 9: 507. = *Bourreria velutina* (DC.) Gurke in Engl. & Prantl, Nat. Pflanzenfam. IV. 3a: 87. 1897; O. Schulz in Urban, Symb. Antill. 7: 54. 1911.

Ehretia tomentosa var. *havanensis* Gómez, Anal. Hist. Nat. Madrid 19: 256. 1890. = *Bourreria succulenta* var. *revoluta* (Kunth in Humb., Bonpl. & Kunth) O. Schulz in Urban, Symb. Antill. 5: 59. 1911.

Ehretia velutina DC., Prodr. 9: 508. 1845. = *Bourreria velutina* (DC.) Gürke in Engl. & Prantl, Nat. Pflanzenfam. IV. 3a: 87. 1897; O. Schulz in Urban, Symb. Antill. 7: 62. 1911.

Ehretia virgata Sw., Prodr. 47. 1788; Flor. Ind. Occ. 1: 463; DC., Prodr. 9: 506. 1845. = *Bourreria virgata* (Sw.) G. Don, Gen. Hist. 4: 389. 1838; O. Schulz in Urban, Symb. Antill. 7: 66. 1911; León & Alain, Fl. Cuba 4: 269. 1957.

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NEW AND CRITICAL TAXA OF EUPHORBIACEAE FROM SOUTH AMERICA[1]

Michael J. Huft[2]

ABSTRACT

Study of neotropical Euphorbiaceae for various floristic and taxonomic projects has uncovered several novelties. New taxa proposed in this paper are *Dalechampia liesneri* from southern Venezuela, *Richeria tomentosa* from Colombia, *Tragia rubiginosa* from Peru, and the genus *Tacarcuna*, including the three new species *T. gentryi*, from the border of Panama and Colombia, *T. amanoifolia* from Peru, and *T. tachirensis* from Venezuela. In addition it is shown that *Caryodendron janeirense* Muell. Arg. is the correct name for the plant hitherto known as *C. grandifolium* (Muell. Arg.) Pax.

The Euphorbiaceae, one of the largest families in the Neotropics, remains one of the least well understood. The largest genera, *Acalypha*, *Croton*, *Euphorbia*, and *Phyllanthus*, have not been critically revised in this century, and only a handful of other, smaller genera have been the subject of modern study. Even at the most basic descriptive level, a great deal of work remains to be done, and the mere discovery of a new species can often lead to much insight into the taxonomy of its congeners. Such is the case with the collection of taxa proposed here, which result from study preparatory to the *Flora of the Venezuelan Guayana* (J. Steyermark & collaborators, in prep.), *Checklist of the Flora of Chocó Province, Colombia* (A. Gentry & E. Forero, in prep.), or from serendipitous discovery in the herbarium.

Caryodendron janeirense Muell. Arg. in C. Mart., Fl. Bras. 11(2): 707. 1874. *Centrodiscus grandifolius* Muell. Arg. in C. Mart., Fl. Bras. 11(2): 327. 1874, nom. inval. *Caryodendron grandifolium* (Muell. Arg.) Pax in Engler & Prantl, Nat. Pflanzenfam. III. 5: 52. 1890, nom. illeg. TYPE: Brazil. Rio de Janeiro: *Riedel 1051* (presumably G).

Mueller published the name *Centrodiscus grandifolius* with description and citation of type. Before this went to press however, he added as a separate item on a different page "Addenda and Corrigenda" in which he pointed out that his *Centrodiscus grandifolius* belongs to Karsten's genus *Caryodendron* and that it differs from the only species, *Caryodendron orinocense* Karsten, by, among other things, having smaller leaves. Apparently thinking that the epithet *grandifolium* would be inappropriate in *Caryodendron*, he assigned the new plant the name *Caryodendron janeirense*, which is the correct name for the species. *Centrodiscus grandifolius* was not published before *Caryodendron janeirense*, pp. 273–754 of Volume 11, Part 2, appearing together on May 1, 1874 (Stafleu & Cowan, 1981: 333–337). Mueller was merely making a last-minute correction to text already too far along in press to be changed internally. It is therefore clear that the name *Centrodiscus grandifolius* Muell. Arg. was not accepted by its author when published and therefore is invalid according to Article 34.1 of the *International Code of Botanical Nomenclature* (Greuter, 1988). The combination of Pax based on that name is nomenclaturally superfluous. For the same reason, the generic name *Caryodendron* Muell. Arg., published simultaneously with *Caryodendron grandifolius* Muell. Arg. and likewise not accepted by its author when published, is also invalid.

[1] I am indebted to Dr. W. Scott Armbruster of the University of Alaska for valuable discussions concerning *Dalechampia liesneri*, and to the curators of the herbaria cited for making their specimens available. The excellent drawings were made by Mrs. Carol G. Schneider (Figs. 1 and 3) and Mrs. Wan-Ling Peng (Fig. 2).

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Dalechampia liesneri Huft, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Atures, stream 0.5–2 km E of Río Coro-Coro, W of Serranía de Yutaje, 05°38′N, 66°07′30″W, 200 m, 19 Feb. 1987, *R. L. Liesner & B. Holst 21244* (holotype, MO; isotypes, U, VEN not seen). Figure 1.

Frutex (vel herba) volubilis; caules et folia glabra vel sparsim brevipuberula. Folia simplicia, longipetiolata; laminae ovato-deltatae, basi 5-nerves, apice acutae; basi late cordatae. Inflorescentiae dissitae, longipedunculatae, floribus compactis. Flores masculi ad 8; sepala ovata, acuta, sub anthesi reflexa; stamina 8–10, filamentis connatis, tubum longum gracilem formantibus. Flores feminei 3, subsessilis, pedicello ad fructus maturitatem multo elongato; sepala 6, lineari-lanceolata; stylus gracilis, elongatus. Capsulae glabrae vel brevipuberulae, laeves. Semina ovoidea vel subglobosa, laevia, brunnea.

Twining vine; stems terete or slightly angulate, glabrous or very sparsely short-puberulent. *Leaves* simple, on petioles to 10 cm long, these pinched at apex and at base and puberulent; blades ovate-deltate, membranous, glabrous or the principal veins minutely puberulent, 5-nerved, the secondaries few near apex of blade, ascending, the tertiaries reticulate, conspicuous, the apex acuminate, the base openly cordate, stipellate, the margin minutely and remotely denticulate. *Inflorescences* bisexual, widely spaced, compact, the peduncle slender, densely puberulent, 1–4 cm long. *Staminate flowers* distal, up to 8 present, the pedicels 2–5 mm long; bracts lanceolate, brown puberulent, acute, 2–4 mm long; buds fusiform, acute; sepals 5, ca. 2 mm long, membranous, ovate, acute, sparsely hirtellous, reflexed at anthesis; stamens 8–10, the filaments united nearly their entire length to form a slender tube 4–5 mm long, the anthers free at apex, the tube penicillate toward apex. *Pistillate flowers* 3, 1 or 2 sometimes aborting before maturity, proximal, subsessile at anthesis, the pedicel densely puberulous-hirtellous, greatly elongating in fruit (to 5 cm); sepals 6, linear-lanceolate, 2.8–3.2 mm long, acute, sparsely short-puberulent, the base thickened, the young fruit densely short-pilose; style slender, elongate, to 15 mm long, 0.2–0.3 mm thick, densely puberulent toward the base, otherwise glabrous. *Capsule* smooth, 3-lobed, short-puberulent, not seen entire, apparently 6–7 mm diam.; seeds ovoid to subglobose, smooth, ca. 4 mm diam., brown.

The pantropical genus *Dalechampia* contains over 100 principally neotropical species. Numerous recent discoveries (Armbruster, 1984, 1988, 1989; Huft, 1984; Webster, 1967, 1988; Webster & Armbruster, 1979, 1982), many of them of taxonomic and phylogenetic importance, attest to the need for the critical study this genus is now receiving at the hands of Dr. Grady L. Webster and Dr. W. Scott Armbruster.

Dalechampia liesneri belongs to sect. *Rhopalostylis* Pax & K. Hoffm., the most primitive section of the genus, which apparently is restricted to the northern and western Amazonian basin. Only four species have previously been described from this group: *D. micrantha* Poeppig from western Brazil and eastern Peru, *D. parvibracteata* Lanj. from the Guianas, *D. olympiana* Kuhlm. & Rodrigues from northern Brazil, and the recently described *D. attenuistylus* Armbruster from southern Venezuela (Armbruster, 1989). The genus *Megalostylis* S. Moore, whose only species, *M. poeppigii* S. Moore, appears to be based on an isotype of *D. micrantha*, is synonymous with sect. *Rhopalostylis*.

Section *Rhopalostylis* is characterized by absence of the showy white, pinkish, purplish, or green bracts that are so characteristic of the rest of the genus; absence of resiniferous glands in the inflorescences; and larger, usually basally swollen, styles. *Dalechampia liesneri* is distinctive in its few-flowered, long-pedunculate, inflorescences and long, thin styles that are not at all swollen toward the base. Dr. Armbruster (pers. comm.), who is preparing a revision of this group, has discovered an additional population of this species near San Pedro de Cataniapo (ca. 60 km ESE of Puerto Ayacucho) in southern Venezuela, and he reports that it is probably not uncommon in that region.

It is a pleasure to name this species after Ronald Liesner of the Missouri Botanical Garden who has collected extensively in Venezuela during the past decade and has been responsible for many discoveries and additions to our knowledge of the flora of that country.

Richeria tomentosa Huft, sp. nov. TYPE: Colombia. Chocó: Municipio de Quibdó, bosque frente al barrio Obrero, 24 May 1985, *Espina & García 1518* (holotype, MO).

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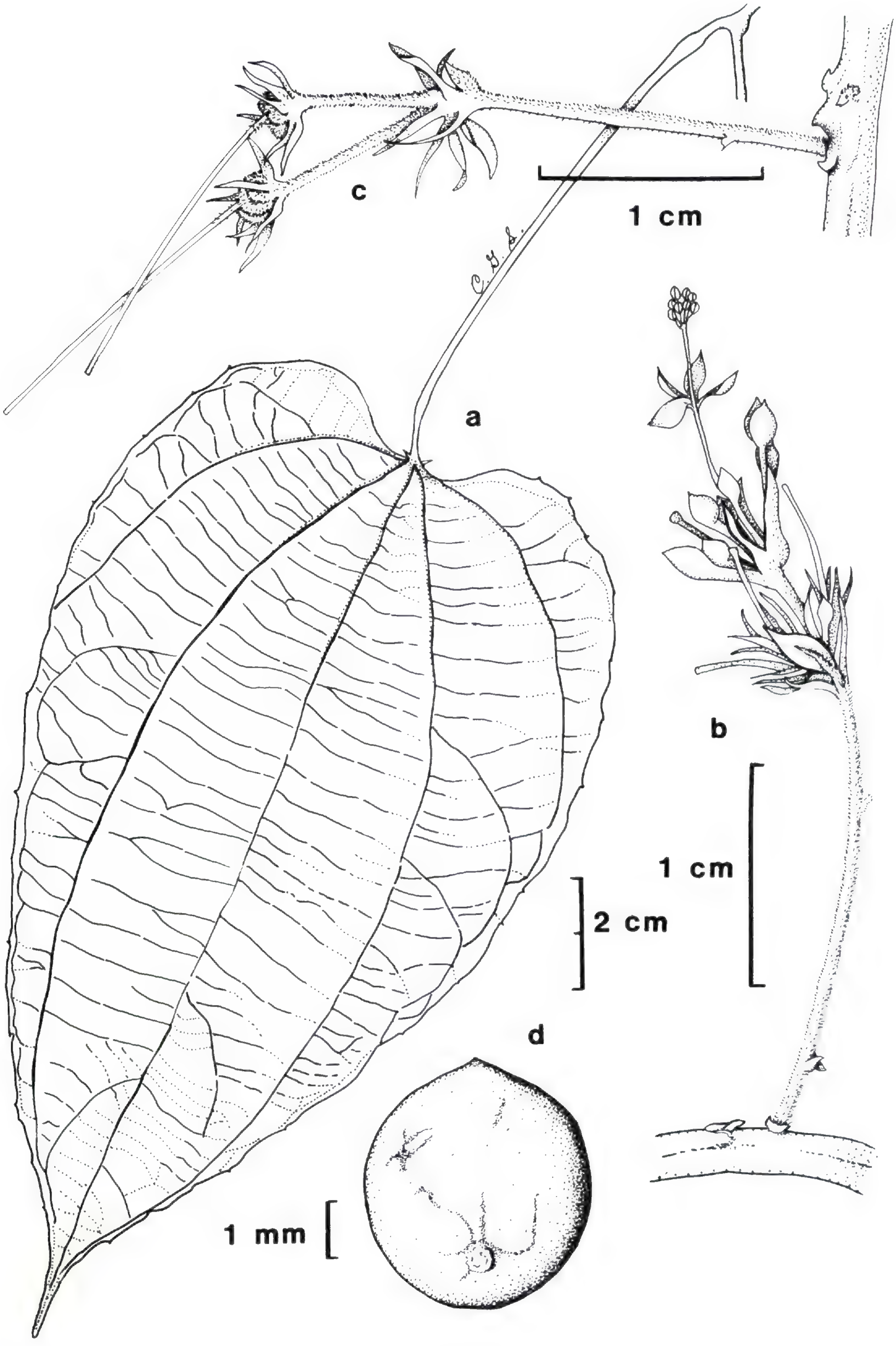
FIGURE 1. *Dalechampia liesneri*.—a. Leaf.—b. Inflorescence at anthesis.—c. Inflorescence with immature fruits.—d. Seed. (Based on *Liesner & Holst 21244*.)


c
1 cm
a
b
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2 cm
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Arbor ad 25 m alta, dioecia; cortex crassus exaratus. Folia alterna brevipetiolata; laminae late obovato-ellipticae, infra dense brunneo-tomentosae vel glabratae, supra moderate pilosae vel glabratae, apice rotundatae, obtusae, vel breviacuminatae, basi rotundatae vel late cuneatae, margine crenato-undulatae. Inflorescentiae numerosae laterales sub foliis, ex paniculis fasciculatis 2–4 cm longis constans. Flores masculi in glomerulis sessilibus vel subsessilibus. Flores feminei non visi, sessiles vel brevipedicellati; fructus juvenes dense brunneo-tomentosi pyriformes, stylis 3 valde recurvis. Capsulae ellipsoideo-oboideae obscuro trigonae glabrae; columella non persistens alis latis papyraceis.

Tree to 25 m high, dioecious; twigs with thick bark formed into flattened ridges and narrow furrows, densely hirsutulous to glabrate toward apex. *Leaves* alternate, short-petiolate; stipules obsolete; petioles 0.5–2.5 cm long, stout, densely hirsutulous to glabrate; blades chartaceous to subcoriaceous, broadly obovate-elliptic, 10–23 cm long, 7–12 cm wide, 1.5–2.8 times as long as wide, densely brown tomentose to glabrate below, moderately pilose to glabrate above, the apex rounded, obtuse, or short-acuminate, the base rounded, obtuse, or broadly cuneate, the margins entire to obscurely crenate-undulate; midrib prominent below, the secondary nerves 14–26 on a side, parallel, arching somewhat toward the margin of the blade, prominent below, light-colored above, neither raised nor impressed, the tertiary veins connecting the secondaries at right angles, regularly spaced, prominulous below. *Inflorescences* numerous, lateral, below current leaves, consisting of clustered panicles 2–4 cm long, the axes densely brown tomentose when young, becoming densely puberulent at maturity. *Staminate flowers* 1–3 in sessile or subsessile glomerules, the buds globose, 0.7–1.1 mm diam. *Pistillate flowers* not seen, sessile or short-pedicellate; calyx persistent on young fruits, tomentose outside, the lobes 1–1.5 mm long, deltate, ca. ⅔ the length of the calyx; young fruits densely brown tomentose, pyriform, the styles 3, ca. 1 mm long, strongly recurved, united at base, glabrous or with a few scattered hairs. *Capsules* ellipsoid-obovoid, obscurely trigonous, glabrous, smooth, 11–16 mm long, 6–9 mm diam., the styles persistent, minute, the columella with broad papery wings, not persistent.

This very distinctive species is easily distinguished from the four to six other species of *Richeria* by the densely tomentose lower leaf surfaces on many specimens and by the short, compact, highly branched inflorescences. The prominent midrib and secondary veins are also distinctive. The widespread *R. racemosa* (Poeppig) Pax & K. Hoffm. has staminate spikes longer than the leaves rather than the short, compact, clustered panicles that are characteristic of *R. tomentosa*, and the cymules are distinctly pedunculate and two- or three-flowered. Two other South American species, *R. grandis* Vahl and *R. obovata* (Muell. Arg.) Pax & K. Hoffm., have longer and less compact inflorescences than *R. tomentosa* and are completely glabrous; their leaf margins are prominently crenate-undulate (vs. entire or obscurely crenate-undulate). The recently described *R. dressleri* Webster (Ann. Missouri Bot. Gard. 75: 1094. 1988), from Panama and apparently Costa Rica, is distinctive in its two-carpellate ovaries and fruits.

Additional specimens examined. COLOMBIA. VALLE: Bajo Calima Concessión, ca. 20 km N of Buenaventura, behind Pulpapel Forest Station, 3°40′N, 77°0′W, 50 m, 26 May 1987, *Faber-Lagoenden et al. 675* (F); Bajo Calima, ca. 15 km N of Buenaventura, Cartón de Colombia Concessión, 3°56′N, 77°08′W, ca. 50 m, 14 Feb. 1983, *Gentry et al. 40219* (F); 18 Feb. 1983, *Gentry & Juncosa 40483* (F); 27 Mar. 1986, *Gentry et al. 53648* (F); Bajo Calima, Dindo area, pluvial forest, 3°59′N, 76°58′W, ca. 100 m, 20 July 1984, *Gentry & Monsalve 48390* (MO); Bajo Calima, Cartón de Colombia Concessión, Dindo 4 area, 11 km E of Buenaventura–Río Calima road, 3°55′N, 77°0′W, 50–100 m, 14 Dec. 1985, *Gentry et al. 53295* (F, MO); 27 Feb. 1985, *Monsalve 716* (F, MO); Bajo Calima, Juanchaco Palmeras area, 3°55′N, 77°02′W, 50 m, 29 Aug. 1986, *Gentry & Cuadros 55602* (F); Bajo Calima, Concessión Pulpapel Buenaventura, 3°55′N, 77°W, ca. 100 m, *Monsalve 876* (F).

Tacarcuna Huft, gen. nov. TYPE: *Tacarcuna gentryi* Huft.

Arbor, ut videtur dioecia; foliis alternatis, simplicibus, petiolatis, stipulatis; inflorescentiis axillaribus, glomeratis; sepalis 3 vel 5, imbricatis; petalis 3 vel 5; staminibus 5, liberis; pistillodio effecto; ovariis 3, uniovulatis; stylis 3; fructibus capsularibus.

Trees, apparently dioecious. *Leaves* alternate, simple petiolate; stipules small, deciduous. *Inflorescences* axillary, sessile or short-petiolate, glomerate. *Staminate flowers* (seen only in *T. gentryi*) short-pedicellate; calyx lobes 5, imbricate, petals 5, equaling or exceeding the sepals; stamens 5, free; pistillode well developed. *Pistillate flowers* pedicellate, the pedicel elongating in fruit; perianth as in the pistillate flowers (sepals and petals only 3 in *T. tachirensis*, in which staminate flowers are unknown), persistent on the mature fruit; carpel 3-locular, the locules uniovulate; styles 3, divided at apex. *Fruits* capsular, the thin outer wall separating from the thicker inner wall at dehiscence; seeds apparently ovoid-lenticular, smooth or perhaps sculptured, often misshapen, rarely seen mature.

This genus of small to medium-sized trees seems

quite unlike any other Euphorbiaceae in the Neotropics, and I have been unable to match it with any Old World representatives of the family. The collections available have mature capsules and young fruits that retain the pistillate calyx and corolla. Only one specimen (*T. gentryi*, *Gentry et al. 16901* MO), however, has staminate flowers, and these are partially embedded in mounting glue. Additional material of *T. gentryi* containing abundant staminate flowers was collected but has apparently been lost or misplaced (A. Gentry, pers. comm.). Since characters of the staminate flowers are of great importance in generic delimitation in the Euphorbiaceae, I have been reluctant for some time to describe this new genus, pending recovery or re-collection of staminate material. However, partial dissection of the available staminate flowers revealed five free stamens and a well-developed staminode; these features along with the glomerate, axillary inflorescences, presence of petals, and imbricate calyx mark this as a previously undescribed genus.

Only recently have collections of two additional species of this remarkable genus come to light, and, even though staminate material is lacking in these species, all three species are described together in the hopes of stimulating further exploration. In addition to the characters already mentioned, the three species of *Tacarcuna* are held together by the combination of ovate-lanceolate or obovate-lanceolate leaves with very short, stout petioles; the sepals and often the petals more or less densely puberulous centrally on the outer surface, and with distinctly hyaline margins; deeply lobed capsules somewhat depressed at the apex; and a network of low ridges on the mature capsules, especially prominent in *T. gentryi*, less so in *T. amanoifolia*, and largely obscured by the velutinous indument in *T. tachirensis*.

KEY TO THE SPECIES OF *TACARCUNA*

1a. Branchlets and petioles brown strigillose; secondary veins 5–7, broadly arching; sepals and petals 5 ..... *T. gentryi*
1b. Branchlets and petioles glabrous; secondary veins more than 12, arching only at margins; sepals and petals 3.
  2a. Capsules glabrous to sparsely puberulent; sepals navicular; leaves strongly cuspidate-acuminate ..... *T. amanoifolia*
  2b. Capsules velutinous; sepals more or less plane; leaves acute or rarely short-acuminate ..... *T. tachirensis*

Tacarcuna gentryi Huft, sp. nov. TYPE: Panama. Darién: lower montane wet forest, S slope of westernmost summit of Cerro Tacarcuna Massif between Pucuro base camp and Tacarcuna summit camp, 1,400–1,600 m, 21 July 1976, *Gentry, Leon & Forero 16869* (holotype, MO; isotypes, COL not seen, DAV not seen, F). Figure 2.

Arbor mediocra, dioecia; ramulis junioribus dense puberulis; foliis lanceolate ovatis vel ellipticis, glabris; nervis secondariis 7–9; sepalis et petalis similibus, extus dense brunneo-puberulis, ad marginem late hyalinis; capsulis fasciculatis, pedicellatis, 8–10 mm altis, 10–12 mm latis, parece brunneo-pubescentibus, leviter porcatis.

Tree 6–10 m high, dioecious; branchlets slender, densely puberulent. *Leaves* alternate; blades lanceovate to elliptic, entire, (8–)10–16 cm long, 3–5.5 cm wide, glabrous or brown strigillose below toward the base; apex acuminate; base obtuse; midvein prominent; lateral veins 7–9 per side, prominent, arching; veinlets forming a prominent reticulum; petioles short, thickened, 3–5 mm long, glabrous or brown-strigillose; stipules deciduous, deltate, 1.6–2.2 mm long, 0.8–1 mm wide, shallowly cucullate, brown strigillose. *Inflorescences* axillary, glomerate. *Staminate flowers* apparently several in each axil; pedicel ca. 2 mm long, finely and densely puberulous with short brown hairs; sepals 5, valvate, 1.2–1.5 mm long, oblong, rounded at apex, densely brown puberulent outside except the broad hyaline margin, glabrous inside; petals similar; stamens 5, free; disk present, the features not clearly seen; pistillode well developed. *Pistillate flowers* 2–5 in each axil (seen only in fruit); fruiting pedicel 8–14 mm long, stout, finely and densely puberulous with short brown hairs; perianth as in staminate flowers, persistent in fruit; styles 3, strongly recurved, densely brown puberulent on the outer surface, glabrous on the inner surface, bifid at apex for ca. ¼–⅓ their length; style branches divergent and recurved. Immature *capsules* brown tomentose; mature capsules prominently 3-lobed, drying black, 8–10 mm high, 10–12 mm diam., pubescent with scattered short brown hairs, covered with a network of low ridges, the columella unknown; seeds (immature, misshapen) apparently reniform, ca. 8 mm long.

Tacarcuna gentryi is known only from montane rainforest and elfin forest on the Cerro Tacarcuna massif on the border of Panama and Colombia. It is distinctive in its brown strigillose stems and petioles, membranous leaf blades with widely spaced and broadly arching secondary nerves, and five-merous perianth.

I am pleased to name this species after Dr. Alwyn H. Gentry, who in the course of two long

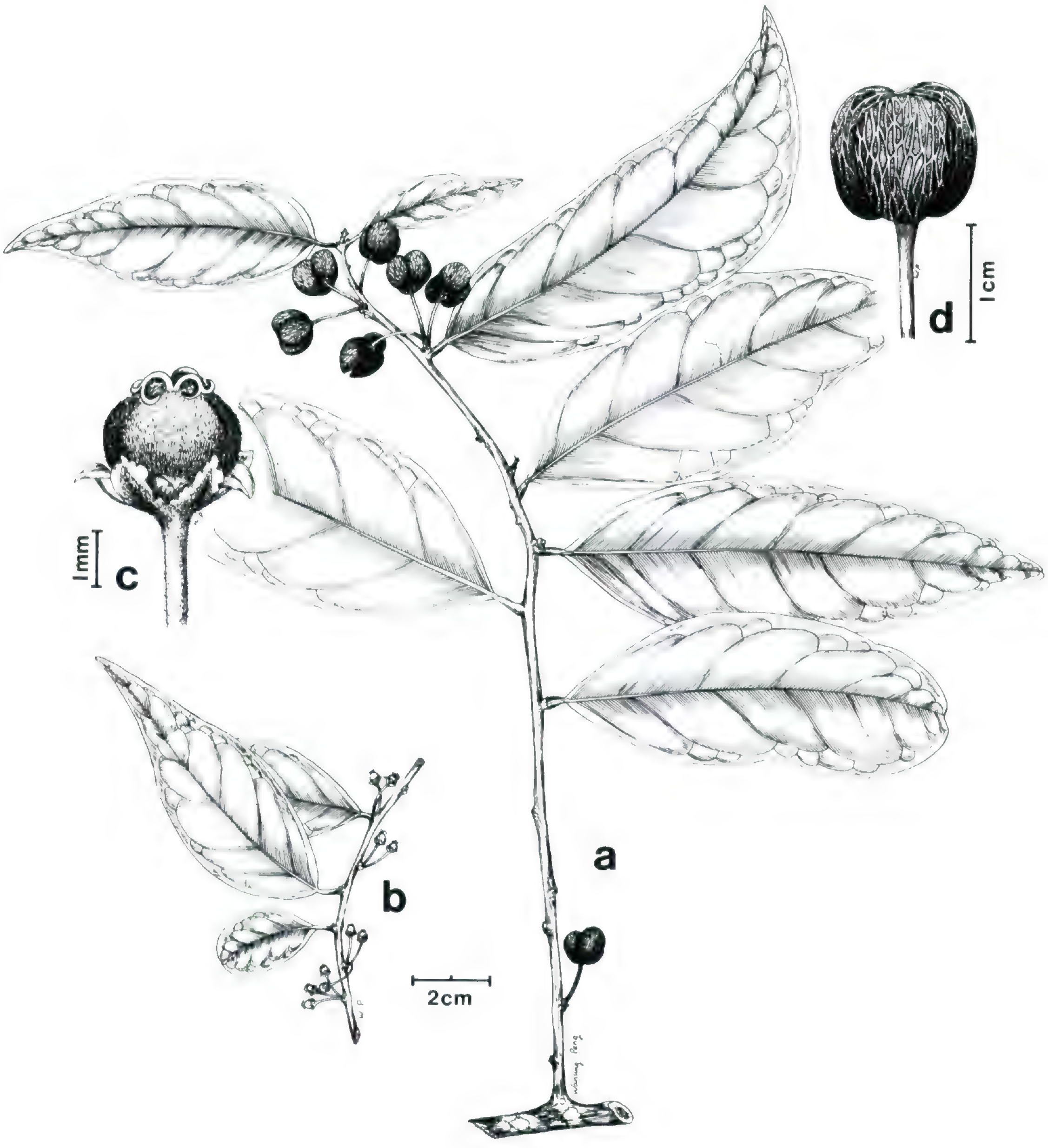


FIGURE 2. *Tacarcuna gentryi.*—a. Leafy branch with mature capsules.—b. Branch with immature capsules. (Same scale for a and b.)—c. Immature capsule.—d. Mature capsule. (Based on *Gentry et al. 16869.*)

expeditions in the mid 1970s was the first botanist to collect the rich and biologically significant flora on the Cerro Tacarcuna Massif on the boundary between Central and South America (Gentry, 1977).

Additional specimens examined. PANAMA. DARIÉN: Cerro Tacarcuna, W ridge, trail toward Río Pucuru just below summit camp, 1,500-1,600 m, *Gentry & Mori 14121* (MO), *14143* (MO); elfin forest near top of westernmost peak of Cerro Tacarcuna Massif, 1,720 m, *Gentry et al. 16901* (F, MO).

Tacarcuna amanoifolia Huft, sp. nov. TYPE: Peru. Maynas: Dtto. Iquitos, Río Momon, 3 km above jct. with Río Nanay, ca. 105 m, 10 Jan. 1976, *S. McDaniel & M. Rimachi Y. 20414* (holotype, MO-3622561).

Arbor mediocra, ut videtur dioecia; ramulis junioribus glabris; foliis lanceolate obovatis, glabris; nervis secondariis 12–16, sepalis 3, navicularibus, extus plus minusve puberulis, ad marginem late hyalinis, petalis 3, glabris, ad apicem cucullatis; capsulis fasciculatis, pedicellatis, 5–6 mm altis, 9 10 mm latis, parece pubescentibus, leviter porcatis.

Tree 7–13 m high, apparently dioecious; branchlets slender, glabrous. *Leaves* alternate,

short-petiolate; blades elliptic to oblanceolate-obovate, entire, (5–)8–12 cm long, (1.8–)3–5 cm wide, 1.9–2.8 times as long as wide, glabrous, somewhat leathery; apex cuspidate-acuminate; base acute to acuminate; midvein prominent on both sides; lateral veins 12–16 per side, arching near the margin of the blade, connected by a fine reticulum; petioles stout, 3–6 cm long, glabrous; stipules fugacious, not seen, leaving a horizontal scar 2–2.5 mm long. *Inflorescences* axillary, glomerate. *Staminate flowers* not seen. *Pistillate flowers* 6–8 in each axil, seen only in fruit; fruiting pedicels 3–4 mm long in immature fruits, 6–9 mm long in mature fruits, ± densely puberulous; sepals 3, imbricate, strongly navicular, ca. 1.8 mm long, ± densely puberulous except on the broad hyaline margins, glabrous inside; petals 3, exceeding the sepals, glabrous, cucullate at apex, the margins hyaline; styles 3, strongly recurved, ca. 2 mm long, ± densely puberulous on the outer surface, especially toward the base, glabrous on the inner surface, bifid ca. ½–⅔ their length; style branches divergent and recurved. Immature *capsules* tomentose, conspicuously 3-lobed; mature capsules deeply 3-lobed, not drying black, 5–6 mm high, 9–10 mm diam., sparsely beset with minute scattered hairs, covered with an inconspicuous network of low ridges, the columella persistent, 3–3.5 mm long, with 3 narrow conspicuous wings running the length of the axis; seeds (misshapen) apparently 5–6 mm long.

This is the only species of *Tacarcuna* known from lowland areas; the two collections were made in occasionally inundated mature forest at ca. 0–100 m elevation. The leaf blades of *T. amanoifolia* are thicker and more lustrous than in *T. gentryi*, and are marked by their more or less broadly obovate-lanceolate outline with a conspicuous cuspidate-acuminate tip. These features along with a sometimes lighter color along the margins impart to the leaves an appearance strikingly similar to that of *Amanoa guianensis* Aublet, a widespread euphorbiaceous tree of the lowland forests of northern South America and southern Central America. Its short mature pedicels give the fruiting branch a more congested appearance than in *T. gentryi*.

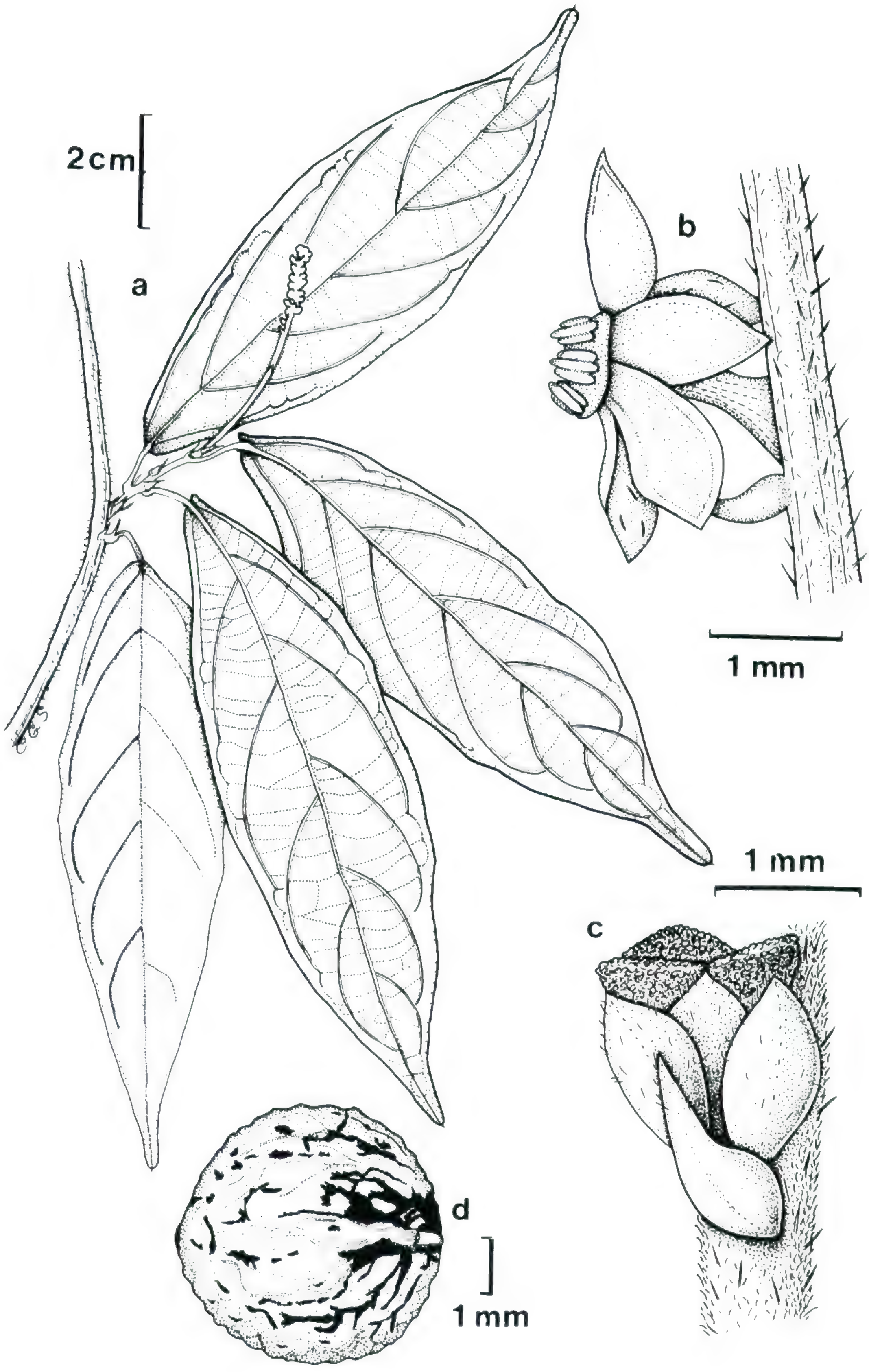
Additional specimen examined. PERU. MAYNAS: Dtto. Iquitos, Río Nanay, two bends below entrance to Mapa Cocha, 14 Jan. 1976, *McDaniel & Rimachi 20465* (MO).

Tacarcuna tachirensis Huft, sp. nov. TYPE: Venezuela. Táchira: Cerro Las Minas, 18 km SE of Santa Ana, along steep slopes leading to Cerro Azul of Cerro Las Minas, 7°36′N, 72°13′W, 1,200–1,380 m, 6 May 1981, *R. Liesner & M. Guariglai 11874* (holotype, MO; isotypes, DAV not seen, F, VEN not seen, and to be distributed).

Arbor parva, ut videtur dioecia; ramulis junioribus glabris; foliis lanceolate ovatis vel lanceolate obovatis, glabris; nervis secondariis 17–25; sepalis 3, extus leviter puberulis vel glabratis, ad marginem hyalinis, petalis 3, similibus; capsulis fasciculatis, pedicellatis, ut videtur 6–8 mm altis, 12–13 mm latis, velutinis, leviter porcatis.

Tree to 3 m high, apparently dioecious; branchlets glabrous. *Leaves* alternate, short-petiolate; blades elliptic, lanceolate-ovate or lanceolate-obovate, entire, 7–12 cm long, 3–5 cm wide, 2–2.8 times as long as wide, glabrous, chartaceous; apex acute or scarcely short-acuminate; base obtuse to rounded; midvein prominent on both sides; lateral veins 17–25 per side, arching near the margin of the blade, scarcely prominulous, ± inconspicuous, connected by a fine reticulum; petioles 2–5 mm long, thickened, glabrous; stipules fugacious, ligulate, ca. 7 mm long, ca. 2.5 mm wide, rounded at apex, leaving a conspicuous horizontal scar. *Inflorescences* axillary, glomerate. *Staminate flowers* not seen. *Pistillate flowers* usually 4 in each axil, seen only in post-mature fruit; fruiting pedicels 1–1.5 cm long, ± puberulous; sepals 3, persistent on mature capsules, imbricate, ovate, ca. 2.5 mm long, glabrous to sparsely puberulous except the hyaline margins, glabrous inside; petals 3, similar to sepals; styles not evident (no intact capsules seen). *Mature capsules* apparently 6–8 mm high, 12–13 mm diam., shallowly 3-lobed, densely velutinous, the network of low ridges barely discernible; columella persistent, ca. 5 mm long, thickened at base, with 3 narrow, scarcely discernible wings running the length of the axis, these rarely larger and membranous; seeds smooth, brown, wrinkled, semiglobose with a vaguely triangular cross section, ca. 6 mm diam.

This species is known only from a single collection on steep forested slopes above 1,200 m. Only post-mature (i.e., already dehisced) capsules are available. The capsules are distinctive in their densely velutinous indument. The leaves are similar to those of *T. amanoifolia* in their thicker texture and lustrous surface, but are more characteristically lanceolate-ovate rather than lanceolate-obovate, and have more closely spaced and more numerous secondary veins; the tips are acute (rarely short-acuminate) rather than prominently cuspidate-acuminate as in *T. amanoifolia*.


2 cm
a
b
1 mm
1 mm
c
d
1 mm

Tragia rubiginosa Huft, sp. nov. TYPE: Peru. Loreto: Mishuyacu, near Iquítos, 100 m, Apr. 1930, *G. Klug 1176* (holotype, US-1456205). Figure 3.

Frutex volubilis, monoeicus; caules pilosi. Folia alternata brevipetiolata; stipulae anguste lanceolatae basi hastatae; laminae lanceolatae vel oblanceolatae, supra glabrae vel ad costam sparsim pubescentes, infra minime pilosae, apice acuminatae, basi cordato-hastatae, margine integrae vel remote denticulatae, basi 3-nerves. Inflorescentiae axillares, spicatae, ut videtur unisexuales, longipeduculatae, plus minusve reflexae. Flores masculi brevipedicellati; lobi calycis 5, 1.5–1.8 mm longi, elliptici, valvati, ad anthesin reflexi; stamina 5; antherae subsessiles, glandulae discorum 5, intrastaminales. Flores feminei lobis calycis 5, ovato-ellipticis, ca. 1.5 mm longis, acutis; stigmata subsessilia, 3, crassa. Capsulae ut videtur 3-lobatae, cristis humilibus reticulatibus, leviter puberulentes; semina globosa, laevia, 4–4.5 mm diametro, ecarunculata.

Vine, monoecious; stem pilose. *Leaves* alternate, on petioles 5–10 mm long, these densely hirsutulous; stipules narrowly lanceolate, appressed, 3.5–5 mm long, sparsely pilose, the base broadly and conspicuously hastate, the lobes rounded; blades lanceolate to oblanceolate, 7.5–11 cm long, 2.7–3.5 cm wide, 2.8–3.7 times as long as wide, glabrous above or sparsely pubescent on midrib, very sparsely pilose below, acuminate at the apex, narrowed to a cordate-hastate base with rounded lobes ca. 1 mm long, the margin entire to remotely denticulate, 3-nerved from base, the central nerve giving rise to another 5–7 pairs of secondaries. *Inflorescences* axillary, spicate, apparently unisexual, ± reflexed, the peduncle densely brown-puberulent, ca. 3 cm long. *Staminate flowers* on pedicels ca. 1 mm long; calyx lobes 5, drying black, 1.0–1.3 mm long, 0.7–0.8 mm wide, elliptic, valvate, reflexed at anthesis; stamens 5, the anthers subsessile, 2-locular, introrse, disk glands 5, intrastaminal. *Pistillate flowers* with calyx lobes 5, ovate-elliptic, ca. 1.5 mm long, acute, lightly hispidulous; stigmas nearly sessile, 3, thick. *Capsules* (not seen entire), apparently 3-lobed, with low reticulate ridges, lightly puberulent, apparently 6–7 mm diam.; seeds globose, cream mottled with reddish brown, smooth, 4–4.5 mm diam., ecarunculate.

This unusual species would key to sect. *Bia* (Klotzsch) Muell. Arg. in the treatment of Pax & Hoffmann (1919) on the basis of its five stamens and the presence of disk glands in the staminate flowers, but it seems hardly related to the other species of that section, which are characterized by their usually deeply cordate leaves (except *T. lessertiana* (Baillon) Muell. Arg.) and especially their robust, bipartite inflorescences with one branch staminate and the other pistillate. Were it not for the presence of the disk glands, however, *Tragia rubiginosa* might seem almost at home in the Cuban genus *Platygyne* Mercier, which Pax & Hoffmann distinguished from *Tragia* by unisexual (vs. androgynous) inflorescences, 5–15 (vs. 2–50 usually near the lower end of the range) stamens, globose hairy receptacles, free filaments, absence of a disk, and wide styles emarginate at the apex.

Liogier (1971: 132, 133) was spurred by his study of the Hispaniolan species *Tragia biflora* Urban, which closely resembles *Platygyne*, to investigate the relationship between *Tragia* and *Platygyne*. He found that the generic characters are intermixed in some species referred to *Platygyne*, and particularly in *T. biflora*, which has a globose, glabrous receptacle with 10–20 stamens and wide, but not emarginate, styles. His conclusion that *Platygyne* cannot be kept separate from *Tragia* is bolstered by the existence of *T. rubiginosa*, which has the five stamens and monoecious inflorescences typical of *Platygyne* but has a disk, flat glabrous receptacle, and nonemarginate styles. The inflorescences of *T. rubiginosa* are reminiscent of those of *T. biflora*, which likewise are monoecious, axillary, and somewhat reflexed, although considerably shorter and with a less pronounced peduncle. The leaves also seem similar but are longer, narrower, and less coarsely crenate in *T. rubiginosa*.

The specific epithet refers to the red-brown color of the flowers.

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FIGURE 3. *Tragia rubiginosa*.—a. Branch with immature inflorescences.—b. Staminate flower.—c. Young pistillate flower.—d. Seed.

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A REVISION OF *AMPELOCERA* (ULMACEAE)[1]

Carol A. Todzia[2]

Abstract

Ampelocera, a genus of Ulmaceae with nine species of low- to mid-elevation rainforest trees, occurs from Mexico to Brazil. This review deals with the systematics and nomenclature, including the description of three new species, *A. albertiae* Todzia from Colombia, *A. longissima* Todzia from Ecuador, and *A. macphersonii* Todzia from Panama, Colombia, and Venezuela. The taxonomic history of *Ampelocera* is outlined, followed by a key to the species. Brief descriptions and geographic ranges are provided for each species.

Ampelocera is a little-known genus of nine species of neotropical trees. Although a frequent component of some low- to mid-elevation neotropical forests (A. Gentry, pers. comm.), *Ampelocera* is poorly represented in herbaria because it is a large rainforest tree and because specimens are not readily identified and often are misfiled. *Ampelocera* is characterized by its large tree habit, buttressed trunk, oblique leaf bases, large number of stamens, bifid style, and asymmetrical drupaceous fruits. The genus ranges from central Mexico to Bolivia and southern coastal Brazil, and it occurs in the West Indies.

In preparing a treatment for the *Flora de Nicaragua*, the literature dealing with *Ampelocera* was reviewed along with all material available from the following herbaria: BM, CAS, F, K, LL, MO, NY, TEX, and US. Three new species as well as changes in the currently accepted nomenclature came to light. Since no summary of the systematics and geography exists, a revision of the genus is now presented. A short history of *Ampelocera* is outlined below, followed by a diagnostic key for the species and a review of their systematics and nomenclature.

Historically included in the Ulmaceae, the genus has been the subject of recent studies on embryology (H. Tobe, Kyoto University, Japan, in prep.) and pollen (M. Takahashi, in prep.) that indicate it is not well placed there. Although past authors have positioned the genus in the subfamily Celtidoideae based on its drupaceous fruit, *Ampelocera* is anomalous within the Ulmaceae by virtue of its 4–16 stamens. On the basis of a summation of evidence from various sources (morphology, anatomy, embryology, palynology, and flavonoid chemistry), Tobe considers *Ampelocera* best classified in a family of its own.

In 1847 Klotzsch described *Ampelocera* with one species, *Ampelocera ruizii*, from a Ruiz & Pavón collection. He placed his new genus near *Celtis*. Since then, *Ampelocera* has generally been aligned within the subfamily Celtidoideae of the Ulmaceae with *Celtis* L., *Trema* Lour., *Aphananthe* Planch., and *Gironniera* Gaudich., although Planchon (1873) considered its placement within the Ulmaceae doubtful due to the anomalous stamen number.

In 1937 Baehni created the genus *Plagioceltis* attributed to Mildbraed on the basis of unpublished notes on the Ruiz & Pavón type specimen at Madrid (Gentry, 1983). I strongly suspect that the unnumbered Ruiz & Pavón type specimen of *Plagioceltis dichotoma* is from the same collection as the type of *Ampelocera ruizii* Klotzsch (Ruiz & Pavón *s.n.*, B!) because both bear leaves and flowers of exactly the same maturity (very young, not fully expanded leaves; flowers at anthesis; no fruits).

Since *Ampelocera* was erected in 1847, ten species have been added to the original *A. ruizii*. The first addition, *Ampelocera cubensis*, was described by Grisebach based on a Wright collection. It was approximately 50 years before the next species of *Ampelocera*, *A. crenulata* Urban and

[1] I thank Guy Nesom for providing the Latin diagnosis, Doris Lee Tischler for the drawing, M. Kubala for field observations, Robbin Moran for help with references, and L. Albert de Escobar, A. Gentry, M. Nee, G. Rogers, and H. van der Werff for their helpful comments on the manuscript. I also wish to thank the curators of the following herbaria for borrowed material and/or help during visits: CAS, F, LL, K, BM, MO, NY, TEX, US.

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A. hondurensis J. D. Smith, were described. Those species, however, were not members of *Ampelocera*, nor even the Ulmaceae, and are presently placed into synonymy in genera in the Flacourtiaceae and Achatocarpaceae, respectively. In 1925 Kuhlmann described *A. glabra* Kuhlm. and *A. verrucosa* Kuhlm. followed by *A. edentula* Kuhlm. (1940) and *A. latifolia* Ducke (1943) all from Brazil. In the protologue of the most recently described species, *A. macrocarpa*, Forero & Gentry (1984) indicated the need for taxonomic study of *Ampelocera*.

Morphology and Taxonomic Characters

Ampelocera species are small to large trees often with slender, channeled buttresses and smooth gray bark. The wood is light brown to cream-colored and hard.

LEAVES

The leaves of all species are pinnately veined except for those of *Ampelocera hottlei*, which are trinerved at the base. The texture of most leaves is coriaceous, but *A. cubensis* and *A. macphersonii* have chartaceous leaves. The leaves of *Ampelocera* are glabrous except for those of *A. cubensis*, which are sometimes softly puberulent beneath. Young leaves in most species are often many times larger than those on fertile branches. Young leaves of *A. hottlei* and *A. macrocarpa* are distinctive for their bright blue metallic color.

Nearly all leaves of *Ampelocera* are oblong to elliptic with characteristic oblique bases and attenuate apices. *Ampelocera cubensis*, *A. glabra*, and *A. ruizii* often have obscurely and coarsely dentate leaves. Petioles are usually thick and have a red flaky epidermis.

INFLORESCENCES

Ampelocera inflorescences are axillary, sometimes simple, usually compound dichasia or rarely are panicles of compound dichasia. In *A. glabra* the rachises are so short that the inflorescences appear fasciculate. The longest and most densely flowered inflorescences in the genus with up to 56 flowers are found in *A. longissima*. Inflorescences have perfect flowers and functionally staminate flowers, the latter being found lower on the inflorescence axis.

FLOWERS

Ampelocera flowers are small, cream-colored, yellow, or green and offer a limited number of characters. All dimensions provided in the descriptions are based on dried material. The perianth consists of a sepalar cup with four or five usually sparsely puberulent lobes. The lobes in *A. cubensis* are villous.

Stamen number varies from 4 to 16 with the staminate flowers often having fewer stamens (4–8) than the perfect flowers. Two kinds of filaments are found in the genus: relatively thick filaments expanded near the base and drying flat characterize *A. edentula* and *A. macrocarpa*, and relatively long, thin filaments that twist upon drying characterize the other seven species. The anther connective is extended beyond the thecae to form a strigose apicule. In the species with the short, broad filaments, the connective extension is very pronounced, while in those with long, thin filaments, the extension is smaller.

The ovary in *Ampelocera* is puberulent and oblong to globose. The two style branches are free to the base in most species, but in *A. cubensis* and *A. ruizii* they are united in the lower one-fourth. Staminate flowers often have cylindrical, ribbed pistillodes with the same vestiture as the ovaries in the perfect flowers.

Size and shape of the drupaceous fruits of each species of *Ampelocera* are quite distinctive. Generally the fruits of *Ampelocera* are yellow, asymmetrical, and transversely obovoid or ellipsoid; they vary from 0.6 to 2.2 cm long. The fruits may be glabrous (*A. glabra*, *A. longissima*), sparsely puberulent (*A. edentula*, *A. macrocarpa*), densely pubescent (*A. macphersonii*), or densely pilose (*A. ruizii*). *Ampelocera hottlei* fruits, the most unusual in the genus, are symmetrically oblong and velutinous with longitudinal striations. *Ampelocera macrocarpa* typically has pyriform fruits with an unusually thick endocarp.

USES

The wood of *Ampelocera* is hard and is used for firewood and lumber. In the Pichis Valley of Peru, the astringent bark of *A. edentula* is used by the Campa Indians to tattoo skin. The bark is wetted and then bound around the arm, where it ulcerates the skin and causes a painful eruption. A coloring agent is then applied to the ulceration and scar tissue forms (A. Gentry, pers. comm.).

Systematic Treatment

Ampelocera Klotzsch, Linnaea 20: 541. 1847.
TYPE SPECIES: *Ampelocera ruizii* Klotzsch.

Plagioceltis Milbr. ex Baehni, Contr. Field Mus. Nat. Hist., Bot. Ser. 13(2): 272. 1937.

Small to large trees with slender buttresses. Leaves petiolate, entire or coarsely dentate, usually glabrous, pinnately veined or palmately veined at base, with paired stipules. Inflorescences axillary, sparsely branched to much-branched dichasia, or the flowers fasciculate, with perfect flowers toward the apex and functionally staminate flowers toward the base; rachises 0.2–7.8 cm long with 2–57 flowers. Flowers white, yellow, or green; calyx with 4–5 lobes, these usually united in the lower half; petals absent; stamens 4–16; filaments 1–4 mm long, 0.5–1 mm broad, of two types, either thick and expanded near base and drying flat, or long, thin, and drying twisted; anther connective extended beyond the anther at the apex; ovary superior, unilocular with a single pendulous ovule, glabrous or pubescent; style branches 2. Fruits drupaceous, yellow or orange, globose, or oblong, or obovoid to transversely obovoid, with persistent stamens and style branches; seeds globose, with thick cotyledons.

KEY TO THE SPECIES OF *AMPELOCERA*

1a. Fruits strongly asymmetrical, broader than long (not known in *A. albertiae*); filaments slender throughout.
  2a. Leaves usually dentate, occasionally entire; inflorescences borne on leafless branches; style branches 3–5 mm long.
    3a. Leaf margins often revolute; filaments ca. 2 mm long; Cuba and Hispaniola ..... 2. *A. cubensis*
    3b. Leaf margins not revolute; filaments ca. 3 mm long; South America.
      4a. Inflorescence rachises 0.9–1.5 cm long with 8–23 flowers; calyx 2–2.5 mm long; fruits 1–1.2 cm tall, 1.2–1.6 cm broad, densely pilose; Peru, Bolivia, Amazonian Brazil ..... 9. *A. ruizii*
      4b. Inflorescence rachises 0.5 0.8 cm long with 4 9 flowers; calyx ca. 1.5 mm long; fruits 1.5 2 cm tall, 2–2.3 cm broad, glabrous; southeastern and central coastal Brazil ..... 4. *A. glabra*
  2b. Leaves always entire; flowers borne on leafy branches; style branches 1–2 mm long.
    5a. Inflorescences with 3–6 flowers; stamens ca. 16; leaves chartaceous, unevenly colored on drying; Panama, northern Colombia, northwestern Venezuela ..... 8. *A. macphersonii*
    5b. Inflorescences with (9)20 56 flowers; stamens 4–12; leaves subcoriaceous, uniformly colored on drying; Colombia (Valle), Ecuador.
      6a. Inflorescence rachises (2.7–)3.5–7.8 cm long, elongate, loosely flowered; ovary sparsely puberulent; Ecuador ..... 6. *A. longissima*
      6b. Inflorescence rachises 0.6–1.9 cm long, congested, densely flowered; ovary densely strigose; Colombia ..... 1. *A. albertiae*
1b. Fruits obovoid to globose, not strongly asymmetrical, longer than broad; filaments broadened basally.
  7a. Leaves trinerved at the base; style branches ca. 4 mm long; stamens ca. 16; fruits densely brown tomentose, with longitudinal striations; Mexico to Nicaragua ..... 5. *A. hottlei*
  7b. Leaves pinnately veined at the base; style branches 1 2 mm long; stamens (6–)8; fruits glabrous to sparsely puberulent, yellow; Honduras to Panama, South America.
    8a. Ovary densely puberulent; fruit with a thin endocarp; greater Amazon Basin in Surinam, Guyana, Brazil, Venezuela, Colombia, Ecuador, Peru, and Bolivia ..... 3. *A. edentula*
    8b. Ovary sparsely puberulent; fruit with a thick endocarp; Honduras to northern Colombia and northern Venezuela ..... 7. *A. macrocarpa*

1. Ampelocera albertiae sp. nov. TYPE. Colombia. Valle: carretera Cali–Buenaventura, km 24, 1,750 m, 15 Oct. 1982, *L. Albert de Escobar, J. Folsom, J. Brand & D. Sánchez 2788* (holotype, TEX; isotypes, HUA, MO). Figure 1.

Ampelocerae longissimae similis sed inflorescentiis densifloris et ovariis dense strigosis differt. Inflorescentiae saepe ad basim ramosissimae, floribus (9–)20–52, sepala 4, 1.5–2 mm longae, stamina 8(–12) in floribus perfectis, filamenta 1.5–2 mm longae, tenues, fructus ignotus.

Trees 4 m tall; younger branches very sparsely puberulent, reddish brown; older branches gray, glabrous; stipules 3–4 mm long, lanceolate, sparsely to moderately strigose. Leaf blades elliptic, 9–12 × 3–6 cm, the apex acute, the base attenuate, drying coriaceous, dull green to brown, uniformly colored, glabrous and smooth above and beneath, the margins entire; lateral veins 5–6, gradually arcuate, raised beneath; petioles 0.5–0.6 cm long, smooth, drying dark brown. Inflorescences axillary, short panicles on leafy branches, often much-branched at base, with perfect and functionally staminate flowers; rachises 0.6–1.9 cm long, densely flowered, with (9–)20–52 flowers, sparsely strigose. Flowers white, subtended by ovate, chartaceous, acute bracts ca. 1 mm long; calyx 1.5–2 mm long, the lobes 4, united at the base, glabrous to sparsely strigose, ciliate; stamens 8(–12) in perfect flowers, 4–8 in functionally staminate flowers, these with a strigose pistillode; filaments 1.5–2 mm long, slender throughout; anthers ca. 1 mm long, with the connective extending into a short strigose

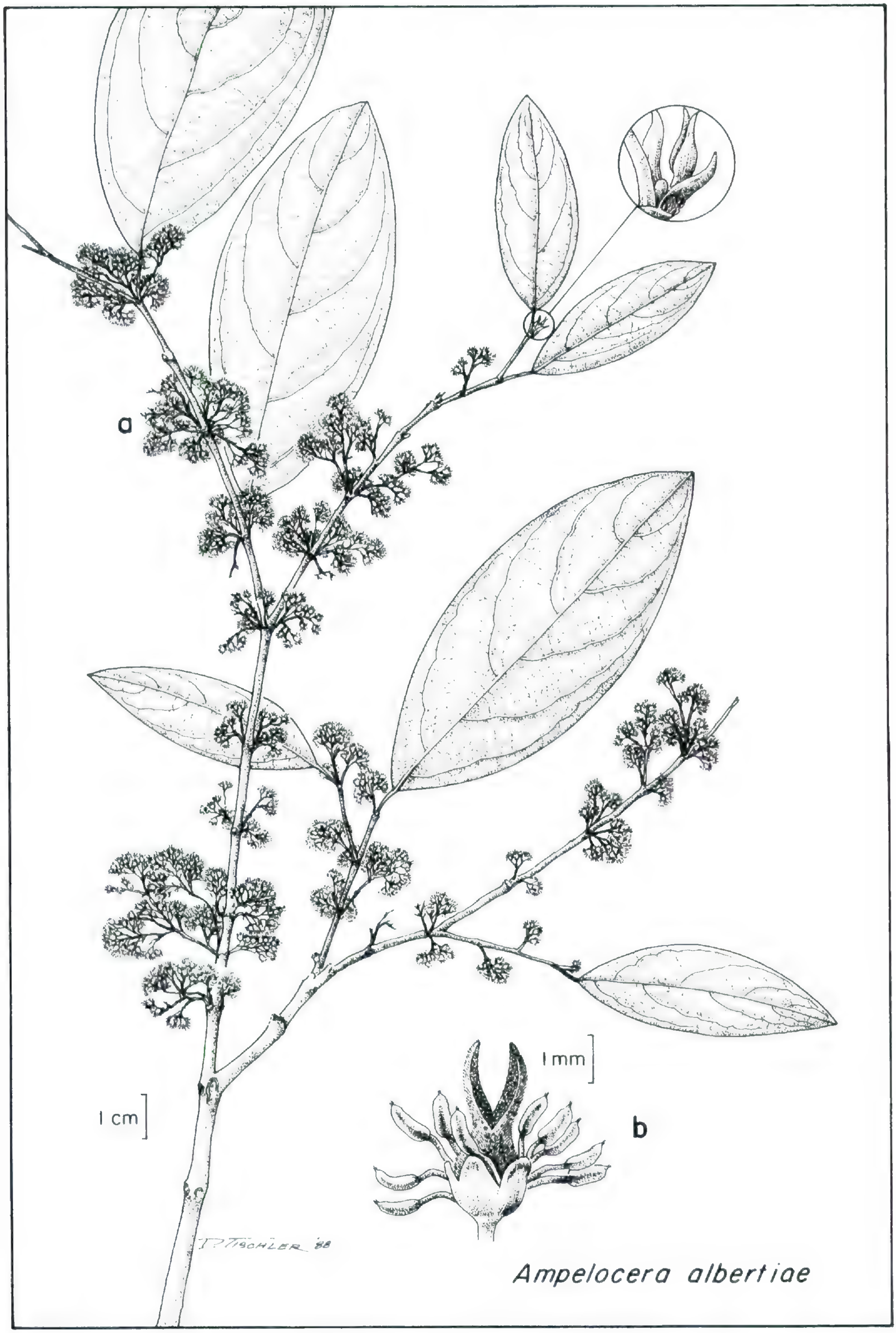


FIGURE 1. *Ampelocera albertiae.*—a. Fertile branch showing close-up of stipules.—b. Perfect flower. (From *Albert de Escobar et al. 2788* TEX.)

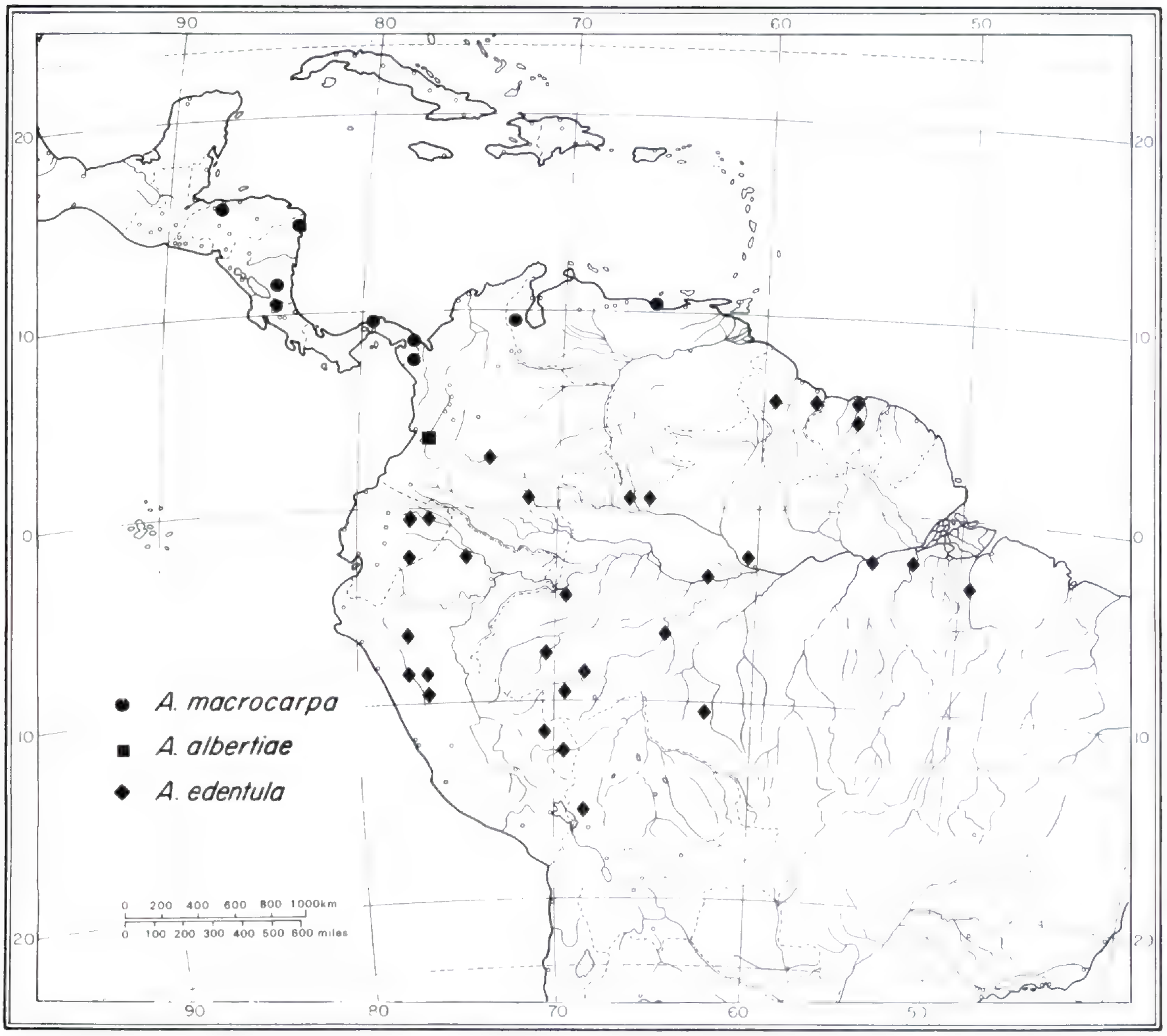


FIGURE 2. Distributions of *Ampelocera albertiae*, *A. edentula*, and *A. macrocarpa*.

apicule ca. 0.1 mm long; ovary densely strigose, the style branches 1.5–2 mm long, free to base. Fruit not seen.

Distribution, habitat, and phenology. This species is known only from the western slope of the western cordillera of Colombia (Fig. 2). Flowering is recorded in October.

Presently known from only one specimen, more collections are needed to understand the morphological variation and relationships of *Ampelocera albertiae*. *Ampelocera albertiae* is characterized by having entire leaves, densely flowered inflorescences on leafy branches, flowers with relatively thin filaments, and style branches 1–2 mm long. This species appears to be most similar to *Ampelocera longissima* but differs by having densely flowered inflorescences and densely strigose ovaries. The unusual, new species is named in honor of its discoverer, Dra. Linda Albert de Escobar, of the Universidad de Antioquia, Colombia (HUA), a student of Passifloraceae.

2. Ampelocera cubensis Griseb., Catalogus Plantarum Cubensium. 57. 1866. TYPE. Cuba. Pinar del Río: Loma de Rangel, 28 May 1863, *Wright 2222* (lectotype [designated by R. A. Howard (1988, Fiche 2, B 11)], GOET; isolectotypes, B, GH, GOET, K, MO).

Ampelocera pubescens C. Morton, Proc. Biol. Soc. Wash. 71: 153. 1958. TYPE. Cuba. Santa Clara: Limones, Soledad, Cienfuegos, 26 Apr. 1928, *J. G. Jack 6036* (holotype, US; isotypes, A—3 sheets, B, F (frag.), K, NY).

Trees 5–30 m tall; younger branches sparsely to densely puberulent, light brown; older branches glabrous, light gray to brown; flowering branches

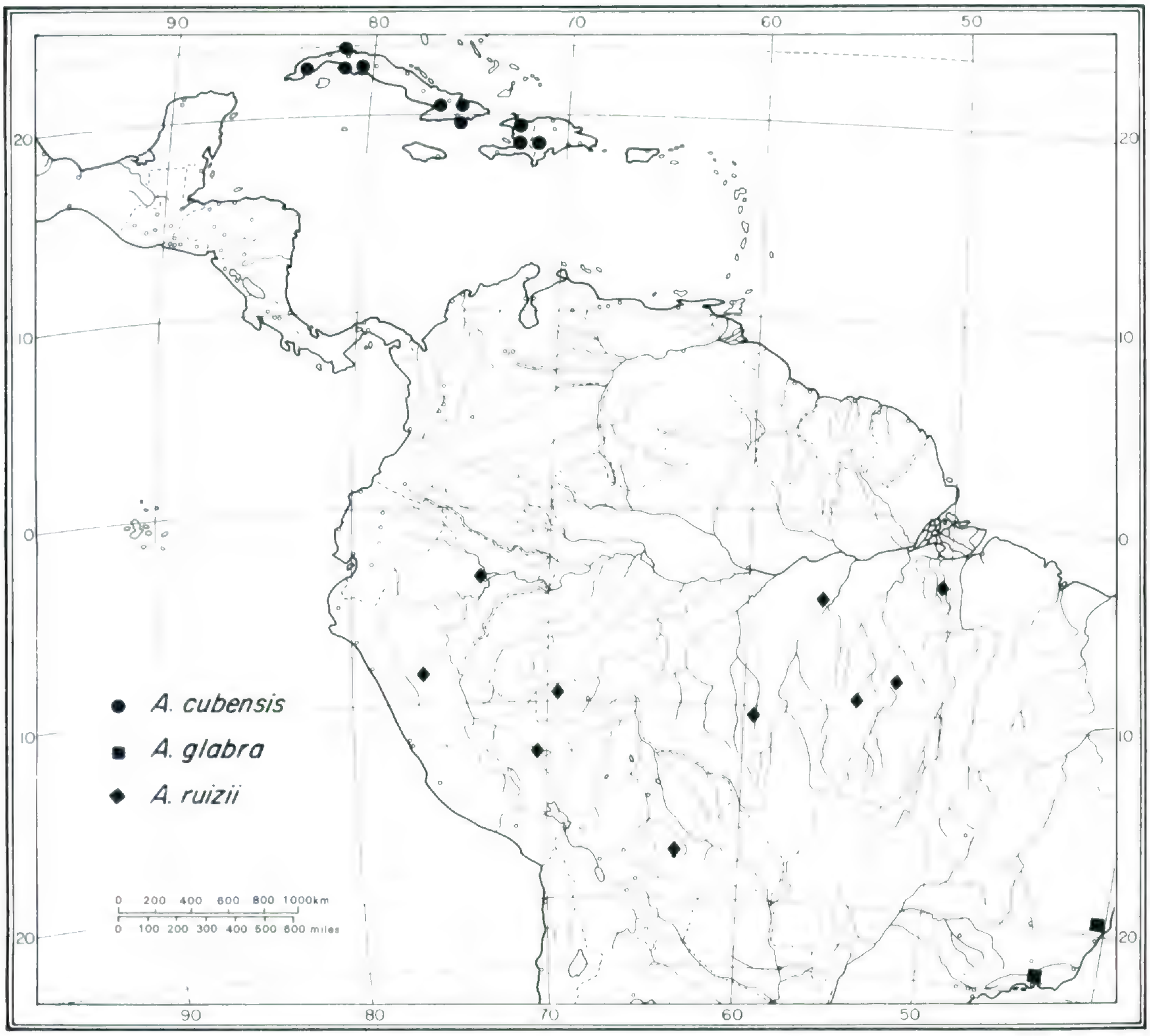


FIGURE 3. Distributions of *Ampelocera cubensis*, *A. glabra*, and *A. ruizii*.

with shortened internodes; stipules 2–5 mm long, lanceolate, sometimes falcate, acute, pilose. Leaf blades narrowly to broadly elliptic, 7.5–17 × 3.5–6(–9.5) cm, the apex gradually acuminate with the acumen 1–2 cm long, obliquely rounded at base, the margins entire, or obscurely dentate with 2–4 teeth per side, or obscurely crenulate, often revolute, drying chartaceous, light brown, the lateral veins 5–7, arcuate, smooth and glabrous above and beneath, the midvein puberulent to glabrous beneath; petioles 0.8–1.2 cm long, puberulent. Inflorescences axillary on leafless branches, fasciculate or in very short racemes with only perfect flowers; rachises 0.2–1 cm long with 2–5 flowers, glabrous to puberulent. Flowers (color not known) subtended by glabrous to sparsely puberulent bracts, the ovate bracteoles 2–3 mm long; calyx ca. 2 mm long, the lobes 4–5, united at base, pilose to villous; stamens 12–16; filaments ca. 2 mm long, linear, slender throughout; anthers 1–1.3 mm long, the connective slightly extended into an apicule; ovary sparsely puberulent, the style branches 3–4 mm long, connate in lower ca. 1 mm. Fruits yellow, asymmetrical, transversely obovoid, 0.8–1.3 cm long, 1–1.4 cm broad, puberulent; endocarp ca. 0.5 mm thick.

Common names. hueso de costa, jatia blanca (Cuba).

Distribution, habitat, and phenology. Uncommon in coastal thickets, limestone cliffs, and rocky woods in Cuba and on western Hispaniola (Fig. 3) from 0 to 300 m. Flowering apparently occurs February to June when the trees are leafless; fruiting specimens have been collected in April, May, July, and December.

Additional specimens examined. CUBA. HAVANA: near Playa de Mariano, Feb. 1922, *Bro. León 10677* (GH, NY, US); Sierra de Anafe, 8 Aug. 1923, *Bro. León 11486* (GH, NY). LAS VILLAS: on limestone outcrop of Potrero Seboruco at Gavilán, 1–20 July 1950, *Howard et al. 21* (A, NY). ORIENTE: Renté, Santiago Bay, July 1943, *Bro. Clemente 2984* (GH). Banes, Puerto Rico, 18 Nov. 1915, *Ekman 6629* (F, K, US); Palmarito de Cauto, 250 m, 2 May 1919, *Ekman 9626* (NY); Papayo, in hills, 21 Feb. 1919, *Ekman 9470* (LL, NY, US 2 sheets). PINAR DEL RÍO: Sierra de Anafe, 18 Dec. 1911, *P. Wilson 11398* (NY—3 sheets, US). SANTA CLARA: Limones, Soledad, Cienfuegos, 12 Mar. 1927, *Jack 4911* (A, NY, US); 3 Sep. 1927, *Jack 5396* (US); 7 Feb. 1928, *Jack 5934* (A—2 sheets, NY, US); 18 July 1929, *Jack 7490* (A, NY, US); Bartolina woods, S coast of eastern Tapata, 1 Aug. 1930, *Bro. León 14625* (GH, NY). DOMINICAN REPUBLIC. SANTO DOMINGO: Peninsula de Barahona, top of Cerro Jean-Josè, ca. 300 m, 23 Sep. 1926, *Ekman 7044* (GH). HAITI: L'ARTIBONITE: Massif des Cahos, Dessalines, limestone cliffs at Case-à-Roche, 13 Mar. 1925, *Ekman 3506* (LL); Gonâve Island, Anse à Galets, Aug. 1927, *Eyerdam 214* (A, GH, NY, US).

This species is characterized by relatively small, thin, sparsely dentate leaves; short, fasciculate inflorescences that are borne on leafless branches; style branches 3–4 mm long; linear filaments; and small, puberulent, strongly asymmetrical fruits. *Ampelocera cubensis* is closely related to *A. glabra* from central coastal and southeastern Brazil and *A. ruizii* from Amazonian Brazil, Peru, and Bolivia. It differs from *A. glabra* by having smaller fruits and less prominently dentate leaves and differs from *A. ruizii* by having shorter inflorescences with 2–5 (vs. 8–23) flowers and by having sepals 1.5 (vs. 2–2.5) mm long.

Morton (1958) described *Ampelocera pubescens*, distinguishing his new species from *A. cubensis* by the vestiture of the lower leaf surface and the length of the stipules (4.5–6 mm in *A. pubescens* vs. 3 mm in *A. cubensis*). I can find no other characters to corroborate the recognition of two taxa, and, in fact, vestiture of material annotated as *A. pubescens* by Morton, including the type (*Jack 6036*), ranges from densely to sparsely pilose.

3. Ampelocera edentula Kuhlm., Annais Prim. Reu. Sul. Amer. Bot. 3: 75. 1940. TYPE. Brazil. Pará: "In silva collina inter locos Piquiatuba et Cipoal," 18 Jan. 1933, *Ducke s.n.* (RB # 24.565) (holotype, RB, n.v.; isotypes, K, US).

Ampelocera latifolia Ducke, Trop. Woods 76: 15. 1943. TYPE. Brazil. Amazonas: Esperança, boca do Javary, 29 Oct. 1942, *Ducke 1039* (holotype, RB, n.v.; isotypes, MG, MO, NY, US).

Trees 12–30 m tall, up to 90 cm dbh, with triangular buttresses 1.5–3 m high; young branches dark reddish brown, glabrous to puberulent, lenticellate, smooth; older branches light grayish brown, with exfoliating bark; stipules 2–6 mm long, narrowly to broadly lanceolate, acute, strigose. Leaf blades elliptic to oblong-elliptic, 8–26(–35) × 3.5–12 cm, apex acuminate with tips 0.2–1.2 cm long, the base rounded, cuneate to oblique, with margins entire, lustrous above, glabrous, drying smooth above and beneath, dull green to brown, pinnately veined; lateral veins 5–7, arcuate, raised beneath; petioles 0.5–1.4 cm long, glabrous or with a red flaky epidermis. Inflorescences 1–2 per axil on leafy branches, short, much-branched, densely flowered panicles, with staminate and perfect flowers; rachises 0.8–2.8 cm long, branching almost to the base, densely flowered, with 6–27(–55) flowers, puberulent. Flowers white to greenish yellow, subtended by bracts 0.5–2 mm long, these reddish, ciliate, ovate, acute, chartaceous; pedicels 0.5–1 mm long, narrower than the rachis and flower base; calyx 1.5–2 mm long, the lobes 4, united in lower half, glabrous to sparsely puberulent; stamens (6–)8 in perfect and staminate flowers; filaments 3–4 mm long, broadened basally; anthers ca. 1 mm long, often curved inward, with the connective extended into an apicule 0.5–1 mm long; ovary in perfect flowers densely puberulent, oblong, 2–3.5 mm long, with style branches 1–1.5 mm long; pistillode in staminate flowers oblong, strigose at the apex and with 5–6 strigose ridges. Fruits yellow, globose to oblong, only slightly asymmetrical, glabrous to sparsely puberulent, scabrous, (0.8–) 1.6–2.2 cm long, 1–1.7 cm broad; endocarp thinner than 0.5 mm.

Common names and uses. Nina-caspi (Peru: San Martín). The fiber of the bark is strong, and when bound around the arm it causes painful eruption; it is toxic and vesicans. The fruit is hypnotic. (Data fide *Woytkowski 5449.*)

Distribution, habitat, and phenology. This species is found throughout the Amazon Basin from near sea level to 750 m in Surinam, Guyana, Venezuela, Brazil, Colombia, Ecuador, Peru, and Bolivia (Fig. 2) in primary tropical moist forest and nonflooded and flooded riverine forests. Flowering and fruiting apparently occur throughout the year.

Additional specimens examined. BRAZIL. ACRE: near mouth of Rio Macauhan (tributary of Rio Yaco), 9°20'S, 69°W, 3 Aug. 1933, *Krukoff 5266* (K, MO 2 sheets, NY, US). AMAZONAS: Manaus, Estrada do Aleixo, 27 Aug. 1945, *Ducke 1736* (A, F, NY, US); Rio Purús, Rio Ituxi, SE of Lábrea, 29 June 1971, *Prance et al. 13979* (MG);

near mouth of Rio Embira (tributary of Rio Tarauaca), 7°30′S, 70°15′W, *Krukoff 4877* (A, F, K—2 sheets, MO, US); Serra da Neblina, Rio Cauaburi, beyond mouth of Tucano Igarapé, 125 m, 16 Nov. 1965, *Maguire et al. 60185* (MO). PARÁ: near EMBRAPA station, at km 23 on road Altamira–Itaituba, 29 Oct. 1977, *Berg et al. 734* (MO); Tucurui, Cagancho, Rio Tocantins, Jan. 1981, *Lisboa et al. 2114* (MG). RONDÔNIA: Município de Ouro Preto do Oeste, BR 364, rodovia Cuiabá–Porto Velho, km 382, rodovia 470, linha 81, em direção a Mirante da Serra, km 17, 10°11′S, 62°63′W, *C. A. Cid 4940* (MO 2 sheets). SURINAM: Kaboerie, Arbor no. 596, Oct. 1950, *B. W. 4964* (K 2 sheets, NY). GUYANA: Mazarumi Station, 9 Jan. 1940, *Fanshawe 3075* (K, NY); Mapenna Creek, Courantyne River, 23 Oct. 1946, *Fanshawe 5369* (K, NY, US). VENEZUELA. AMAZONAS: Cerro Neblina, between base camp and "Puerto Chimo" along Río Mawarinuma, 150 180 m, 0°50′N, ca. 66°8′W, 26 Apr. 1984, *Gentry & Stein 46979* (MO, TEX). COLOMBIA. META: Sierra de la Macarena, Caño Entrada, 550 m, 13 Jan. 1950, *Philipson et al. 2107* (US). VAUPÉS: Río Apaporis, entre el Río Pacoa y el Río Kananarí, Soratama, 250 m, 28 Sep. 1951, *Schultes & Cabrera 14147* (ECON 2 sheets). ECUADOR. NAPO: Estación Experimental INIAP-Payamino, 5 km al N de Coca, 0°25′S, 77°00′W, 250 m, 10–15 Sep. 1986, *Neill et al. 7320* (TEX); Añangu, Parque Nacional Yasuní, 0°31–32′S, 76°23′W, 260–350 m, *Studies of Ecuadorian Forests 9154* (NY). PERU. HUÁNUCO: vicinity of Tingo María, along Río Huallaga above docks by coffee tanks, 25 June 1960, *Mathias & Taylor 5002* (F). MADRE DE DIOS: Tambopata Tourist Camp at junction of ríos Tambopata and La Torre, 280 m, 12°49′S, 69°43′W, 24 July 1985, *Gentry et al. 51256* (MO). SAN MARTÍN: Prov. Mariscal Cáceres, Dtto. Tocache Nuevo, 15 Sep. 1970, *Schunke 4395* (F, GH, K, MO, NY, US); Gramalote ad Saposoa, 600 m, 1 Oct. 1959, *Woytkowski 5449* (MO); 17 Apr. 1962, *Woytkowski 7307* (F, GH, MO, NY, TEX, US); Sanango ad Saposoa, 600 m, 14 Apr. 1962, *Woytkowski 7291* (F, MO 2 sheets); 20 Apr. 1962, *Woytkowski 7312* (MO). BOLIVIA. LA PAZ: Prov. Larecaja, Tuiri, near Mapiri (on left bank of Río Mapiri), 490 750 m, 12–30 Sep. 1939, *Krukoff 10732* (A, F, K, MO, US), *10727* (A, F, K, MO, US).

Ampelocera edentula is characterized by having flowers with eight stamens; broad filaments with a pronounced terminal extension of the connective; and large yellow, globose, symmetrical fruits. This species is most closely related to *A. macrocarpa* from which it differs in having generally oblong fruits and a thin endocarp (vs. globose fruits and a thick endocarp).

In his description of *Ampelocera latifolia*, Ducke (1943) stated that his new species might be just an upper-Amazonian variant of *A. edentula*. The fruit on the type of *A. latifolia* is distinctly oblong while that on the type of *A. edentula* is smaller and round. This variation, however, may reflect only a difference in fruit maturity, and since I could find no other consistently correlated characters, *A. latifolia* is placed into synonymy with *A. edentula*.

Although *Ampelocera edentula* occurs throughout a broad geographic area in the Amazon Basin, it is poorly represented in herbaria, and consequently, its morphological variation is difficult to assess. Leaves are generally shorter on fertile branches, 12–20 cm long, while sterile branches have leaves up to 30 cm long. Some collections from Peru and Bolivia (*Schunke 4395*, *Woytkowski 7307* (Perú: Dept. San Martín); *Krukoff 10727* (Bolivia: La Paz)) have leaves up to 35 cm on fertile branches. These populations differ further from typical Brazilian *A. edentula* in having shorter petioles, more oblique leaf bases, and more pubescent fruits. A sterile specimen from Peru (Dept. Loreto: Prov. Requena, Jenaro Herrera, Río Ucayali, 73°45′W, 4°55′S, 22 Feb. 1987, *Gentry et al. 56289* (MO)) is unusual in having sparsely pubescent stems, petioles, and the lower surface of the primary and secondary veins. As more specimens become available, the variation presently included in *A. edentula* may warrant recognition of other taxa.

4. **Ampelocera glabra** Kuhlm., Arch. Jard. Bot. Rio de Janeiro 4: 351, pl. 28. 1925. TYPE. Brazil: "Rio de Janeiro ad urbem in selva loco Fabrica Alliança," 8 Nov. 1922, *Kuhlmann 6794* (holotype, B; isotypes, K, MO, US).

Trees 3–20 m tall, with a spreading crown; trunk brown, up to 66 cm diam.; older stems gray, glabrous; younger stems brown, glabrous; stipules ca. 5 mm long, lanceolate, glabrous or sparsely pilose. Leaf blades elliptic, 7.5–14 cm long, 2.7–7.2 cm wide, the apex acuminate, the tip 0.3–1.5 cm long, obliquely rounded at base, the margins dentate with 4–6 teeth, seldom entire, smooth, glabrous, drying subcoriaceous, the lateral veins 5–8, straight in lower ¾, slightly arcuate near margin; petioles 0.5–1 cm long, glabrous, drying dark brown. Inflorescences fasciculate or very short racemes or cymes, axillary on leafless stems, with perfect and staminate flowers having rudimentary pistils; rachises 0.5–0.8 cm long, sparsely puberulent, with 4–9 flowers. Flowers green, subtended by bracts ca. 1.5 mm long, glabrous to sparsely pilose; calyx ca. 1.5 mm long, the lobes 4, united at the base, ovate, sparsely pilose; stamens 16 in bisexual flowers, 12–14 in functionally staminate flowers; filaments ca. 3 mm long, slender throughout, with the connective extended into an apicule ca. 0.3 mm long; anthers 1–1.5 mm long; ovary sparsely puberulent and verrucose, the style branches ca. 4 mm long. Fruits yellow, asymmetrical, transversely obovoid, 1.5–2 cm tall, 2–2.3

cm broad, glabrous, with persistent style branches; endocarp thin.

Common name. Mentira (Brazil).

Distribution, habitat, and phenology. This species occurs in primary forest in southern coastal Brazil (Fig. 3). Flowering August to November usually on leafless branches.

Additional specimens examined. BRAZIL. ESPIRITO SANTO: Reserva Florestal da CVRD, Linhares, Est. Gavea, ant. X-2, KM 20,790, 20 Aug. 1979, *Foli 98* (MO). MINAS GERAIS: Distr. Rio Branco, retiro de Antonio Avelino, 750 m, 27 Dec. 1930, *Mexia 5456* (MO). RIO DE JANEIRO: cultivadad no Horto Florestal da Gávea, 7 Jan. 1932, *Victorio s.n.* [RB no. 139428] (B); Huto Florestal, 19 Jan. 1928, *Kuhlmann s.n.* [RB no. 139426] (F); Mata das Obras Públicas, 23 Dec. 1926, *Kuhlmann s.n.* [RB no. 139430] (F, US).

Ampelocera glabra is distinguished by its small fascicles of flowers; large, strongly asymmetrical, glabrous fruits; and toothed leaves. It is clearly most closely related to and can be easily confused with *A. ruizii* but is geographically disjunct. The straight instead of arcuate lateral veins in *A. glabra* are distinctive in the genus.

5. Ampelocera hottlei (Standley) Standley, Trop. Woods 51: 11. 1937.

Celtis hottlei Standley, Trop. Woods 20: 20. 1929. TYPE: Honduras. Yoro, near Progreso, 4 Apr. 1929, *Hottle 32* (holotype, F).

Trees 10–30 m tall; trunk 10–50 cm dbh, with narrow buttresses, ca. 2 m tall; crown subglobose or spreading; bark smooth, white to gray with dark lenticels, hard, with a sweet odor; sapwood creamy yellow to light brown; branches light brown-gray, lenticellate; stipules ca. 4 mm long, linear-lanceolate, puberulent. Leaf blades oblong to elliptic, (7–)8.5–16(–26) × (2.6–)3.3–8(–10.5) cm, the apex acuminate with an acumen 0.2–3 cm long, obliquely attenuate to rounded at base, the margins entire, drying chartaceous to subcoriaceous, dull dark green above, dull light green beneath, the young leaves blue to purple, glabrous and smooth above and beneath, the lateral veins 3–4(–5), arcuate, only slightly raised beneath, the base palmately veined with basal pair arising at the petiole; petioles 0.6–1.2 cm long, glabrous, minutely verrucose, usually drying dark brown. Inflorescences axillary on leafy branches, 1–2.5 cm long, compound dichasia with perfect flowers toward the apex and functionally staminate flowers toward the base; rachises 0.7–1.5 cm long with 8–17 flowers, puberulent. Flowers purplish to yellowish green, subtended by puberulent bracteoles 1–2 mm long; calyx 1–2 mm long, the lobes 5, united at base, puberulent abaxially; stamens ca. 16 in perfect flowers, ca. 8 in staminate flowers; filaments ca. 2 mm long, linear-lanceolate, broadened basally; anthers ca. 1 mm long, anther connective extended ca. 1 mm into a puberulent apicule; ovary puberulent, the style branches ca. 4 mm long, united in lower 2–3 mm. Fruits yellow, symmetrical, obovoid, 1.2–1.5 cm tall, 1–1.2 cm wide, velutinous, with persistent style branches; endocarp ca. 1 mm thick.

Common names and uses. Mexico: coquito, cautivo, guaya, ojoche blanco, popo mojo. Belize: bullhoof, luin. Guatemala: luín, tisón. El Salvador: tisón. Nicaragua: cuscano, yayo. The wood is used for house construction and railroad ties.

Distribution, habitat, and phenology. This species occurs from central Mexico to Nicaragua (Fig. 4) in primary, undisturbed rainforest or tropical wet forest, sometimes on limestone. Flowering reported from February and fruiting from March to June.

Representative specimens examined. MEXICO. CAMPECHE: El Tormento, near Escárega, 17 May 1968, *Pennington & Sarukhán 9639* (A, K, NY). CHIAPAS: zona comprendida entre los ríos Chancaláh, Chocoljahíto, y Tulijá, Selva Lacandona, 250–450, 29 Nov. 1967, *Pennington & Sarukhán 9363* (NY); road to the ruins, La Arena, 13 Mar. 1958, *Schubert & Gómez Pompa 1731* (A). OAXACA: Mpio. Sta. María Chimalapa, ca. 7 km al oeste de Santa María en la vereda de Chicusaja, 250 m, 30 June 1984, *H. Hernández G. 163* (CAS); Ubero, 30–90 m, June 1937, *Ll. Williams 9497* (A, F, US). TABASCO: Villahermosa (Centro), Selva Dos Montes, atrás del aeropuerto 3.6 km (2.3 mi.) por camino rural de la entrada al aeropuerto, 8 May 1984, *Cowan & Zamudio 4672* (TEX). VERACRUZ: Estación de Biología Tropical "Los Tuxtlas," Mpio. San Andrés Tuxtla, 26 Mar. 1974, *Calzada 1166* (CAS, MO); Estación de Biología Los Tuxtlas, 170–200 m, 1 June 1981, *Gentry et al. 32522* (MO); Mpio. Minatitlán, 2 km al N de Uxpanapa (Pob. 12) en camino al Pob. 13, 17°13′N, 94°13′W, 150 m, 25 Apr. 1985, *Wendt et al. 4803* (TEX). BELIZE. EL CAYO: Valentin, June–July 1936, *Lundell 6225* (F, NY), *6346* (F, NY), *6423* (F). EL TOLEDO: Temash River, 21 Feb. 1945, *Gentle 5212* (F, LL, TEX); near Moffredye Lagoon, 27 Mar. 1945, *Gentle 5291* (GH LL, TEX, US); Temash River, 200 ft., 4 Mar. 1935, *Schipp 1347* (F, K, MO, NY). GUATEMALA. ALTA VERAPAZ: along Río Icvolay between Río Apia and Río Soctelá, 220–210 m, 14 Mar. 1942, *Steyermark 45038* (F); woods SE of Finca Yalpemech, near Alta Verapaz–Petén boundary line, 100 150 m, 23 Mar. 1942, *Steyermark 45205* (F, LL). HUEHUETENANGO: between Ixcan and Río Ixcan, Sierra de los Cuchumatanes, 150–200 m, 23 July 1942, *Steyermark 49219* (F). IZABAL: between Bananera and "La Presa" in Montaña del Mico, 40–300 m, 28 Mar. 1940, *Steyermark 38175* (F); Escoba, ca. 0 m, 3 May 1939, *Standley 72886* (A, F), *72953* (F, NY); Río Juyamá,

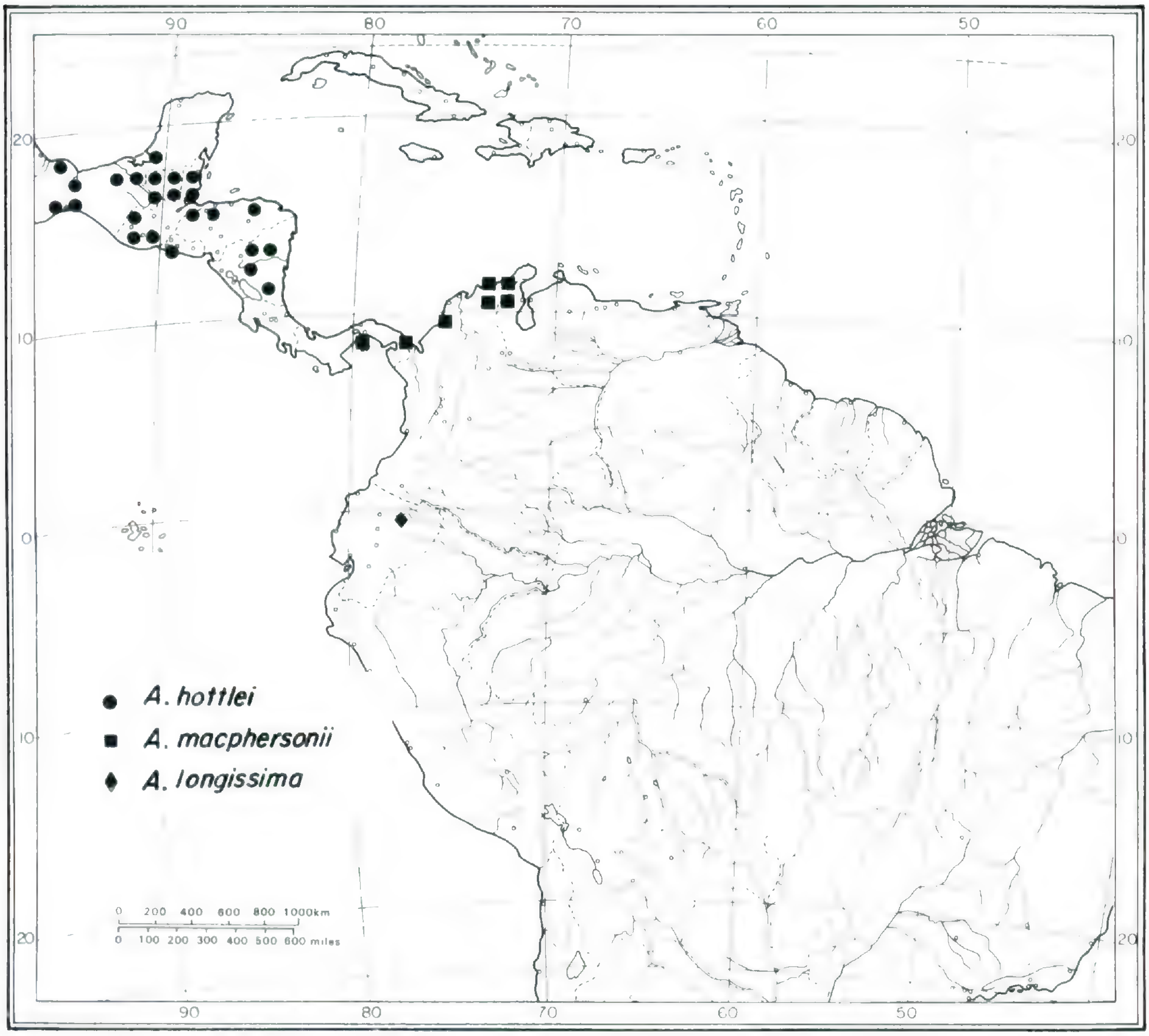


FIGURE 4. Distributions of *Ampelocera hottlei*, *A. macphersonii*, and *A. longissima*.

SE of Cheyenne, ca. 15 mi. SW of Bananera, 50–100 m, 8 Apr. 1940, *Steyermark 39153* (F). PETÉN: Paso Caballos, 5 Apr. 1965, *Contreras 5387* (LL, TEX); Tikal National Park on Remate Road, 4 Mar. 1961, *Lundell 16877* (F, LL); W and NW of Chinajá and 6 mi. W of Río San Román, 50–70 m, 29 Mar. 1942, *Steyermark 45500* (F). RETALHULEU: between Retalhuleu and Nueva Linda, 120–220 m, 18 Feb. 1941, *Standley 87284* (F), *88487* (F), *88520* (A, F). SANTA ROSA: Río de las Pitas, E of Taxisco, ca. 225 m, 2 Dec. 1940, *Standley 78928* (F). EL SALVADOR. AHUACHAPÁN: Sierra de Apaneca, in the region of Finca Colima, 17–19 Jan. 1922, *Standley 20149* (GH). HONDURAS. COLÓN: Guarunta, Wispermini Camp, 75–100 ft., Mar. 1938, *Hagen & Hagen 1372* (F, NY), *1376* (F, NY). YORO: near Progreso, 11 Apr. 1929, *Hottle 108* (F). NICARAGUA. MATAGALPA: Paiwita, 15 km W of Matiguás, 500 m, 5 May 1984, *Moreno 24122* (MO). ZELAYA: Kurinwacito, 80–100 m, 18–22 Mar. 1984, *Moreno 23654* (MO); near Caño San Antonio, 2 km N of Kuikainita, 100 m, 23 May 1978, *Veill 4157* (MO); Mpio. Siuna, La Pimienta, 1 June 1984, *Ortiz 1938* (MO); El Zapote, 40 km NE of Nueva Guinea, 25–31 Mar. 1984, *Sandino 4914* (MO); along Río Iyas between Quebrada El Toro, 260–280 m, 13 May 1978, *Vincelli 367* (MO).

Ampelocera hottlei is represented by the most collections and thus is the best-known species in the genus. Unlike other species, description of the trunk, bark, and sap is available from collection data. It is distinguished from all other species by its trinerved leaf base, and obovoid, densely pubescent, longitudinally lined fruits. As with *A. macrocarpa*, the young leaves are bright metallic blue.

6. **Ampelocera longissima** Todzia. TYPE. Ecuador, Napo: Estación Biológica Jatun Sacha, Río Napo, 8 km al E de Misahuallí 01°04′S, 77°36′W, 450 m, 28 Dec. 1987, *Neill, Gentry & Manning 8135* (holotype, TEX; isotype, MO). Figure 5.

Inflorescentiae pro genere longissimae, (2.7–)3.5–7.8 cm longae, flores 33–56. Sepala 4 glabra in dimidio inferno connata, stamina 8–10 filamentis ca. 3 mm longis tenuibus. Ovaria sparsim puberula. Rami styli 1–2 mm longi. Fructus leviter lutei transverse obovoidei glabri endocarpium tenuissimum.

Trees up to 20 m tall, with a large, round crown, and shallowly channeled buttresses to 1 m high; bark light gray; wood cream-colored to light brown; young branches very minutely puberulent, dark brown; older branches glabrous, gray; stipules 2–3 mm long, narrowly triangular. Leaf blades elliptic, 8.5–17.4 × 3.5–7.1 cm, the apex acute to gradually acuminate, the tips up to 1 cm long, attenuate at the base, rarely oblique, drying subcoriaceous, green to light brown, uniformly colored, smooth and glabrous above and beneath, the margins entire; lateral veins 4–6, arcuate; petioles 5–14 mm long, glabrous, smooth, and dark brown, becoming flaky and gray with age. Inflorescences axillary on leafy branches, flat-topped panicles or compound dichasia, often curving upward; rachises (2.7–)3.5–7.8 cm long, very minutely puberulent, loosely flowered, with 33–56 flowers. Flowers bisexual or staminate with pistillodes, light green; sepals 4, glabrous, connate in lower half; stamens 8–10; filaments ca. 3 mm long, linear, slender throughout; anthers ca. 1 mm long; ovary sparsely puberulent; style branches 1–2 mm long, papillate on inner surface, glabrous to sparsely strigulose on outer surface. Fruits light yellow, asymmetrical, transversely obovoid, 0.6–1 cm tall, 1–1.4 cm broad, glabrous, with persistent style branches; endocarp very thin, thinner than 0.5 mm.

Distribution, habitat, and phenology. This species is known only from Napo Province in Amazonian Ecuador (Fig. 4) in primary forest. Flowering reported in March on leafy branches; fruiting reported in January, May, and December.

Additional specimens examined. ECUADOR. NAPO: Reserva Biológica Jatun Sacha, Río Napo, 8 km al E de Misahuallí, 01°04′S, 77°36′W, 450 m, 19–28 Mar. 1987, *Cerón 973* (MO, TEX); 8 Nov. 1987, *Cerón 2633* (MO, TEX); 18–30 May 1985, *Palacios et al. 519* (MO); 25 Jan. 1986, *Palacios & Neill 965* (MO).

Ampelocera longissima is distinctive in having the longest inflorescences known in the genus, as well as glabrous, asymmetrical, transversely obovoid fruits. Vegetatively, *A. longissima* is somewhat similar to *A. edentula*, which grows in the same area, but can be separated easily by the latter's shorter inflorescences and pubescent, symmetrical fruits.

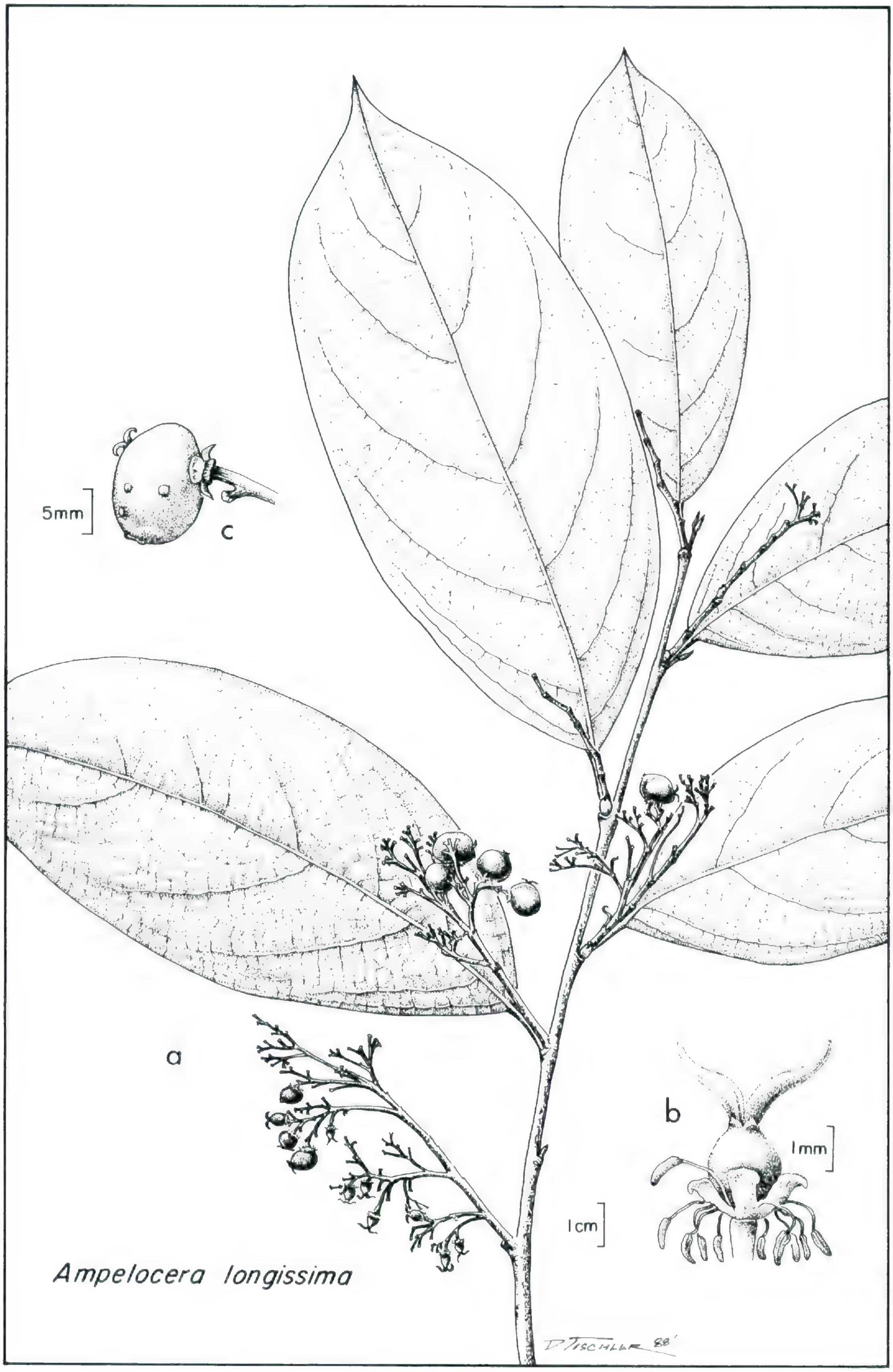
7. Ampelocera macrocarpa Forero & A. Gentry, Phytologia 55: 365. 1984. TYPE. Colombia. Chocó: upper Río Truandó between La Teresita and mouth of Río Ramón, 20 Jan. 1974, *Gentry 9436* (holotype, COL, n.v.; isotypes, MO, NY).

Trees 10–30 m tall; trunk to 50 cm dbh; younger branches sparsely puberulent; older branches glabrous; stipules ca. 6 mm long, linear-lanceolate, sparsely puberulent. Leaf blades oblong to elliptic, 8–22 × 3.7–10 cm (sapling leaves 22–38 cm long), the apex acute to acuminate with tips 1–3 cm long, very strongly oblique, base rounded to subcordate, the margins entire, drying coriaceous, dull green to brown, glabrous and smooth above and beneath, pinnately veined; lateral veins 4–11, arcuate, raised beneath; petioles 0.6–1 cm long, with a flaky red epidermis. Inflorescences axillary on leafy branches, compound dichasia with perfect flowers toward the apex and functionally staminate flowers at the base; rachises (1.8–)2.5–3.7 cm long, with 11–34(–57) flowers, glabrous, sometimes purple. Flowers green, subtended by minute floral bracts, ca. 1 mm long, ovate, acute, chartaceous; sepals 4–5, 1–2.5 mm long, united at base, glabrous; stamens 8 in perfect flowers, 4–6 in staminate flowers; filaments 1.5–2 cm long, broadened basally; anthers ca. 1 mm long, the connective extended into a short apicule less than 0.5 mm long; ovary in perfect flowers sparsely puberulent, with style branches 1–2 mm long; pistillode in staminate flowers cylindrical with longitudinal strigose ribs. Fruits yellow, globose or drying pyriform, 1.8–2.2 cm diam., essentially symmetrical, glabrous or very sparsely strigose, scabrous, with persistent style branches ca. 2 mm long; endocarp 1–2 mm thick.

Common names. Nicaragua: cuscano, yayo. Costa Rica: rescaldo.

Distribution, habitat, and phenology. This species occurs in the Atlantic lowland rainforest of Honduras, Nicaragua, Costa Rica, Panama, northern Venezuela, and northwestern Colombia (Fig. 2). It has been reported in second growth evergreen forest and on limestone. Flowering specimens have been collected in February; fruiting collections are known from January, March, May, and August.

Additional specimens examined. HONDURAS. ATLÁNTIDA: Lancetilla Valley, near Tela, 20–600 m, 6 Dec. 1927–20 Mar. 1928, *Standley 53125* (F), *54159* (F). NICARAGUA. RÍO SAN JUAN: edge of Río Santa Cruz, tributary of the Río San Juan, 42 m, 22 Mar. 1985, *Moreno 25531* (MO). ZELAYA: Comarca de San Isidro,


5mm
c
a
1cm
b
1mm
Ampelocera longissima
D TISCHLER 88'

above Río Pajarito, 3 Oct. 1982, *Laguna 85* (MO); S of Río Wawa, 60 km NW of Puerto Cabezas, 40 m, 13 Mar. 1971, *Little 25135* (F, MO); 16 Mar. 1971, *Little 25165* (MO); along road from Siuna to El Dos, ca. 1 km E of Cerro Livico, 400–600 m, 12 Dec. 1980, *Stevens 18687* (MO). COSTA RICA. HEREDIA: Finca La Selva, 100 m, 25 Mar. 1981, *Folsom 9488* (F, LL, MO, TEX); Finca La Selva, 30 May 1974, *Hartshorn 1495* (MO, NY). PANAMA. COLON: Santa Rita East Ridge lumber road, 23 Feb. 1968, *Correa 738* (MO—2 sheets). DARIÉN: Parque Nacional del Darién, ridge between Río Topalisa & Río Pucuro, ca. 17 km E of Pucuro, 8°03.5′N, 77°17′W, 850 m, 17 Oct. 1987, *Hammel et al. 16276* (MO); S of El Real, region called Alturas de Nique, near Cana mine, 07°45′N, 77°40′W, 650–800 m, 21 Aug. 1987, *McPherson 11518* (MO, TEX). PANAMÁ: Pilota de Toro, 4 Dec. 1977, *Folsom et al. 6776* (TEX). SAN BLAS: forests around Puerto Obaldía, San Blas coast, 0–50 m, Aug. 1911, *Pittier 4319* (F). VENEZUELA. MIRANDA: Cerros del Bachiller, western sector: virgin evergreen forest, between base and summit, above Quebrada Bachiller, S of Caño Rico and Bachiller, 11 km (by air) SSE of El Guapo, 10°6–7′N, 65°53′W, 20 690 m, 27–28 Mar. 1978, *Steyermark & Davidse 117010* (MO). ZULIA: 6 km W of main road and 2 km S of Río Catatumbo, ca. 20–100 m, 9°6′N, 72°42′W, 29 Mar. 1982, *Liesner & González 13348* (LL, MO). COLOMBIA. CHOCÓ: trail from Río Tigre base camp up Serranía del Darién W of Unguía, 300 600 m, 17 July 1975, *Gentry & Aguirre 15286A* (NY, MO).

Ampelocera macrocarpa is characterized by its large fruits with a very thick endocarp, relatively short petioles with flaky red epidermis, and short style branches. The leaves of this species are bright metallic blue when young and have strongly oblique bases. On saplings and young branches the leaves are extremely long and narrow (22–38 cm long). *Ampelocera macrocarpa* appears to be most closely related to *A. edentula* by virtue of the characters given in the key.

8. Ampelocera macphersonii Todzia, sp. nov. TYPE. Panama. Panamá: Canal Area, on hilltop W of canal and Panama City, 8°50′N, 79°34′W, 300 m, 3 May 1987, *McPherson & Stockwell 10901* (holotype, MO; isotypes, NY, PMA, TEX). Figure 6.

Arbores foliis ellipticis chartaceis. Inflorescentiae breves, racemi ramosi vel simplices, 0.8–1.2 cm longi, flores 3–6. Sepala 4, in dimidio distali villosa vel sericea, stamina ca. 16, filamenta 1.5–2 mm longa. Fructus aurantiaci, dense pubescentes, ramis styli persistentibus, transverse obovoidei valde asymmetrici, endocarpium tenue.

Trees up to 20 m tall; younger branches dark brown, puberulent; older branches gray to brown, glabrous, sparsely lenticulate; stipules narrowly triangular to lanceolate, 2–4 mm long, villous. Leaf blades elliptic, 7.5–21 × 4–7 cm, the apex acute or with acuminate tips up to 1.2 cm long, the base rounded to subcordate, sometimes oblique, the margins entire, dark green and shiny above, paler beneath, drying chartaceous, smooth and glabrous above and beneath, light brown to tan, unevenly colored on drying, lateral veins 5–10, arcuate; petioles 0.5–1 cm long, sparsely puberulent, with a smooth epidermis, drying dark brown. Inflorescences axillary, short, simple or compound dichasia, often paired at the node, borne on leafy branches; rachises 0.8–1.2 cm long, strigose to sparsely villous, with 3–6 flowers; subtending floral bracts 1–2 mm long, glabrous. Flowers not seen (the following description based on persistent floral parts on fruits); calyx ca. 2 mm long, the lobes 4, villous to sericeous in distal half; stamens ca. 16; filaments 1.5–2 mm long, linear-lanceolate, slender throughout; anthers ca. 1–1.5 mm long, connective not extended. Fruits yellow to orange, strongly asymmetrical, transversely obovoid, 1.2–1.6 cm long, 1.6–1.8 cm broad, densely pubescent, sweet, with persistent style branches 2 mm long; endocarp thin, less than 0.5 mm thick.

Common name and uses. Panama: Carasuma. Used as firewood.

Distribution, habitat, and phenology. This species occurs in Panama, northern Colombia, and northwestern Venezuela (Fig. 4). It is found in undisturbed deciduous forest and in moist forest, sometimes on limestone. Fruiting is in May, June, and October on leafy stems.

Representative specimens examined. PANAMA. DARIÉN: 110 mi. from Bayano Dam Bridge, vicinity of Canglón, trail to S from road to good forest, 50 ft., 14 May 1980, *Antonio 4568* (MO); Loma Piriauqe, 14 Apr. 1966, *Duke 8108* (MO); Río Pucro, below village of Pucro, 23 June 1967, *Duke 13126* (MO). COLOMBIA. BOLÍVAR: Loma de los Colorados, Mun. San Juan Nepomuceno, ca. 2 km S of San Juan, Cartagena Magangue rd., 9°58′N, 75°10′W, 200 250 m, 7 May 1987, *Gentry & Cuadros 57496* (MO). SUCRE: Estación de Primatas de Colosó, 340 m, 75°30′W, 9°30′N, 17 Nov. 1981, *Gentry et al. 34819A* (MO). VENEZUELA. ZULIA: Dtto. Mara, vía entre Embalse Manuelote y el Campamento Carichuano, ca. 1–4 km al sureste de Carichuanao, al borde de la vía, en zona de bosque seco, 100 m, 29 Oct. 1982, *Bunting & Smith 11924* (NY); Dtto. Mara, en el área de reserva carbonífera de Guasare, unos 1.5 km al suroeste del Campamento

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FIGURE 5. *Ampelocera longissima.* a. Fertile branch showing inflorescences.—b. Perfect flower. (a & b from *Cerón 2633* TEX.) c. Fruit (from *Palacios et al. 519* MO.)

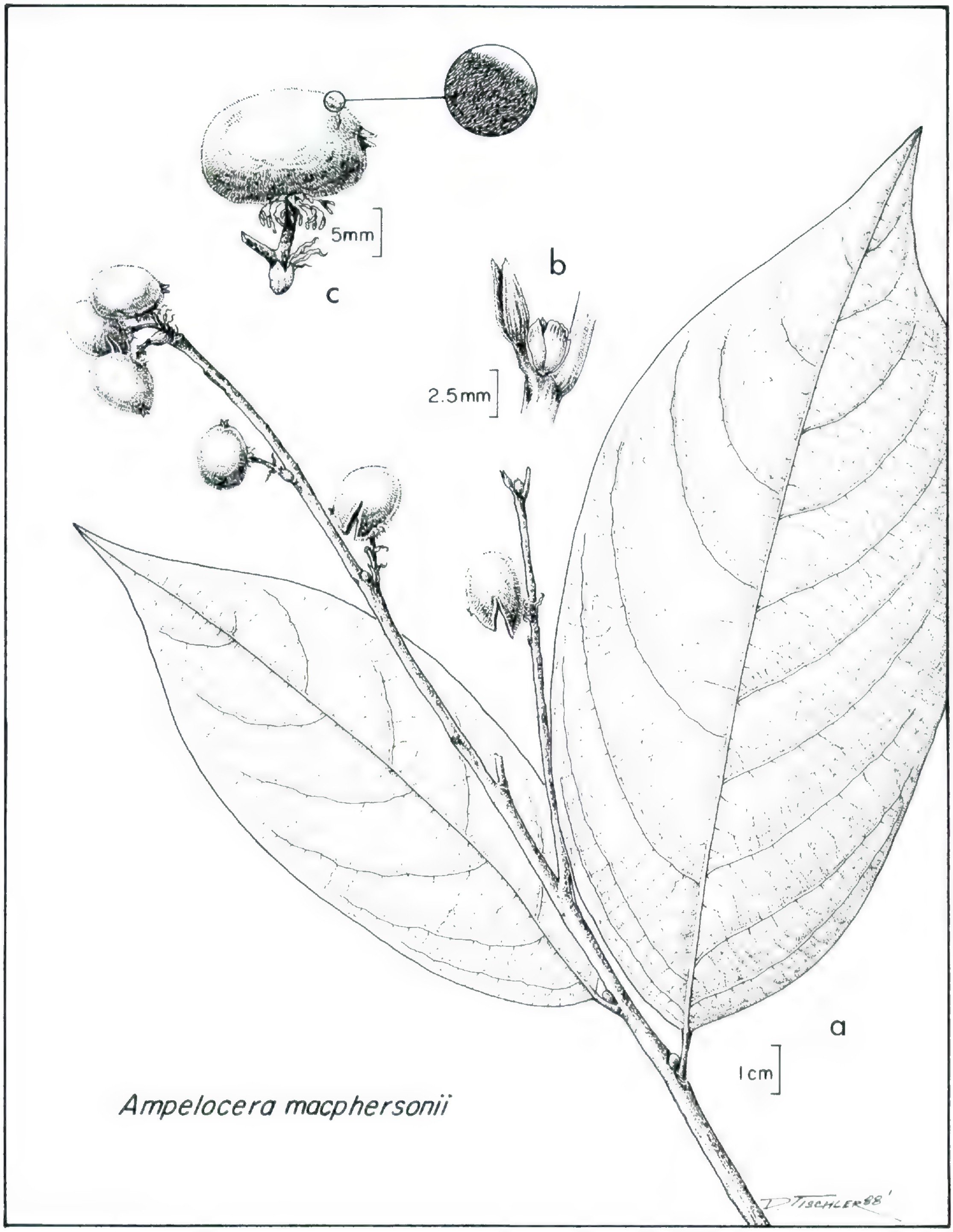

FIGURE 6. *Ampelocera macphersonii*.—a. Branch with infructescences.—b. Close-up of stipules.—c. Mature fruit with pubescence enlarged in inset. (a–c from *McPherson & Stockwell 10901* TEX.)

Carichuano, en bosque seco pero poco decíduo, 150 m, 28 Oct. 1982, *Bunting & Smith 11964* (NY); Dtto. Mara, semievergreen forest bordering Caño del Norte, tributary to Río Socuy, 6 km S of Corpozulia, Campamento Carichuano, 10°58′N, 72°16′W, *Steyermark et al. 122921* (MO); Dtto. Mara, undisturbed deciduous forest remnant on low hills, 4 km (by air) N of Corpozulia, Campamento Carichuano, 11°2′30″N, 72°16′30″W, 150–200 m, 1 June 1980, *Steyermark et al. 123074* (MO, NY); Cerro Cinco de Julio, W slopes to Río Guasare,

8.5–10 km (by air) NW Corpozulia, Campamento Carichuano, 11°2′30″N, 72°21–22′W, 120–400 m, 4 June 1980, *Steyermark et al. 123297* (MO).

Ampelocera macphersonii is distinctive in having entire leaves and small, orange, strongly asymmetrical, transversely obovoid fruits. By virtue of its 16 stamens it is allied to *A. pubescens*, *A. glabra*, and *A. ruizii*. It differs from *A. pubescens* by having glabrous leaves and racemose (not glomerulate) inflorescences, and from both *A. glabra* and *A. ruizii* by having entire (not dentate) leaves and larger fruits. Vegetatively *A. macphersonii* resembles *A. longissima* but can be separated easily by the characters provided in the key. The occurrence of *A. macphersonii* in deciduous and semievergreen forests is unusual for the genus.

This species is named in honor of Dr. Gordon McPherson whose collecting efforts in Panama have yielded many new and interesting plants.

9. Ampelocera ruizii Klotzsch, Linnaea 20: 541. 1847. TYPE. Peru: *Ruiz & Pavón s.n.* (holotype, B).

Ampelocera verrucosa Kuhlm., Arch. Jard. Bot. Rio de Janeiro 4: 352. 1925. TYPE. Brazil. Pará: Itaituba, Rio Tapajoz, 20 Oct. 1922, *Ducke 19135* (holotype, B; isotypes, K, US).

Plagioceltis dichotoma Mildbr. ex Baehni, Contrib. Field Mus. Nat. Hist., Bot. Ser. 13: 272. 1937. TYPE. Peru: *Ruiz & Pavón s.n.* (holotype, MA, n.v.; isotype, F).

Trees 10–35 m tall; trunk up to 2.5 m dbh, with brown, flaky bark, and medium-sized buttresses; younger stems brown, glabrous to sparsely puberulent; older stems gray, glabrous; stipules 3–5 mm long, lanceolate, sparsely puberulent to pilose. Leaf blades elliptic to obovate, 6.5–13 × 2.5–6.5 cm, the acuminate tips 0.5–1 cm long and 2–3 mm broad, attenuate to rounded at the base, often oblique, drying stiffly chartaceous to subcoriaceous, glabrous and smooth above and beneath, with 3–5 teeth per side, occasionally entire; lateral veins 5–8, arcuate, raised beneath, puberulent beneath when young, becoming glabrous with age; petioles 0.5–1 cm long, sparsely puberulent, drying dark brown. Inflorescences of axillary, compound dichasia, on leafless branches, apparently with bisexual and staminate flowers (staminate flowers not seen); rachises 0.9–1.5 cm long, sparsely puberulent, with 8–15(–23) flowers. Flowers subtended by ovate bracteoles, these 1.5–2 mm long, glabrous to sparsely puberulent; calyx 2–2.5 mm long, the lobes 4, united at the base, sparsely villous; stamens 16 in perfect flowers; filaments ca. 3 mm long, linear, slender throughout; anthers ca. 1 mm long, the connective extended into an apicule ca. 0.5 mm long; ovary very densely pilose, with style branches 3–5 mm long, united in lower 1 mm. Fruits yellow, asymmetrical, transversely ellipsoid, 1–1.2 cm tall, 1.2–1.6 cm broad, slightly flattened, densely pilose, with persistent style branches; endocarp thin, ca. 0.3 mm thick.

Distribution, habitat, and phenology. This species is known from 0–500 m in lowland rainforest in Brazil, Peru, and Bolivia (Fig. 3). Flowering time is not known; fruiting is reported from August to January.

Additional specimens examined. BRAZIL. ACRE: near mouth of Rio Macauhan (tributary of Rio Yaco), 7 Aug. 1933, *Krukoff 5316* (MO). MATO GROSSO: Serra do Cachimbo, 12 Nov. 1976, *Nascimento 445* (MG); Aripuanã, Projeto Juina, 6 June 1979, *Silva & Rosário 4805* (NY). PARÁ: Fazenda Rio Dourado, Rio Dourado, afluente do Rio Fresco, 28 June 1978, *Pires 16046* (MG); basin of Rio Xingu, Gleba Bacaja, lote 88, just below mouth of Rio Bacaja, 27 Nov. 1980, *Prance et al. 26502* (MO). PERU. LORETO: Veradero de Mazán from the Río Amazonas to Río Napo, 22 Aug. 1972, *Croat 19516* (MO). MADRE DE DIOS: Parque Nacional del Manu, Río Manu, vicinity of Cocha Cashu Station, 18 Nov. 1976, *Foster & Terborgh 5209* (F, US); 23 Nov. 1976, *Foster & Terborgh 5239* (F, NY); 350 m, 27 Nov. 1980, *Foster 5956* (F, MO); 380 m, 22 Oct. 1979, *Gentry et al. 27135* (MO). SAN MARTÍN: Prov. Mariscal Cáceres, Dtto. Uchiza, Caserío Nueva Unión Huicte, 450–500 m, 1 Aug. 1974, *Schunke 7964* (MO). BOLIVIA. SANTA CRUZ: Prov. Sara, Buena Vista, 450 m, *J. Steinbach 1309* (GH, NY, MO).

Ampelocera ruizii is distinguished from *A. glabra* by having smaller fruits and longer inflorescences. They are similar in having dentate, glabrous leaves and transversely ellipsoid, asymmetrical fruits.

Baehni (1937) separated *Ampelocera* from *Plagioceltis* and the other Peruvian genera of the Ulmaceae on the basis of the former having twice as many stamens as the latter. The isotype of *Plagioceltis dichotoma* at F, however, has a greater number of stamens than perianth parts. Since stamen number is not mentioned in the *Plagioceltis* description, Baehni's misplacement of the genus in the *Flora of Peru* key alongside genera possessing equal numbers of stamens and perianth segments is probably due to Mildbraed's inadequate notes (Gentry, 1983). As mentioned under taxonomic history, the similarity of the unnumbered Ruiz & Pavón type specimen of *Plagioceltis dichotoma* and the type of *Ampelocera ruizii* is the most likely because both originated from the same collection.

EXCLUDED TAXA

Ampelocera crenulata Urban, Repert. Spec. Nov. Regni Veg. 15: 399. 1919. TYPE. Cuba: *Ra-*

mon de la Sagra 413 (B, n.v.). = *Casearia praecox* Griseb. (Flacourtiaceae).

Ampelocera hondurensis J. D. Smith, Bot. Gaz. (Crawfordsville) 54: 244. 1912. TYPE. Honduras: Dept. Santa Bárbara, San Pedro Sula, 200 m, May 1890, *Thieme 5606* (US—3 sheets). = *Achatocarpus nigricans* Triana (Achatocarpaceae).

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POLLEN MORPHOLOGY OF THE SHRUBBY IRIDACEAE *NIVENIA, KLATTIA,* AND *WITSENIA*[1]

Peter Goldblatt[2] *and*
John C. Manning[3]

ABSTRACT

Nivenia, Klattia, and *Witsenia,* a monophyletic assemblage of 13 species of the southwestern Cape, South Africa, have pollen grains with sculpturing similar to the basic type for Iridaceae (and for the monocots). The nearly spherical grains have a broad sulcus and reticulate to microreticulate exine. The supratectal gemmae, found only in *Witsenia,* are unique in Iridaceae. In *Nivenia* species the walls of the reticulum are lightly sculptured, sometimes laterally verrucate or micropapillate, the degree of sulpturing varying with the species. The pollen grains differ in size for all the species examined, and in four of the five heterostylous species of *Nivenia* there are statistically significant size differences between the long- and short-styled morphs.

The genera *Nivenia* (nine species), *Klattia* (three species), and *Witsenia* (one species) comprise a natural alliance of Iridaceae, restricted in distribution to the southwestern Cape region of southern Africa. Uniting the genera are the following specialized characters: a shrubby evergreen habit; a woody rootstock and aerial stems both having appreciable secondary growth; nonfugacious flowers with a well-developed perianth tube and bearing septal nectaries; tangentially compressed seeds; and a specialized leaf anatomy with submarginal sclerenchyma and girders produced by the extension to the epidermis of the sclerenchyma surrounding some of the vascular bundles (Goldblatt, in prep.; Goldblatt & Bernhardt, in press; Manning & Goldblatt, in prep.; Rudall & Burns, 1989).

This study of the pollen morphology of the three genera was undertaken in conjunction with a broadly based investigation of their systematics and reproductive biology, the latter focusing particularly on the heterostylous condition in five species of *Nivenia.* These distylous species are made up of populations of plants with either long styles and short stamens or short styles and long stamens. In many plants heterostyly is often associated with pollen dimorphism (Ganders, 1979; Richards, 1986) and this phenomenon has been considered in our examination of exine structure. The homostylous *Klattia* and *Witsenia* were included in our study for the sake of completeness. *Klattia* and *Witsenia* are probably bird pollinated (Rebelo, 1988; Goldblatt, in prep.) in contrast to species of *Nivenia* which are pollinated by long-tongued insects, either anthophorid bees or nemastrinid flies (Goldblatt & Bernhardt, in press). Any differences in the pollen of the three genera may be significant in light of the differences in their pollination biology.

MATERIALS AND METHODS

Pollen taken from herbarium specimens of 11 species (Table 1) was treated in one of two ways. For examination of exine sculpturing alone, untreated grains were glued on aluminum stubs and sputter coated with gold. For examination of whole grains, unacetolyzed pollen was rehydrated by warming in 10% KOH for ca. 10 minutes, then dehydrated in ethanol, rinsed twice in 50% acetone

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TABLE 1. Species of *Vivenia*, *Klattia*, and *Witsenia* studied with locality and voucher data. All localities are in the Cape Province, South Africa. Herbarium vouchers are preserved at MO, NBG, and PRE.

Klattia	
K. flava (G. Lewis) Goldbl.	slopes of Landdrost Kop, *Goldblatt 8347*
K. partita Ker ex Baker	Langeberg, Swellendam, *Goldblatt 8698*
K. stokoei L. Guthrie	Steenbras Ridge, *Goldblatt 8342*
Vivenia	
Distylous Species	
V. binata Klatt	Swartberg Pass, upper slopes, *Goldblatt 7959*
V. capitata (Klatt) Weim.	Little Karoo, Rooiberg slopes, *Vlok 1794*
V. corymbosa (Ker) Baker	Bains Kloof, Tweede Tol camp, *Goldblatt 7631*
V. dispar N. E. Br.	Olifantskloof, Riviersonderend, *Goldblatt 8480*
V. stenosiphon Goldbl.	Klein Swartberg, Buffelsrivierpoort, *Goldblatt & Manning 8864*
Homostylous Species	
V. concinna N. E. Br.	Viljoens Pass, *Goldblatt 7624*
V. fruticosa (L. f.) Baker	Swellendam Langeberg, *Esterhuysen 36149*
V. levynsiae Weim.	Highlands hiking trail, Caledon Div., *Goldblatt 8463*
V. stokoei (L. Guthrie) N. E. Br.	Palmiet R. Mountains, *Levyns 5344*
Witsenia	
W. maura L.	Bettys Bay, *Goldblatt & Gentry 1600*

and four times in 100% acetone, and critical point dried before mounting and coating. Specimens were observed at an accelerating voltage of 15–20 kV. *Klattia partita* and *K. flava* are listed in Table 1 but were not included in the SEM study. Descriptive terminology used follows Walker & Doyle (1975). Pollen grains mounted in FLP orcein were measured under the light microscope. Measurements (Table 2) represent the means of 10 grains except in the case of the heterostylous species

TABLE 2. Pollen characteristics of *Nivenia*, *Klattia*, and *Witsenia*. Only the equatorial diameter is listed. For heterostylous species of *Vivenia* the diameter of the long-styled morph precedes that of the short-styled morph. The asterisk (*) indicates species not examined under the scanning electron microscope (SEM).

Species	Shape	Diameter μm	Sculpturing	Muri
Nivenia				
N. binata	spherical	51.26/55.55	reticulate	granulate and ridged
N. capitata	spherical	59.88/62.79	reticulate	granulate
N. concinna	spherical	71.43	microreticulate	granulate
N. corymbosa	spherical	44.69/49.69	reticulate	granulate
N. dispar	spherical	53.50/52.02	reticulate	*
N. fruticosa	spherical-subprolate	63.93	microreticulate	granulate
N. levynsiae	spherical	65.00	reticulate	granulate
N. stenosiphon	spherical	65.00/68.69	reticulate	granulate and ridged
N. stokoei	spherical	61.43	reticulate	granulate
Klattia				
K. flava	subprolate	63.89	reticulate	*
K. partita	subprolate	64.12	reticulate	*
K. stokoei	spherical	80.16	reticulate	smooth
Witsenia				
W. maura	oblate-spheroidal	81.55	microreticulate with supratectal gemmae	granulate

TABLE 3. Pollen size comparison between long- and short-styled morphs of the five distylous species of *Nivenia*: N = total number of pollen grains measured from three (or four) individuals; $\bar{X}$ = mean pollen grain diameter in μm; S.D. = standard deviation; P = probability (from Goldblatt & Bernhardt, in press).

	Pollen morph measurements (equatorial diameters)						
	Long-styled			Short-styled			
Species	N	$\bar{X}$	S.D.	N	$\bar{X}$	S.D.	P[1]
N. binata	39	51.26	3.30	30	55.55	5.12	0.001[2]
N. capitata	30	59.88	3.75	30	62.79	4.44	0.008[2]
N. corymbosa	40	44.69	3.80	40	49.69	2.78	0.000[2]
N. dispar	30	53.50	3.36	30	52.02	4.07	0.128[3]
N. stenosiphon	30	65.00	3.75	30	68.69	4.07	0.014[2]

[1] Two-tailed *t*-test.
[2] Significant.
[3] Not significant.

(listed in Table 3), where nine or ten grains in three or four individuals per style morph were measured (Table 3).

OBSERVATIONS

Grains of all species of all three genera are more or less spherical (Figs. 1–6), ranging from near prolate to near oblate depending on the species (Table 2). The monosulcate grains have a prominent elliptic to oblong sulcus (Figs. 2, 5, 6); they are tectate-perforate in *Witsenia* with a microreticulate tectum (Figs. 4–6, 9, 10) and semitectate with a reticulate tectum in *Nivenia* and *Klattia* (Figs. 1–3, 7, 8). The floors of the lumina in all the species are granulate (e.g., Fig. 7). The muri are smooth in *Klattia* (Fig. 8) but minutely granulate in *Nivenia* and *Witsenia* (e.g., Figs. 7, 9, 10). In *N. binata* and *N. stenisiphon* the sides of the muri are irregularly ridged (e.g., Fig. 7) (Table 2).

In *Nivenia* the luminae range from about as wide as the muri (microreticulate), e.g., *N. concinna* (Fig. 12), to about twice as wide (reticulate), or up to four times as wide in *N. capitata* (Fig. 11).

Supratectal gemmae (ca. 4 μm in diameter) are restricted to *Witsenia* (Figs. 5, 6) and are scattered more or less evenly across the surface.

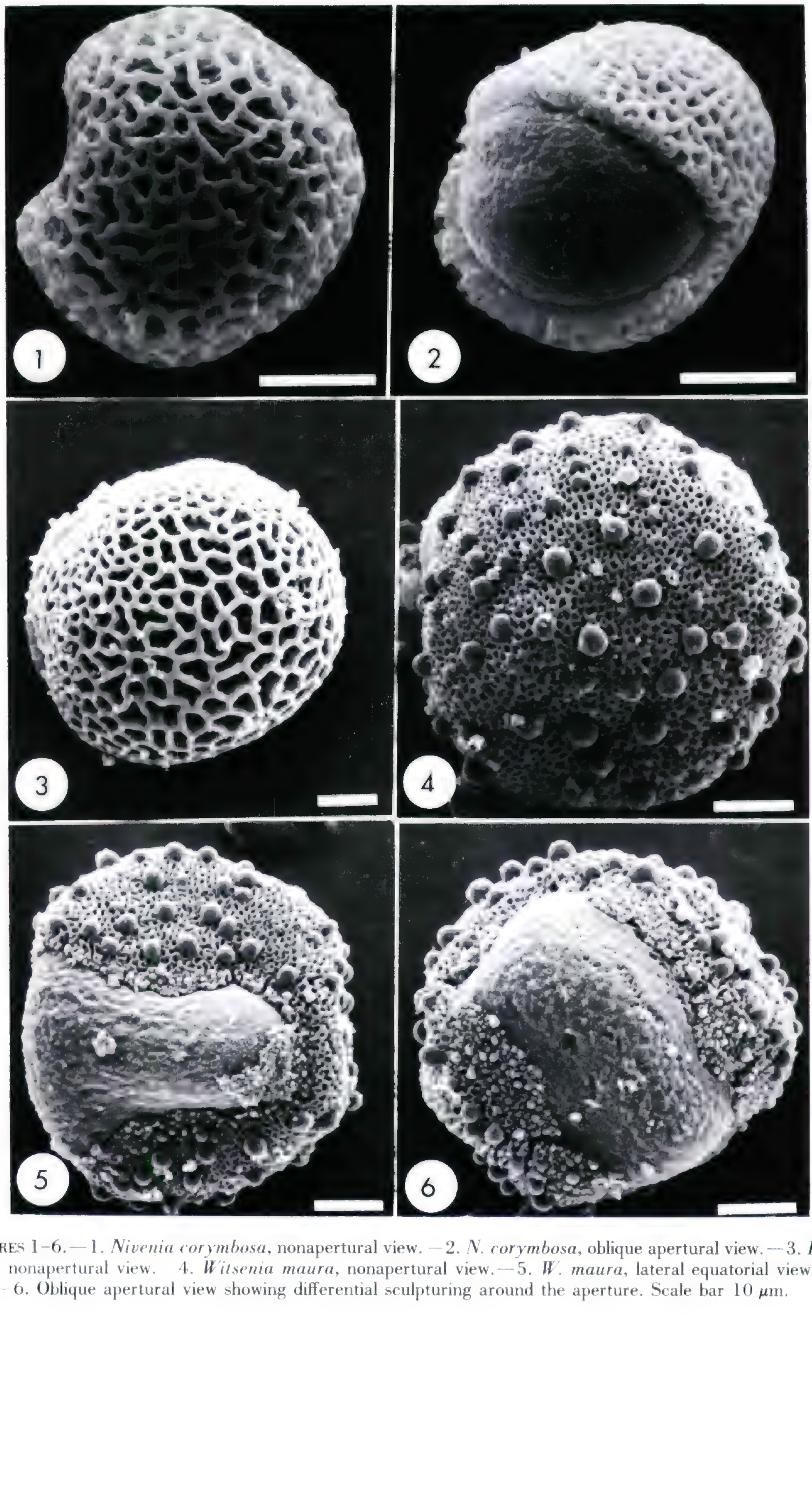
The exine sculpturing ends abruptly at the sulcus (Fig. 2) in *Nivenia* and *Klattia*, but in *Witsenia* the muri become disrupted into pilae and baculae (Fig. 10) along the sulcus margins.

Pollen grain diameter ranges from 44.69 μm in the long-styled morph of *Nivenia corymbosa* to over 80 μm in *Klattia stokoei* and *Witsenia maura* (Table 2). Differences in pollen grain size among the species correlate generally with differences in style length. *Klattia* and *Witsenia* have the longest styles and largest pollen in the group, and *K. stokoei* the longest styles in that genus. *Nivenia levynsiae* and *N. concinna*, however, do not follow this trend, having shorter styles than one would expect from their comparatively large pollen grains.

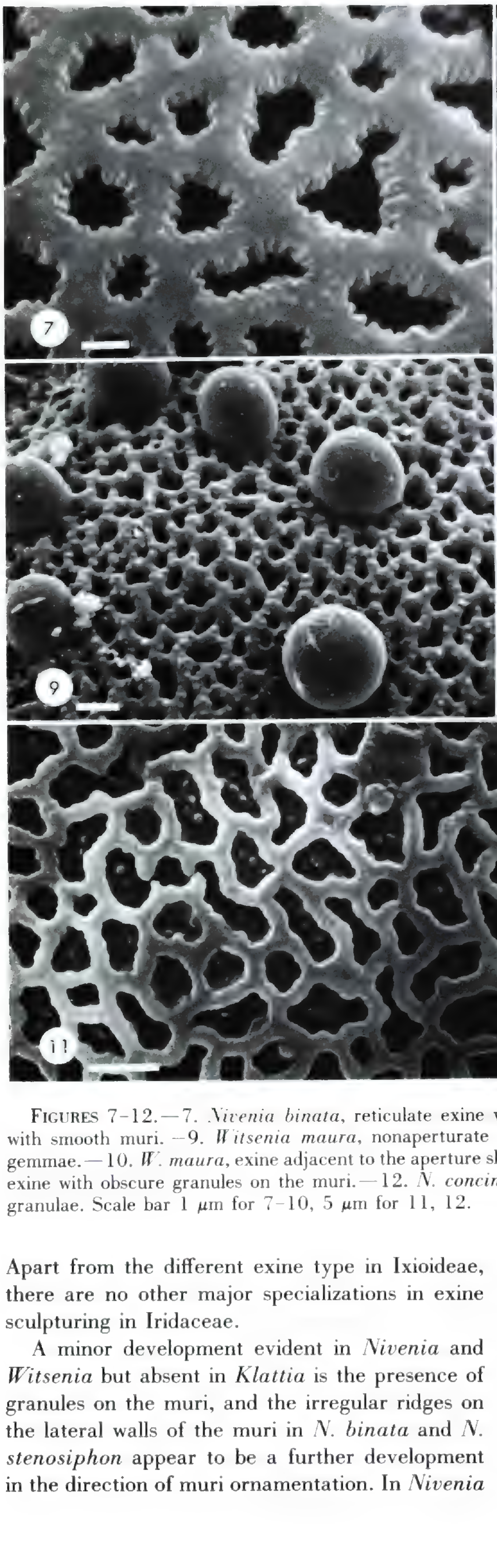
In four of the five heterostylous species of *Nivenia* the grains of the long-styled morph are significantly smaller (Table 3). Pollen size differences between morphs of the four heterostylous species also correlate directly with differences in style length in the complementary morph (Goldblatt & Bernhardt, in press). Exine sculpturing does not differ between morphs within the heterostylous species, but there are notable differences between the species. *Nivenia binata* exhibits the greatest degree of sculpturing and *N. capitata* the least (Figs. 7, 11).

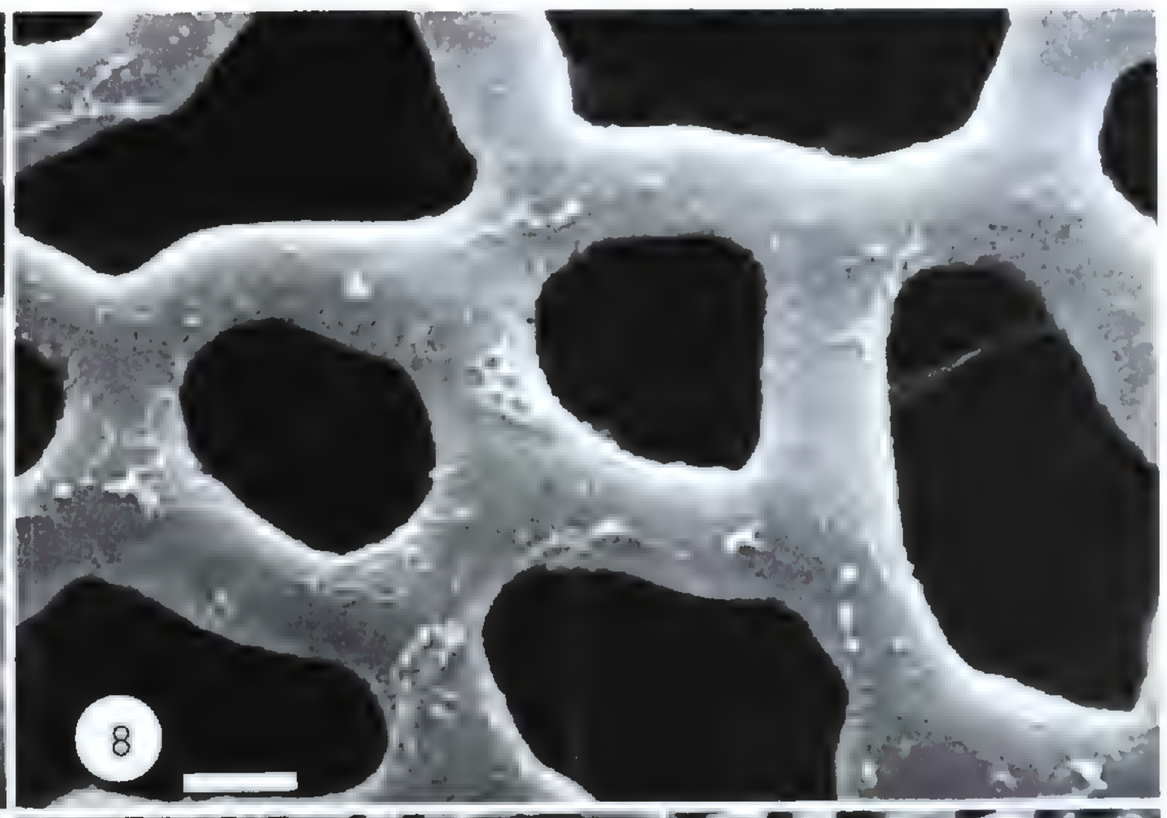
DISCUSSION

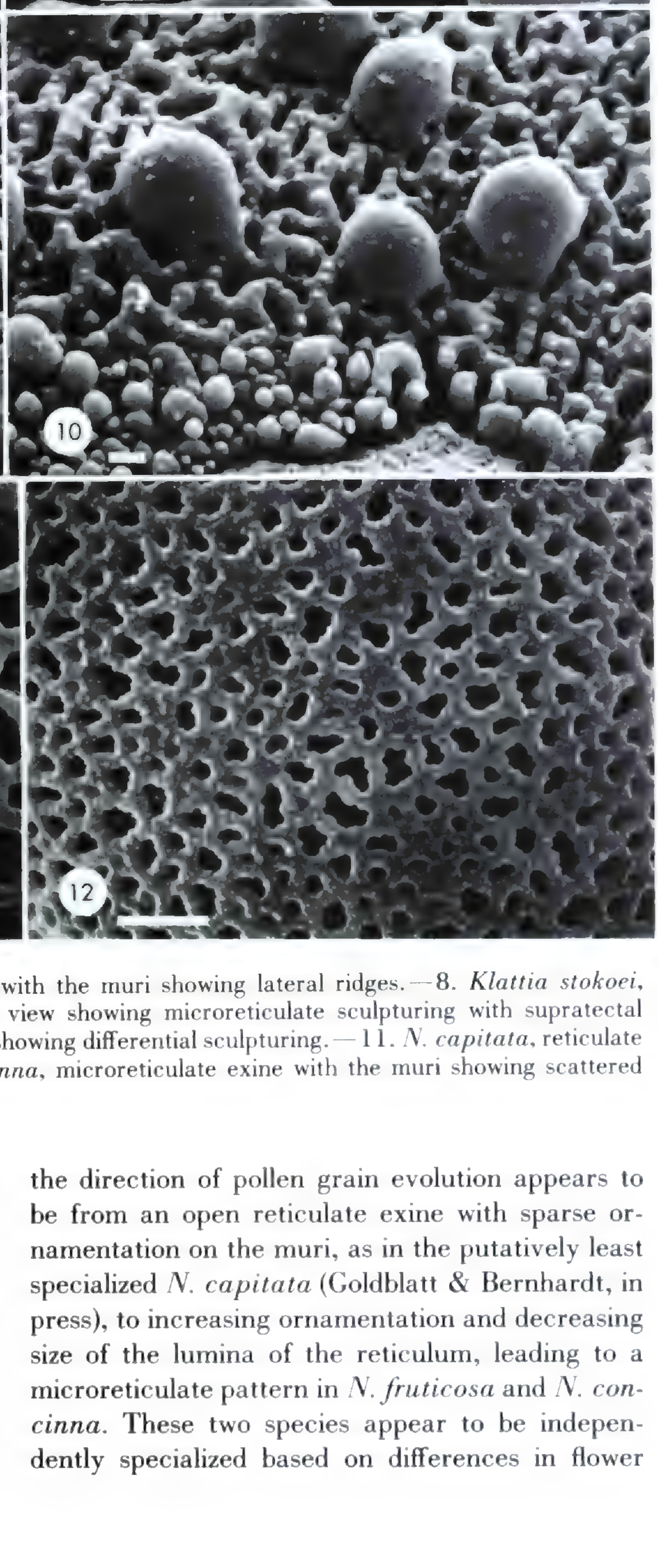
The pollen grains of *Nivenia* and *Klattia* conform fairly closely to the presumed basic type for Iridaceae and for the monocots in general, in which reticulate grains appear to be fundamental (Schulze, 1971; J. Walker, pers. comm.). Similar grains are found in species of *Aristea* (likewise Nivenioideae) and in numerous genera of Iridoideae, excluding *Iris*, in which there are multiple unusual specializations, particularly in the form of the aperture (Schulze, 1971). A group of New World genera of Iridoideae belonging to the tribe Tigridieae stand out in having bisulcate grains (Schulze, 1971), clearly a secondary condition in the tribe. Members of subfamily Ixioideae also differ markedly from this basic pollen type, having a tectate-microperforate exine with supratectal spinules (Erdtman, 1952; Schulze, 1971; Goldblatt & Stein, 1988).



FIGURES 1–6.—1. *Nivenia corymbosa*, nonapertural view. —2. *N. corymbosa*, oblique apertural view.—3. *Klattia stokoei*, nonapertural view. 4. *Witsenia maura*, nonapertural view.—5. *W. maura*, lateral equatorial view of the sulcus.—6. Oblique apertural view showing differential sculpturing around the aperture. Scale bar 10 μm.







FIGURES 7–12.—7. *Nivenia binata*, reticulate exine with the muri showing lateral ridges.—8. *Klattia stokoei*, with smooth muri. —9. *Witsenia maura*, nonaperturate view showing microreticulate sculpturing with supratectal gemmae.—10. *W. maura*, exine adjacent to the aperture showing differential sculpturing.—11. *N. capitata*, reticulate exine with obscure granules on the muri.—12. *N. concinna*, microreticulate exine with the muri showing scattered granulae. Scale bar 1 μm for 7–10, 5 μm for 11, 12.

Apart from the different exine type in Ixioideae, there are no other major specializations in exine sculpturing in Iridaceae.

A minor development evident in *Nivenia* and *Witsenia* but absent in *Klattia* is the presence of granules on the muri, and the irregular ridges on the lateral walls of the muri in *N. binata* and *N. stenosiphon* appear to be a further development in the direction of muri ornamentation. In *Nivenia* the direction of pollen grain evolution appears to be from an open reticulate exine with sparse ornamentation on the muri, as in the putatively least specialized *N. capitata* (Goldblatt & Bernhardt, in press), to increasing ornamentation and decreasing size of the lumina of the reticulum, leading to a microreticulate pattern in *N. fruticosa* and *N. concinna*. These two species appear to be independently specialized based on differences in flower

and inflorescence morphology (Goldblatt, in prep.), and their similar pollen sculpturing is presumably convergent. The occurrence of ridged muri in *N. binata* and *N. stenosiphon*, however, appears to be an indication of close taxonomic relationship as it is correlated with two specialized characters restricted to these species: blue anthers and pollen, and large, dry, brown, crisped bracts (Goldblatt, in prep.).

The grains of *Witsenia*, with their large supratectal gemmae, are clearly derived. These distinctive gemmae, observed by Schulze (1971) under light microscopy, are unique in Iridaceae and make the pollen grains of this genus immediately recognizable. The presence of an unusual exine in *Witsenia* emphasizes the taxonomic isolation of this genus, distinctive in its unusual floral and inflorescence morphology. Any significance in the elaborate exine sculpturing of *Witsenia* in relation to its mode of pollination remains to be demonstrated.

Pollen sculpturing does not provide any character uniting the three shrubby genera of Cape Iridaceae, but within the alliance trends of specialization are evident in *Nivenia*, and the supratectal gemmae in *Witsenia* constitute an autapomorphy for this genus.

Mulcahy's (1965) report of a difference in size between the grains of the short- and long-styled morphs of *N. binata* is substantiated by our observations, although we noted a smaller size difference (ratio of grain size between short- vs. long-styled morph 1.11 compared with 1.3 reported by Mulcahy). We were unable to confirm Mulcahy's observation of differences in the size of the lumina of the exine reticulum between short- and long-styled grains in *N. binata*, nor did we record measurable differences in lumina size in the other heterostylous species.

The close similarity of the exine sculpturing and small, though statistically significant, differences in pollen grain size between the two style morphs in four of the observed heterostylous species of *Nivenia* are consistent with similar observations in many heterostylous taxa (Ganders, 1979; Richards, 1986). In *Nivenia* the morphological differences between the style morphs of the heterostylous species appear not to be accompanied by the expected self-incompatibility characteristic of most heterostylous plants (Goldblatt & Bernhardt, in press).

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SEED MORPHOLOGY OF *SISYRINCHIUM* (IRIDACEAE—SISYRINCHIEAE) AND ITS ALLIES[1]

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ABSTRACT

Seeds of 25 species of sects. *Sisyrinchium*, *Echthronema*, *Eriphilema*, and *Nuno* of the large North and South American genus *Sisyrinchium* were examined using the scanning electron microscope and light microscope and compared with seeds of representative species of related genera in tribe Sisyrinchieae. Seeds of sects. *Sisyrinchium* and *Echthronema* are more or less rounded, are blackish with reticulate surfaces, and often have a large depression, the umbilicus, along the raphe. Species of sects. *Eriphilema* and *Nuno* have brown, more or less angular seeds with a strongly reticulate surface, and they lack an umbilicus. The genera *Libertia*, *Ona*, *Orthrosanthus*, *Phaiophleps*, *Solenomelus*, and *Tapeinia* have similar brown, usually angular seeds without an umbilicus. Seeds of *Solenomelus* have distinctive longitudinal lines of nearly circular depressions along the seed body, and one species has seeds with a large, half-circumferential wing. Seeds of sects. *Sisyrinchium* and *Echthronema* appear to embody important, probably derived specializations. Based on seed characters, sects. *Eriphilema* and *Nuno* seem more closely related to the other genera of Sisyrinchieae, particularly *Phaiophleps*, than to sects. *Sisyrinchium* or *Echthronema*.

In the course of a systematic study of the New World genus *Sisyrinchium* for *Flora Mesoamericana* (Henrich & Goldblatt, 1987, in press a) and *Flora de Nicaragua* (Henrich & Goldblatt, in press b) our attention was drawn to the unusual rounded, blackish, umbilicoid seeds of the genus. The seeds were novel to us in Iridaceae and distinguish *Sisyrinchium* from all other genera in the family. Seed characters were also useful in establishing species limits within the genus. We found no adequate description or record of *Sisyrinchium* seeds in the literature, and Huber (1969) did not specifically describe them in his extensive study of the seeds of lilioid monocots. However, Cholewa & Henderson (1984) included SEM examination of six North American species of sect. *Sisyrinchium*, and Rodriguez (1986) mentioned color and surface texture in his revision of the Chilean species of *Sisyrinchium*.

With this background we undertook the present survey of the seeds of *Sisyrinchium* and its allies in tribe Sisyrinchieae of subfamily Iridoideae (classification after Goldblatt, 1990). *Sisyrinchium* as presently constituted (Bentham & Hooker, 1883; Baker, 1892) comprises over 100 species. Our study includes a small but representative sample of the total and is sufficient to satisfy our purpose in documenting the basic seed types found in the genus and to allow a valid comparison with allied genera. We included taxa from the two large and apparently natural sects. *Sisyrinchium* (= sect. *Bermudiana* of several authors) and *Echthronema* (Bentham & Hooker, 1883) and the smaller sects. *Eriphilema* and *Nuno*. Related genera of tribe Sisyrinchieae (sensu Goldblatt, 1990) examined for comparison were *Libertia*, *Ona*, *Orthrosanthus*, *Phaiophleps*, *Solenomelus*, and *Tapeinia*. Seeds of *Chamelum*, which belongs in this alliance, were not available. The southern African *Bobartia* and the Australian *Diplarrhena*, the remaining genera of the tribe, appear to be more distantly related to the *Sisyrinchium* complex and neither was included in our survey. Sections *Eriphilema* and *Nuno* and the other genera examined have seeds

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fairly typical of Iridaceae in their brownish color and more or less angular shapes (Huber, 1969) and are very different from the seeds found in sects. *Sisyrinchium* and *Echthronema*.

Materials and Methods

Mature seeds were assembled from herbarium material, and in a few cases fresh field-collected seeds were examined (Table 1). We excluded seeds that appeared deformed or showed signs of fungal infection. Seeds were examined under the light microscope for size and color, and then prepared for the scanning electron microscope (SEM) study by attachment with water-soluble white glue to aluminum stubs and sputter coating with 500–700 Å of gold. They were examined in an ISI Super IIIA SEM at 15 kV.

Observations

color

Seeds of all the species of *Sisyrinchium* sects. *Sisyrinchium* and *Echthronema* are blackish (Table 2). Surface color intensity ranges from a fairly glossy, intense black to matte and dark gray. As we used seeds almost exclusively from herbarium specimens, we are uncertain how much significance to attribute to the color variation as ripening may have been affected by the rapid drying, and the final seed appearance may thus not be the same as in nature.

Seeds of *Sisyrinchium* sects. *Eriphilema* and *Nuno* and of the genera *Libertia*, *Ona*, *Orthrosanthus*, *Phaiophleps*, *Solenomelus*, and *Tapeinia* are shades of brown (Table 2), most often red-brown, presumably the basic condition in the family (Huber, 1969) and an indication of the presence of the pigment phlobaphene. Some species, for example *Orthrosanthus occissapungus*, have light brown seeds, an apparently significant character at the species level.

shape and size

The number of seeds per locule of the three-chambered capsules of Sisyrinchieae was not recorded in our study, but all species examined have multiseeded loculi. The effect of crowding and alteration of shape by mutual pressure within the locules (Huber, 1969; Wagner & Goldblatt, 1984) was noted to some degree in most species. Angular seeds characterize *Libertia* and *Orthrosanthus* (Figs. 1–3). *Phaiophleps* and *Sisyrinchium* sect. *Eriphilema* have less sharply angular seeds (not illustrated), sometimes tending toward rather obtusely angled and differing consistently in basic shape from the rounded seeds of sects. *Sisyrinchium* and *Echthronema*. Seeds of two species of *Solenomelus* are cylindric to barrel-shaped with distorted angular ends (e.g., *S. segethii*, Fig. 5). In a third, possibly new, species of *Solenomelus* (Fig. 6) the seeds have a broad, membranous, half-circumferential wing. The seeds of *Orthrosanthus occissapungus* (Fig. 3) have the proximal and distal ends produced into winglike processes, but other species of the genus have angular seeds, as illustrated by Takhtajan (1985) for *O. chimboracensis*. In *Tapeinia* (Fig. 4) the seeds are nearly pyriform to elongate-pyriform, narrowest at the chalazal end. The raphe is usually distinct and terminates in a small depression in which we assume the micropyle is located. The least effect of crowding was found in sects. *Sisyrinchium* and *Echthronema*. There, except for the small persistent funicle, the seeds (Figs. 7–18) are nearly regularly spherical to rounded or sometimes somewhat depressed (e.g., *S. chiricanum*, Fig. 16).

Seed size varies considerably (Table 2) within genera. Thus in *Sisyrinchium*, *S. minus* has seeds 0.6 × 0.4 mm, whereas those of *S. chiricanum* are ca. 2.5 mm in diameter. The seeds of *Solenomelus* are even larger, with a maximum length of 5.5 mm attained by *Solenomelus* sp.

There is a regular pattern of small, evenly spaced, irregularly rounded depressions oriented in lines running along the long axis of the seeds of all three species of *Solenomelus* (Figs. 5, 6). In *Solenomelus* sp. these depressions are limited to the area covering the seed body.

A conspicuous, often large pit, which we here call an umbilicus, is an outstanding feature of the seeds of most species of sects. *Sisyrinchium* (Figs. 9, 10) and *Echthronema* (Figs. 13–18) (Table 2). The umbilicus straddles the raphe, either between the hilum and the micropyle (Figs. 17, 18), or the umbilicus includes the micropyle (Figs. 13, 15).

surface morphology and microsculpturing

Outlines of the testa cells often form a pronounced reticulum owing to the typical condition in Iridaceae for the outer periclinal walls to collapse while the thickened anticlinal walls persist (e.g., Figs. 1–4). The seed surfaces thus have a reticulate appearance. In some species of sect. *Echthronema* the surfaces exhibit little texture and in *S. trinerve* (Fig. 15) are nearly smooth. We did not find examples of the somewhat irregularly granular surfaces and diffuse reticulation without cell outlines

TABLE 1. Voucher data for the species studied (acronyms in parentheses after *Index Herbarium* (Holmgren et al., 1981)).

Species	Voucher information
Sisyrinchium sect. *Sisyrinchium*	
arenarium Poeppig	Chile: *Zollner 11298* (MO)
campestre Bickn.	U.S.A. Nebraska: *Tolstead 9715* (MO)
chilense Hook.	Chile: *Mexia 7994* (MO)
dimorphum Bickn.	Guatemala. Huehuetenango: *Breedlove 8730* (F)
johnstonii Standley	Costa Rica. Cartago: *Lent 2221* (F)
miamiense Bickn.	U.S.A. Florida: *Moldenke 446* (MO)
micranthum Cav.	Costa Rica. San José: *Khan et al. 137* (MO)
minus Engelm. & Gray	U.S.A. Texas: *Oliver 417* (MO)
montanum Greene	U.S.A. New Hampshire: *Churchill 302* (MO)
nashii Bickn.	U.S.A. Georgia: *Ravenal s.n.* (MO)
pruinosum Bickn.	U.S.A. Texas: *Reverchon 2791* (MO)
Sisyrinchium sect. *Echthronema*	
chiricanum Woodson	Guatemala: *Steyermark 46760* (F)
commutatum Klatt	Brazil. Paraná: *Hatschbach 25417* (MO)
convolutum Nocca	Honduras: *Standley 15493* (MO)
mandonii Baker	Costa Rica: *Allen 698* (MO)
prealtum Kraenzl	Peru. Cuzco: *West 7029* (MO)
tenuifolium Kunth	Guatemala: *Steyermark 50670* (F)
tinctorium Kunth	Belize: *Gentle 2225* (MO)
trinerve Baker	Costa Rica: *Davidse & Herrera 29375* (MO)
Sisyrinchium sect. *Eriphilema*	
douglasii A. Dietr.	U.S.A. Oregon: *Henderson 478* (MO)
scirpiforme Poeppig	Chile. Santiago: *Böcher et al. 614* (MO)
Sisyrinchium sect. *Nuno*	
filifolium Gaudich.	Falkland Islands. Port William: *Hooker 98* (K)
Libertia	
sp.	Bolivia. Nor Yungas, La Paz: *Solomon 17343* (MO)
ixioides Spreng.	New Zealand. South Island: *Anderson 243* (MO)
Ona	
obscura (Cav.) Ravenna	Chile. Port Famine: *King 113* (K)
Orthrosanthus	
chimboracensis (Kunth) Baker	Venezuela: *Dorr et al. 5044* (MO)
occissapungus (Ruiz ex Klatt) Diels	Bolivia. Murillo, La Paz: *Solomon 18360* (MO)
Phaiophleps	
biflora (Thunb.) R. Foster	Chile: *Pfister 12279* (CONC)
Solenomelus	
pedunculatus (Gillies) Johnst.	Chile. Talcar, Camarica: *Moreira s.n.* (GH)
segethii (Philippi) Kuntze	Chile. Santiago: *Wilkes s.n.* (GH)
? sp. nov.	Chile/Argentina. Calenfen Valley: *Elwes s.n.* (K)
Tapeinia	
pumila (Forster f.) Baillon	*Ricardi et al. 1156* (CONC)

reported in some North American species of sect. *Sisyrinchium* (*S. idahoense*, *S. radicatum*, *S. montanum*) by Cholewa & Henderson (1984) except in a possibly fungal-infected sample of *S. prealatum*.

Although details of the surface of individual cells were not our primary concern, we noted a characteristic "bumpy" or granular texture (Fig. 19) within the outlines of the anticlinal cell walls similar to that illustrated by Cholewa & Henderson (1984)

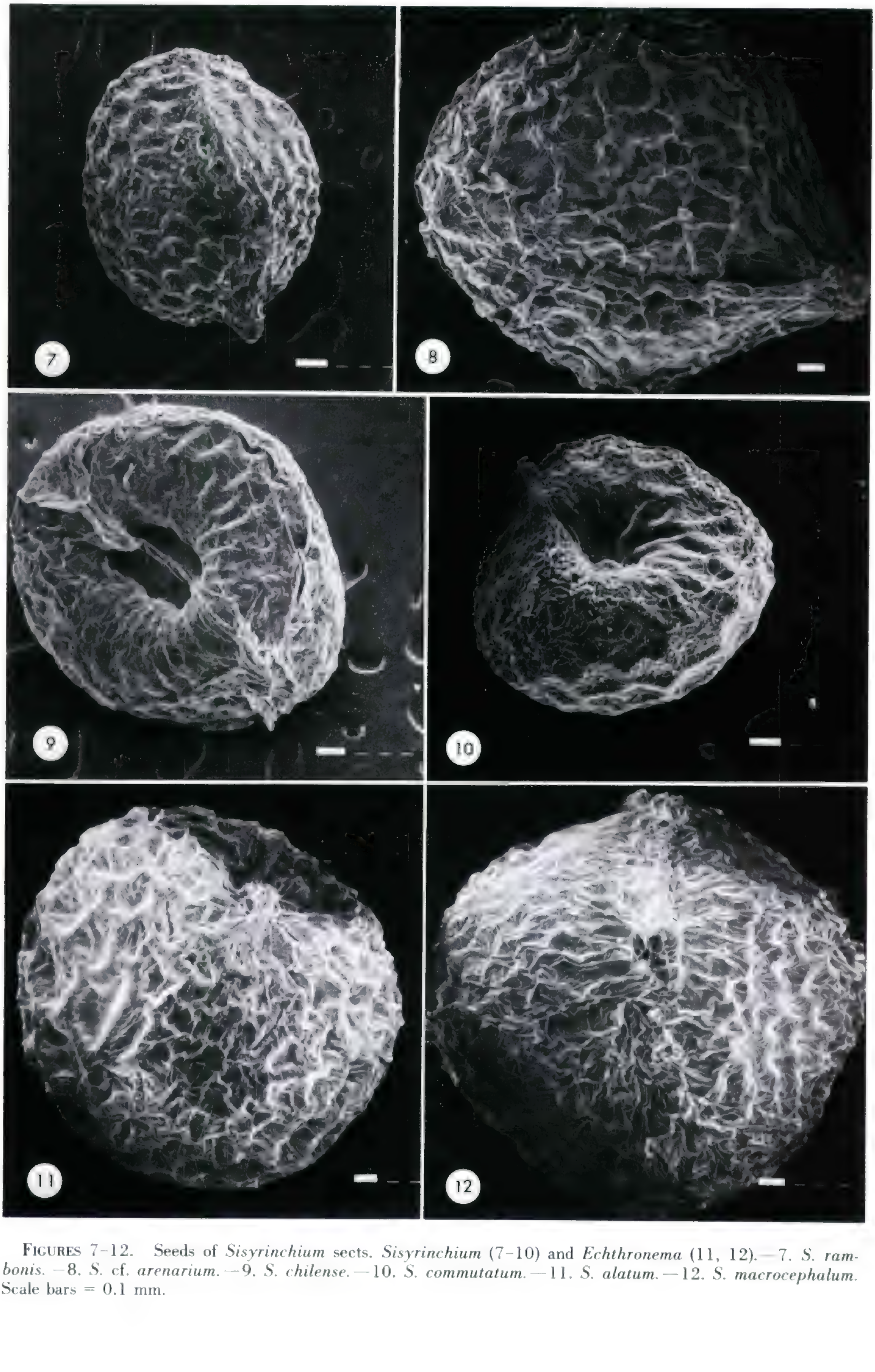
TABLE 2. Seed characteristics in Iridaceae tribe Sisyrinchieae. Presence of a character is indicated as X, absence by —. Measurements of seeds are diameter, or if two sizes given, long axis first followed by short axis.

Species	Shape	Size (mm)	Color	Umbilicus
Sisyrinchium sect. *Sisyrinchium*				
arenarium	± spherical	ca. 1.5	black	X
campestre	spherical	0.9	black	X
chilense	rounded	1–4 × 1–1.1	black	X
dimorphum	± spherical	ca. 1.1	black	X
johnstonii	± spherical	ca. 1.1	black	X
luzula	rounded	0.8–1 × 0.8	black	X
miamiense	spherical	1–1.1	black	—
micranthum	broadly trianguloid	0.8–0.9	black	X
minus	rounded	0.6 × 0.4	black	X
montanum	± spherical	1–1.3	black	X
nashii	spherical	0.8	black	X
pruinosum	spherical	0.9	black	X
rambonis	spherical-oblong	0.8 × 0.8–1	black	—
Sisyrinchium sect. *Echthronema*				
alatum	± spherical	ca. 1.7	black	—
chiricanum	spherical-depressed	2.5 × 2	black	X
commutatum	rounded	ca. 0.7	black	X
convolutum	spherical-depressed	1.2–1.5	black	X
macrocephalum	± spherical	ca. 1.8	black	—
mandonii	spherical	1.2	black	X
prealtum	± spherical-rounded	1.7–2 × 1–1.5	black	X
tenuifolium	rounded	0.9 × 0.6	black	X
tinctorium	spherical	ca. 1.5	black	X
trinerve	spherical-depressed	1.1–1.2	black	X
Sisyrinchium sect. *Eriphilema*				
douglasii	± angular	2–2.5 × 1.8–2	red-brown	—
scirpiforme	± rounded	1.9–2.1	light brown	—
Sisyrinchium sect. *Vuno*				
filifolium	angular	2–2.5 × 1.5–2	red-brown	—
Libertia				
sp.	angular	1 × 1	dark brown	—
ixioides	angular	1.8 × 1.5	red-brown	—
Ona				
obscura	ovoid	ca. 1.9 × 1.5	dark brown	—
Orthrosanthus				
chimboracensis	angular	1.1–1.6 × 1	red-brown	—
occissapungus	angular-elongate[1]	3–3.5 × 0.8–1.1	light brown	—
Phaiophleps				
biflora	angular	ca. 2.5 × 2	brown	—
Solenomelus				
pedunculatus	barrel-shaped[2]	2 × 1.3	red-brown	—
segethii	short-cylindric[2]	2.3 × ca. 1.4	dark brown	—
sp. nov.	nearly discoid[2,3]	5–5.5 × ca. 3.5	red-brown	—
Tapeinia				
pumila	elongate pyriform	1.1 × 0.5	red-brown	?[4]

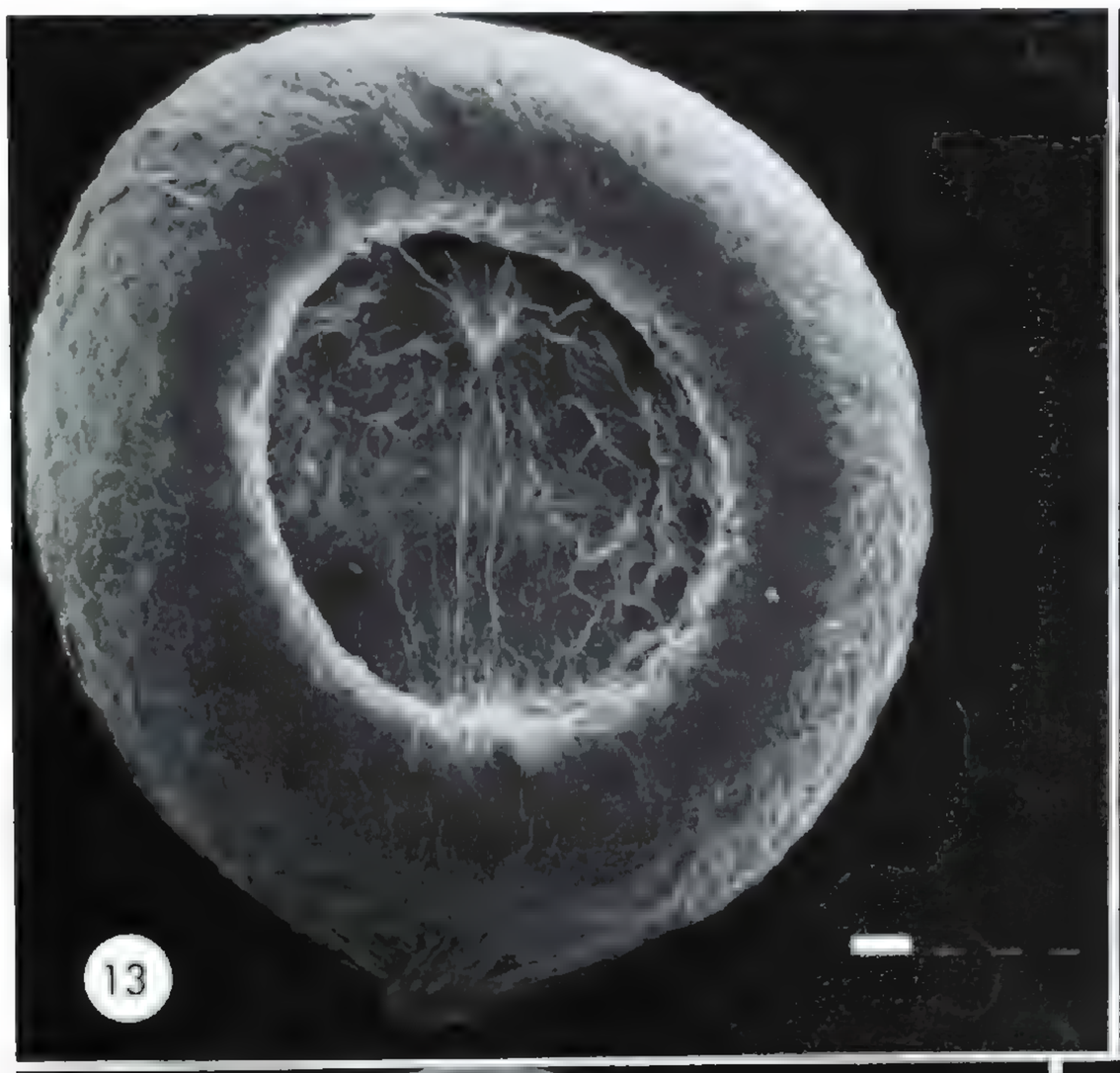
[1] With a distal and proximal wing.
[2] With linear arranged depressions.
[3] With a broad half-circumferential wing.
[4] With a small depression around the micropyle.

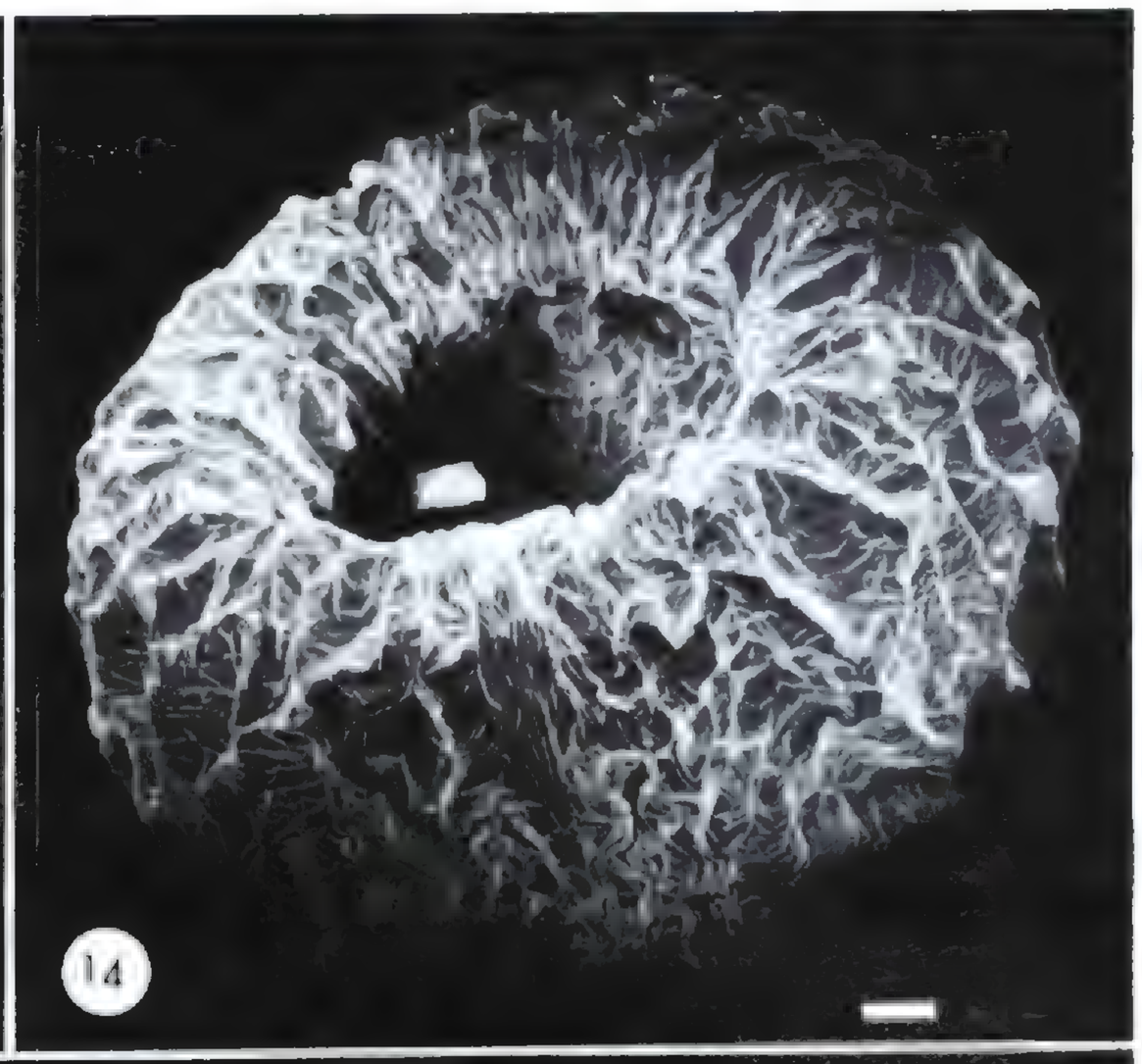
FIGURES 1–6. Seeds of genera of Sisyrinchieae.—1. *Libertia* sp.—2. *Orthrosanthus chimboracencis*.—3. *O. occissapungus*.—4. *Tapeinia pumila*.—5. *Solenomelus segethii*.—6. *Solenomelus* sp. Scale bars = 0.1 mm.

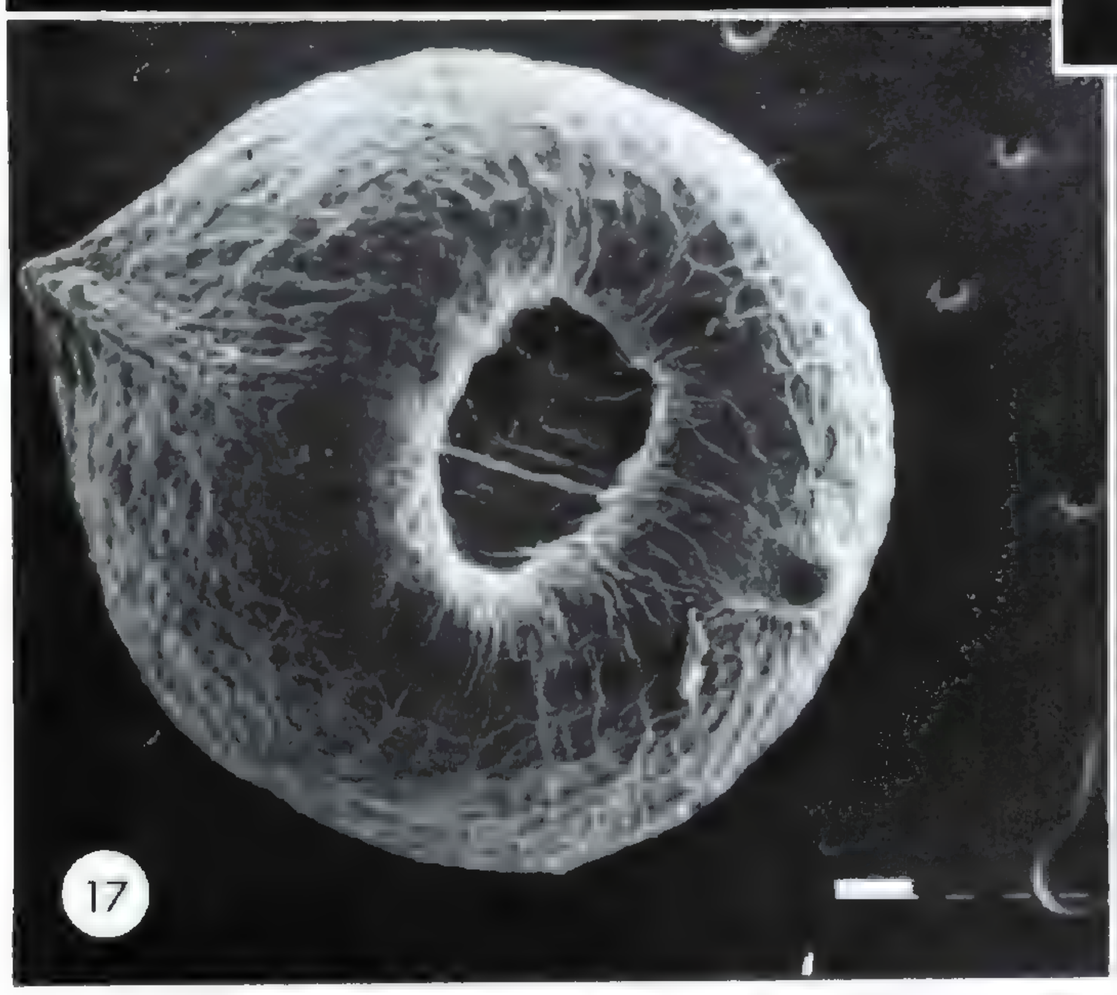
for *Sisyrinchium montanum*, and *S. pallidum*, and by Rodriguez (1986) for the Chilean *S. azureum*, all sect. *Sisyrinchium*. Among the species that we examined, this was noted particularly in *S. chiricanum*, *S. convolutum*, *S. commutatum* (Fig. 19), and *S. tinctorium* (all sect. *Echthronema*). Even the apparently smooth seed surface of *S. trinerve* shows this granularity at very high magnification.

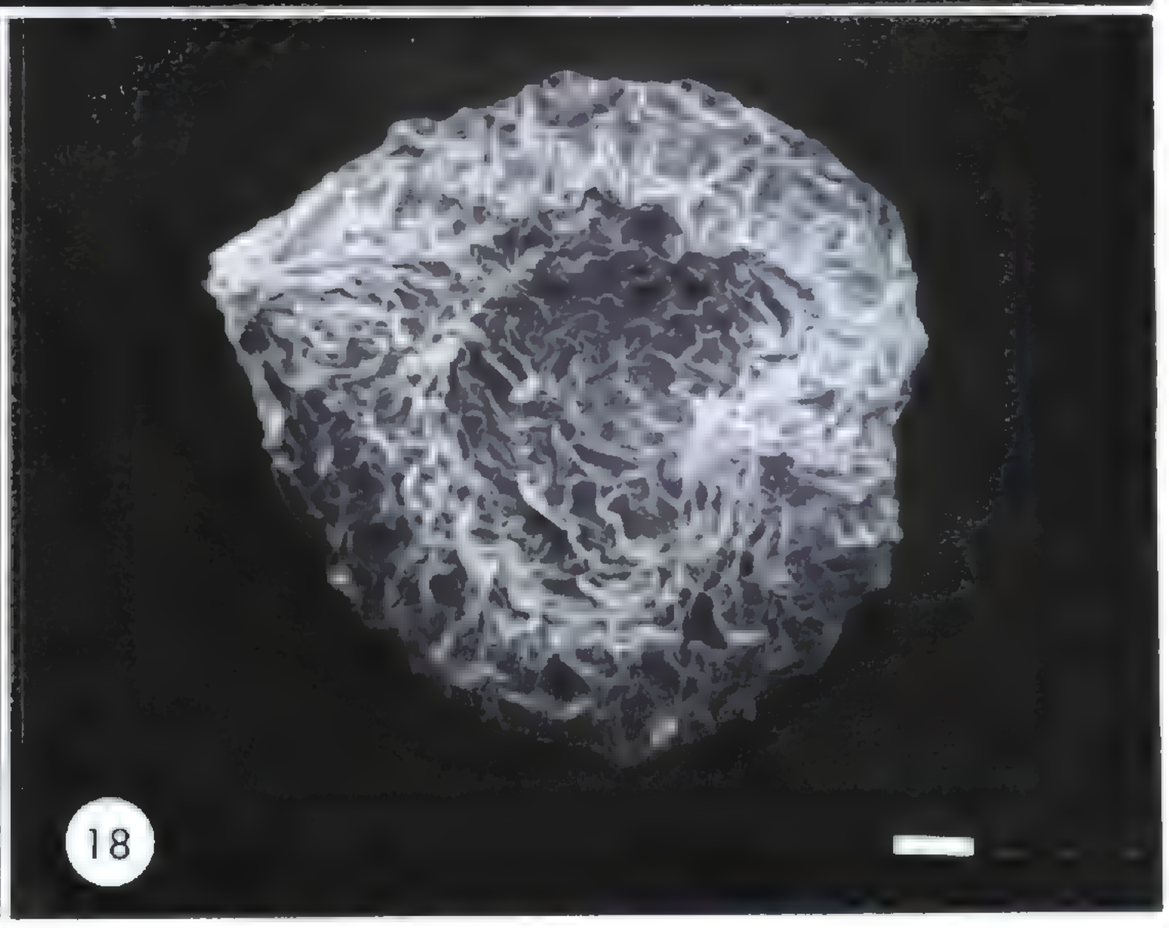


FIGURES 7–12. Seeds of *Sisyrinchium* sects. *Sisyrinchium* (7–10) and *Echthronema* (11, 12).—7. *S. rambonis*. —8. *S.* cf. *arenarium*.—9. *S. chilense*.—10. *S. commutatum*.—11. *S. alatum*.—12. *S. macrocephalum*. Scale bars = 0.1 mm.

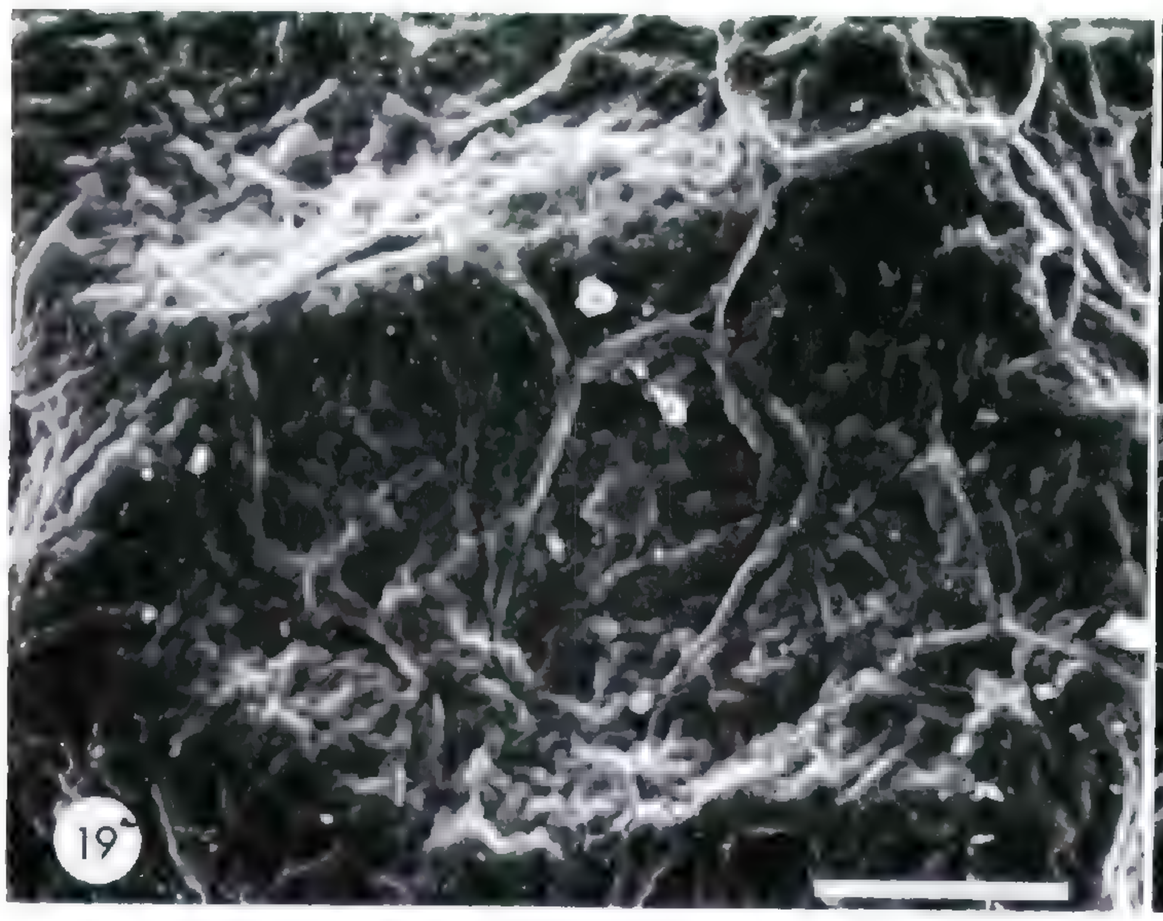


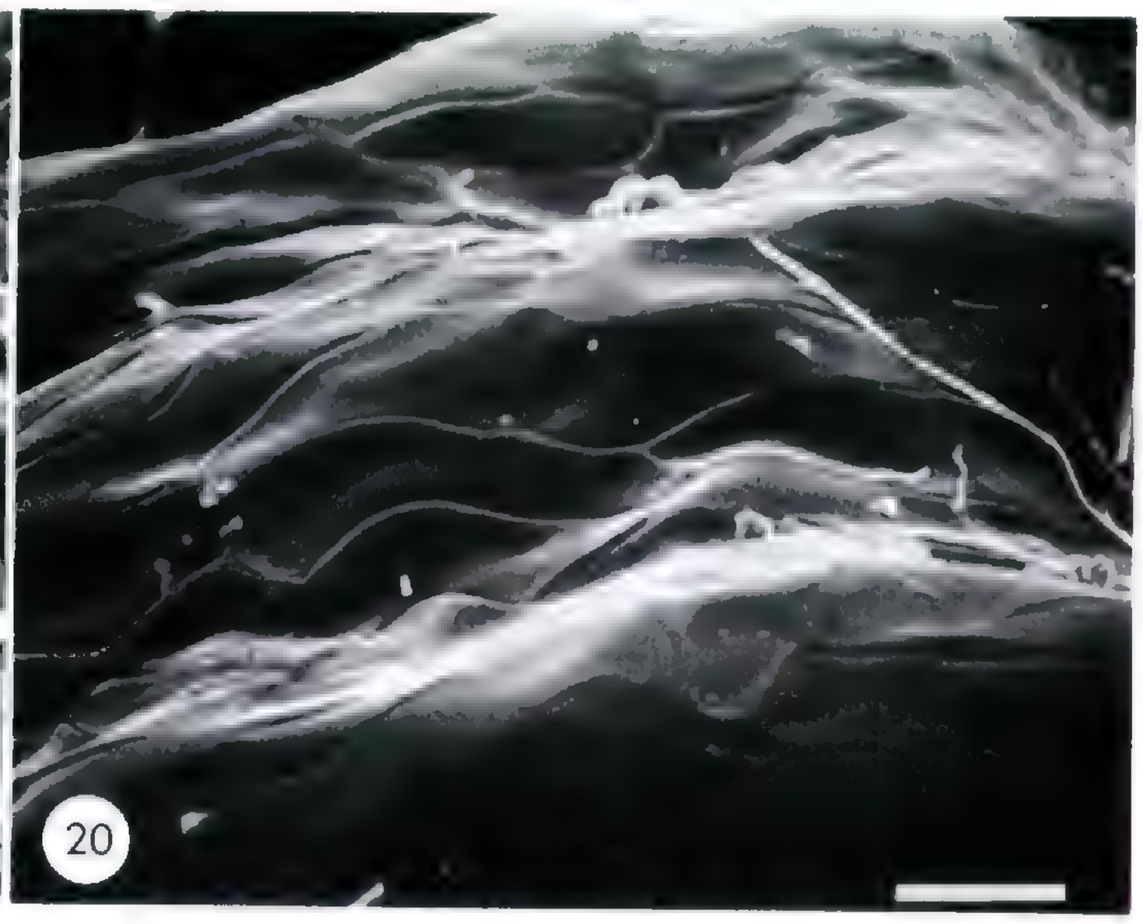






FIGURES 13–18. Seeds of *Sisyrinchium* sect. *Echthronema*. —13. *S. prealtum*. —14. *S. tinctorium*. —15. *S. trinerve*. —16. *S. chiricanum*. —17. *S. mandonii*. —18. *S. tenuifolium*. Scale bars = 0.1 mm.





FIGURES 19, 20. Surface details of seeds of *Sisyrinchium commutatum* (19) and *Solenomelus pedunculatus* (20). Scale bars = 50 μm.

very high magnification. No granular microsculpturing was noted in species of any other genus included in our survey.

In *Solenomelus* the longitudinal lines of more or less circular depressions do not correspond to the surface cells. The depressions are larger than the individual cells, the outlines of which can be clearly seen over the entire seed surface in *S. segethii* (Fig. 5), but are rather obscure in *Solenomelus* sp. (Fig. 6) and *S. pedunculatus*. In the latter the peripheral cells of the seed are unusual in being elongate and they have a remarkably smooth surface (Fig. 20).

DISCUSSION

Most Iridaceae have seeds of a light to middle brown, sometimes reddish brown (Huber, 1969; Wagner & Goldblatt, 1984), the coloration attributed to the presence of phlobaphene (Huber, 1969). A few exceptions include the glossy black seeds of *Belamcanda* (tribe Iridoideae) and *Babiana* and *Antholyza* (tribe Ixioideae), and the bright orange seeds of *Chasmanthe* (also Ixioideae) and *Neomarica variegata* (Iridoideae tribe Mariceae). Whether the black color in the above genera or in *Sisyrinchium* can be attributed to the presence of phytomelan, a dense carbon substance that is regarded as important in the higher systematics of the lilioid monocots (Dahlgren & Rasmussen, 1983; Dahlgren et al., 1985), is unknown.

The most common seed shape in Iridaceae is more or less regularly angular (Huber, 1969) but globose or subglobose seeds are not uncommon. Winged seeds occur in *Gladiolus* and its close allies (Ixioideae), and discoid seeds are characteristic of some species of *Iris* and *Moraea* (both Iridoideae–Irideae) and *Diplarrhena* (Sisyrinchieae). The half-circumferentially winged seeds of *Solenomelus* sp. are reminiscent of those of *Gladiolus* (which have completely circumferential wings) and represent a notable example of convergence.

Until now the blackish seeds encountered in *Sisyrinchium* appear not to have been regarded as particularly significant, although the basic differences in seed color have been noted by Rodriguez (1986), black in species attributable to sects. *Sisyrinchium* and *Echthronema* and brownish in sect. *Eriphilema*. Moreover, the more or less globose shape and the frequent presence of a large umbilicus along the raphe, either between the hilum and micropyle or including the latter, appear to have attracted little attention except for occasional mention in species descriptions. We believe that these features have considerable taxonomic significance, particularly in a genus that is relatively unspecialized in the family and has few other distinguishing characteristics.

A conclusion that appears warranted is that the black, globose, and umbilicoid seeds are a derived (apomorphic) condition in sects. *Sisyrinchium* and *Echthronema*. It is likely, though by no means certain, that this seed, including the umbilicus, is the basic type in the two sections despite the fact that an umbilicus is not present in a few North and South American species of both sections.

Seed data indicate that sects. *Sisyrinchium* and *Echthronema* should be considered sister taxa more closely allied to each other than to sects. *Eriphilema* and *Nuno*. The possibility that sects. *Eriphilema* and *Nuno* may be more closely allied to other genera of Sisyrinchieae, *Phaiophleps* in par-

ticular, than to the rest of *Sisyrinchium* will be explored in a future paper dealing with the phylogeny of Sisyrinchieae.

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NEW SPECIES OF *MENDONCIA* (ACANTHACEAE) FROM THE VENEZUELAN GUAYANA[1]

Dieter C. Wasshausen[2]

ABSTRACT

Recent expeditions in the Venezuelan Guayana have resulted in additional new taxa in the genus *Mendoncia* (Acanthaceae). The following is an effort to place these novelties on record for the convenience of other taxonomists prior to the publication of the *Flora of the Venezuelan Guayana*. Four new Venezuelan Guayana species of *Mendoncia*, *M. steyermarkii*, *M. neblinensis*, *M. williamsii*, and *M. coriacea*, are described, illustrated, and compared with their closest relatives.

There are approximately 60 species of *Mendoncia* in Central and South America and in tropical Africa and Madagascar. The genus, named for Cardinal Mendonça, Patriarch of Lisbon, consists of twining herbaceous or sometimes suffrutescent climbers bearing cylindric red, white, or cream-colored axillary flowers with purple streaks in the throat. Each flower is subtended by a pair of conspicuous, green, more or less connate bracts. Most taxa are limited to wet virgin forests and thickets at elevations between 50 and 1,000 m. Due to the fact that lianas and vines are generally poorly known and collected in the tropics, and given the superficial similarity of many of the species, the taxonomy of the genus is rather difficult. In an attempt to identify recent collections of *Mendoncia* from the Venezuelan Guayana, I have found four undescribed species of the genus.

KEY TO THE VENEZUELAN GUAYANA SPECIES OF *MENDONCIA*

1a. Bracts ovate or oblong-ovate.
  2a. Flowers 4 or 5 in each axil ..... *M. cardonae*
  2b. Flowers solitary or in pairs in each axil.
    3a. Corolla cream-colored with purple streaks in the throat; bracts 2 cm long and 1 cm broad ..... *M. sprucei*
    3b. Corolla bright to deep red; bracts 2.3–3 cm long, 1.3–1.7 cm broad.
      4a. Bracts yellowish green to brownish green, 2.5–3 cm long, hirsute; leaf blades membranous, dark green and lustrous above, glabrous; corolla 3.5 cm long ..... *M. neblinensis*
      4b. Bracts dull green, 2.3 2.5 cm long, densely hirsute; leaf blades firmly membranous, dull dark green above, sparingly hirsute; corolla 3 cm long ..... *M. steyermarkii*
1b. Bracts oblong, oblong-elliptic, or oblong-obovate.
  5a. Bracts narrowly oblong or oblong-lanceolate.
    6a. Leaf blades narrowly to broadly elliptic, rather thin, densely pubescent; bracts narrowly oblong, 3.5 cm long, 0.8 cm broad, densely velvety pubescent ..... *M. hoffmannseggiana*
    6b. Leaf blades elliptic, chartaceous, minutely and sparingly hirtellous; bracts oblong-lanceolate, 2 to 2.5 cm long, 1 cm broad, densely brown strigose ..... *M. williamsii*
  5b. Bracts oblong, oblong-elliptic or oblong-obovate.
    7a. Bracts oblong or oblong-elliptic, coriaceous; leaf blades subcoriaceous to thick-coriaceous.
      8a. Leaf blades elliptic to oblong, 3 6 cm broad; bracts vinaceous-lavender with green, oblong ..... *M. coriacea*
      8b. Leaf blades oblong-elliptic, 7.5 9 cm broad; bracts green, oblong-elliptic ..... *M. phalacra*
    7b. Bracts oblong-obovate to oblong-elliptic, not coriaceous; leaf blades membranous, not coriaceous.
      9a. Bracts oblong-obovate, 1–1.3 cm broad, essentially glabrous; stem glabrous; leaf blades glabrous, chartaceous, the veins prominent on the lower surface ..... *M. obovata*
      9b. Bracts oblong-elliptic, 1.5 1.8 cm broad, long-hirsute; stem hirsute; leaf blades hirsute, membranous, the veins inconspicuous on the lower surface ..... *M. bivalvis*

[1] My special thanks to Alice Tangerini, who skillfully prepared the line drawings, and the staff of the National Museum of Natural History SEM Laboratory for their high-quality pollen photomicrographs.

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FIGURE 1. A, B. *Mendoncia neblinensis.* —A. Habit (*W. W. Thomas 3196*).—B. Corolla (*M. Nee 30578*). C–E. *Mendoncia steyermarkii* (*Steyermark & G. C. K. & E. Dunsterville 104353*).—C. Habit.—D. Bract.—E. Corolla.

Mendoncia neblinensis Wasshausen, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: along Río Baria just upstream from Base Camp on SW side of Cerro de la Neblina, 0°49′50″N, 66°09′40″W, 140 m, 27 Jan. 1985, *M. Nee 30578* (holotype, US; isotype, NY). Figure 1A, B.

Frutex volubilis, caulibus subquadrangularibus, parce hirsutis et lepidotis, pilis ascendentibus. Foliorum lamina elliptica vel ovata, apice abrupte acuminata et aristata, basi abrupte acuta, supra atroviridis et subnitida, glabra vel parce puberula, subtus pallide viridis, glabra vel parce hirsuta, costa et venis lateralibus subtus prominentibus; petioli subquadrangulares, parce hirsuti; flores (1 vel 2) axillares; pedicelli tortiles, parce hirtelli, pilis appressis; bracteae ovatae, flavido- vel brunneolo-virides, apice apiculatae, extus hirsutae et minute muricatae, intus glabrae et minute rugosae; corolla vivido rubra vel atrosanguinea, glabra vel parce hirsuta versus faucem, lobis ellipticis vel obovatis, leviter emarginatis; drupa ellipsoidalis, glabra.

Climbing vine; stem subquadrangular, sparingly hirsute and lepidote with stellate scales, the trichomes ascending. Leaves petiolate, the petioles 1–2.5 cm long, subquadrangular, sparingly hirsute, the blades elliptic to ovate, thinly membranaceous, 5–11 cm long, 3–5.5 cm broad, abruptly acuminate, the tip aristate, the awn to 6 mm long, abruptly acute at the base, the upper surface dark green and lustrous, glabrous or bearing a few appressed trichomes arising from stellate bases, minutely punctate, the lower surface paler and dull green, glabrous or sparsely hirsute (especially the costa and lateral veins bearing a few appressed trichomes), the venation prominent beneath, lateral veins 3 or 4 pairs, veinlets coarsely reticulate. Flowers axillary, 1 or 2 in each axil, the pedicels 3.5–5.5 cm long, twisted, gradually enlarged towards tip, sparingly hirtellous, the trichomes appressed upward, straight; bracts ovate, yellowish green to brownish green, 2.5–3 cm long, 1.3–1.7 cm broad, apiculate, the apicula about 1 mm long, the outer surface minutely muricate and hirsute, the trichomes straight, rigid, appressed upward, the costa rather prominent, the inner surface glabrous, minutely rugose; corolla bright to dark red, 3.5 cm long, the lobes pink within, base of tube white, glabrous or sparingly hirsute towards the throat, the tube 5 mm broad at base, narrowed to 2.5 mm at 8 mm above base, the throat 8 mm broad, the upper lip about 8 mm long, the lobes subequal, elliptic to obovate, 5 mm long and 3.5 mm broad, shallowly emarginate at apex, the lower lip somewhat shorter than the upper lip; pollen grains 5-colporate (brevissimicolpate), prolate-spheroidal, 34 × 30 μm, sexine punctitegillate; calyx annular, 0.5 mm long, glabrous; style 2.5 cm long, glabrous; ovary glabrous. Drupe fleshy, black, ellipsoid, 17 mm long, 8 mm wide, glabrous.

Distribution. Lowland evergreen tropical forest on hummocks along gravelly black-water rivers, Territorio Federal Amazonas at elevations between 100 and 180 m.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro de la Neblina, along Río Mawarinuma, 0°50′N, 66°10′W, 140 m, *Stein, Gentry & Thomas 1716* (MO, US); same locality, *Davidse & Miller 27452* (MO, US); same locality, *Liesner 15667* (MO, US); same locality, *Liesner 17273* (MO, US); same locality, *Liesner & Funk, 15822* (MO, US); same locality, *Thomas 3318* (MO, US); same locality, *Kral 71816* (US); same locality, *Thomas 3374* (NY, US); upper Río Baria, ca. 0°55′N, 66°15′W, 100 m, *Davidse & Miller 26899* (MO, US); between base camp and "Puerto Chimo" along Río Mawarinuma, 0°50′N, ca. 66°8′W, 150 180 m, *Gentry & Stein 46967* (MO, US); 2 6 km E of base camp, 0°50′N, 66°08′W, 160 m, *Thomas 3196* (NY, US).

Mendoncia neblinensis is probably related to *M. sprucei* Lindau. It differs markedly from *M. sprucei* in that the latter species has green bracts 2 cm long and 1 cm broad, sparingly appressed-pilose pubescence on the leaf blades, and corollas 3 cm long. In contrast, *M. neblinensis* has yellowish to brownish green bracts 2.5–3 cm long and 1.3–1.7 cm broad, glabrous leaf blades, and corollas 3.5 cm long. Lindau (1897) in his description of *M. sprucei* did not indicate the color of the corolla, nor did Turrill (1919) in his revision of the genus. Leonard (1951) described the corolla of *M. sprucei* as cream colored with purple streaks in the throat. I believe this to be in error; the corolla of *M. sprucei* is also bright red. Turrill (1919) stated in his discussion that *M. sprucei* appears to be very closely related to the red-flowered *M. aspera* Nees and that perhaps *M. sprucei* was only a variety of *M. aspera*.

Mendoncia steyermarkii Wasshausen, sp. nov. TYPE: Venezuela. Estado Bolivar, en el drenaje del Río Cuyuní, al sur de El Dorado, 1,300–1,380 m, 22 28 Dec. 1979, *Julian A. Steyermark & G. C. K. & E. Dunsterville 104353* (holotype, US; isotype, VEN). Figure 1C–E.

Frutex volubilis, caulibus subquadrangularibus, sulcatis, parce lepidotis, parce hirsutis, pilis ascendentibus. Foliorum lamina ovata, abrupte acuminata apice aristata, base abrupte acuta vel obtusa, aliquanto membranacea, integra, supra atroviridis, parce hirsuta, subtus fulvo-viridis, glabra vel costa et venis lateralibus parce strigosis; petioli glabri vel in canalibus parce hirsuti; flores (1 vel 2) axillares; pedicelli recti, flavo-virentes, dense hirtelli; bracteae ovatae, obscure virides, apiculatae, externe dense hirsutae, minute muricatae, intus glabrae et minute ru-

gosae; corolla atrosanguinea, glabra, lobis rotundatis vel leviter emarginatis; drupa subglobosa, nitida, glabra.

Trailing vine; stems subquadrangular, grooved, sparingly lepidote (the scales stellate), bearing numerous ascending, erect, hirsute trichomes. Leaves on petioles 1–2.5 cm long, subquadrangular, glabrous or the channels sparingly hirsute with straight ascending trichomes, the blades firmly membranous, ovate, 9–11 cm long and 4–6.5 cm broad, apically abruptly acuminate (the tip aristate, the awn 6 mm long), the base abruptly acute to obtuse, the upper surface dull dark green, sparingly hirsute, the trichomes straight, ± ascending, arising from stellate bases, the lower surface dull tawny green, glabrous or the costa and lateral veins bearing a few scattered, stiff, straight, ascending trichomes, lateral veins 3 or 4 pairs, veinlets coarsely reticulate, the venation prominent and raised beneath, less so above. Flowers axillary, 1 to 2 in each axil, the pedicels yellow-green, 4–6 cm long, straight, densely hirtellous, the trichomes appressed upward, straight, rigid; bracts dull green ovate, 2.3–2.5 cm long, 1.3–1.5 cm broad, with an apicula about 1 mm long, the outer surface minutely muricate and densely hirsute with straight, rigid, trichomes, these appressed upward, the costa rather prominent, the inner surface glabrous, minutely rugose; corolla deep red, glabrous, 3 cm long, the tube 5.5 mm broad at base, narrowed to 3 mm at 5 mm above base, the throat 8 mm broad, the upper lip about 5 mm long, the lobes rounded, 3.5 mm broad, shallowly emarginate at apex, the lower lip somewhat shorter than the upper lip; pollen grains 5-colporate (brevissimicolpate), prolate-spheroidal, 42 × 37 μm, sexine punctitegillate; calyx annular, 0.5 mm long, glabrous; style 2.8 cm long, the lower portion hirsute; ovary glabrous. Drupe subglobose, black, shining, 15–18 mm diam., glabrous.

Distribution. Wooded ridge and tall, moist forests with trees on the average 25–30 m tall, Estado Bolívar, Venezuela, at 1,100–1,400 m.

Paratypes. VENEZUELA. BOLIVAR: Gran Sabana, El Dorado Sta. Elena de Uairen road, km 131, 1,200 1,400 m, *J. Steyermark, L. & R. Smith, G. C. K. & E. Dunsterville 105454* (US, VEN); El Dorado–Sta. Elena de Uairen road, km 127 131, 1,300–1,350 m, *Badillo & Holmquist 6094* (MY, US); El Dorado–Sta. Elena de Uairen road, km 119–122, S of El Dorado, ca. 1,100 m, *Gentry, G. Morillo & B. de Morillo 10460* (MO, US); carretera between campamento 125 and km 127, between Luepa and Cerro Venamo, 1,200 m, *Steyermark & Nilsson 194* (US, VEN); 134 km S of El Dorado, 1,300 1,350 m, *Steyermark & G. C. K. & E. Dunsterville 104450* (US); carretera El Dorado–Gran Sabana, La Dante, 1,250 m, *Ruiz-Terán & López-Palacios 11460* (MERF, US).

Mendoncia steyermarkii superficially resembles the Colombian lowland forest species *M. caquetensis* Leonard. However, in *M. caquetensis* the bracts are green and sparingly and inconspicuously hirsute; and the corollas are white(?) (*fide* Leonard, 1961) with the tube 4 mm broad at the base and narrowed to 2.5 mm at 1 cm above the base, and the upper lip is about 1 cm long. In *M. steyermarkii*, the bracts are dull green and densely hirsute, the corollas are deep red with the tube 5.5 mm broad at the base and narrowed to 3 mm at 0.5 cm above the base, and the upper lip is about 0.5 cm long.

Mendoncia williamsii Wasshausen, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: forest at Capihuara, Casiquiare, 120 m, 30 May 1942, *Llewelyn Williams 15697* (holotype, US; isotype, VEN). Figure 2A–C.

Frutex volubilis, caulibus subquadrangularibus, strigosis, pilis brunneis. Foliorum lamina elliptica, breve acuminata, cuspidata, basi acuta, chartacea, integra, supra (in sicco) subnigra, parce et minute hirtella, pilis a basibus planis stellatis orientibus, subtus (in sicco) brunnea, aequaliter strigosa; petioli strigosi; flores 2, axillares; pedicelli dense brunneo-strigosi; bracteae oblongo-ovatae, apice acutae, extus dense brunneo-strigosae, costa aperta; corolla non visa; drupa ovoidea, leviter compressa, minute pubescens.

Vine; stem subquadrangular, rather densely strigose upward, the trichomes brownish, to 2.5 mm long. Leaves on petioles 1–2 cm long, strigose, the blades elliptic, to 15 cm long and 9 cm broad, apically short-acuminate with a cusp to 5 mm long, basally acute, chartaceous, entire, the upper surface drying blackish, minutely and sparingly hirtellous with the ascending hairs 0.25–0.50 mm long and arising from flat, stellate bases, the costa and lateral veins (4 or 5 pairs) rather prominent, strigose with brown trichomes about 1 mm long, the lower surface drying brown, ± evenly strigose, both surfaces bearing rather prominent coarsely reticulate veinlets. Flowers usually 2 in each axil; pedicels 4 cm long, densely brown strigose; bracts oblong-lanceolate, 2–2.5 cm long, 1 cm broad just above base, gradually narrowed to an acute tip, densely brown-strigose, the costa evident, the inner surface glabrous; flowers not seen. Drupes 1.5 cm long, 6 mm wide, 4 or 5 mm thick, oblique at tip, the surface minutely and rather densely pubescent.

Distribution. In dense forest of terra firma, Territorio Federal Amazonas, Venezuela. Known only from the type locality.

FIGURE 2. A–C. *Mendoncia williamsii* (*L. Williams 15697*).—A. Habit.—B. Bracts.—C. Drupe and bract. D–F. *Mendoncia coriacea* (*Steyermark & G. C. K. & E. Dunsterville 104474*).—D. Habit.—E. Bracts.—F. Corolla.

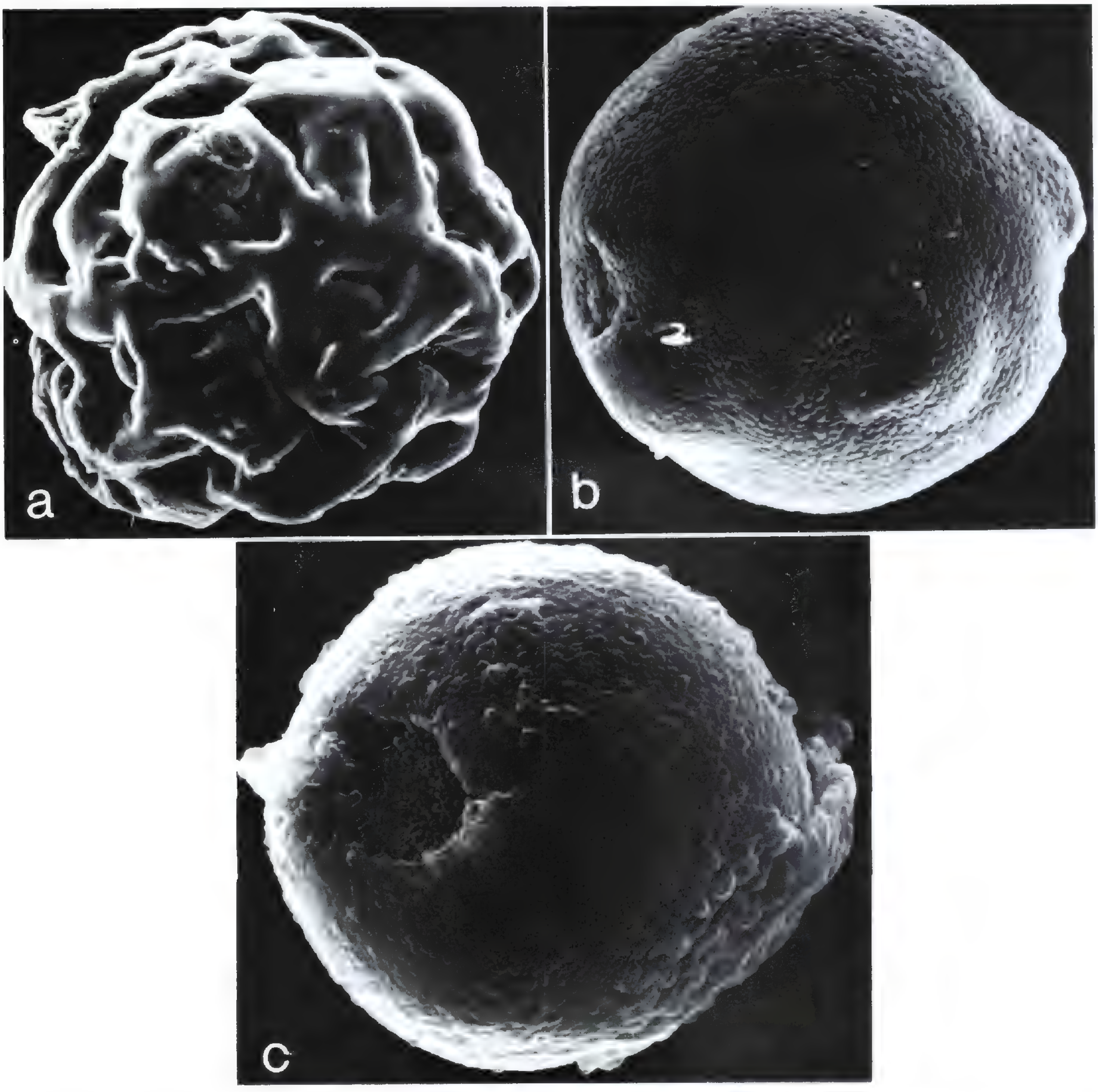

FIGURE 3. Scanning electron microscope (SEM) photomicrographs of *Mendoncia* pollen. — a. *Mendoncia coriacea*, equatorial view, × 1,200 (*Steyermark & G. C. K. & E. Dunsterville 104474*).—b. *M. steyermarkii*, equatorial view, ×1,750 (*Steyermark & G. C. K. & E. Dunsterville 104353*).— c. *M. neblinensis*, equatorial view, ×2,200 (*R. Liesner 15667*).

Mendoncia williamsii is most closely (but distantly) related to *M. sprucei* Lindau. In *M. sprucei* the bracts are ovate and sparingly appressed-hirtellous without; the flowers are usually solitary; and the leaf blades are ovate to oblong-ovate, firmly membranous, and about 6 cm broad. In contrast, in *M. williamsii* the bracts are oblong-lanceolate and densely brown strigose without; the flowers are usually in twos; and the leaf blades are elliptic, chartaceous, and considerably wider (about 7.5 cm broad).

Mendoncia coriacea Wasshausen, sp. nov. TYPE: Venezuela. Bolívar: km 133.5, drenaje del Río Cuyuní, al sur de El Dorado, 1,300–1,380 m, 22–28 Dec. 1970, *Julian A. Steyermark & G. C. K. & E. Dunsterville 104474* (holotype, US; isotype, MO). Figure 2D–F.

Suffrutex volubilis, caulibus subquadrangularibus, glabris. Foliorum lamina elliptica vel oblonga, apice abrupte acuminata et mucronata, basi acuta, coriacea, integra, glabra, costa et venis lateralibus prominentibus subtus; petioli subqudrangulares, glabri; flores 2, axillares; pedi-

celli graciles, glabri, olivacei suffuso marronini; bracteae oblongae, coriaceae, vinaceo-lavandulae viridi-vittatae, apice rotundatae vel obtusae, mucronulatae, extus glabrae et minute rugosae, intus glabrae minute punctatae; corolla alba, in tubo lineis lavandulaceis notato, glabra, limbo obliquo, lobis suborbicularibus, leviter emarginatis; drupa subglobosa, glabra.

Large suffruticose liana, 25–30 m high; stem subquadrangular, glabrous. Leaves on petioles 2–3.5 cm long, subquadrangular, glabrous, the blades subcoriaceous to thick-coriaceous, elliptic to oblong, 8–14 cm long, 3.5–6 cm broad, the tip abruptly acuminate (the tip blunt and terminating in a mucro 1 mm long), acute at base, entire or undulate, both surfaces glabrous, dark green and minutely punctate above, dull green below, the costa and lateral veins (3–5 pairs) obscure above and prominent and raised beneath, the veinlets of the middle lower leaves forming a conspicuous reticulation on the lower surface. Flowers axillary, usually 2 in each axil; pedicels 3–4 cm long, slender, 0.75 mm broad at base, gradually enlarged to 2 mm at tip, glabrous, olive green suffused maroon; bracts coriaceous, vinaceous-lavender with green, oblong, 2.5–3.5 cm long, 1–1.4 cm broad, rounded or obtuse at apex and tipped by a mucro 1 mm long, rounded at base, glabrous and minutely rugose without, glabrous and minutely punctate within; corolla white with lavender stripes in the tube within, glabrous, 4.5 cm long, the tube 4 mm broad at base, narrowed to 3 mm at 10 mm above base, the throat 8 mm broad, the upper lip about 1 cm long, the lobes unequal, suborbicular, 6 mm long and 9 mm broad, shallowly emarginate at apex, the lower lip somewhat shorter than the upper lip; pollen grains 5-colporate (brevissimicolpate), prolate-spheroidal, 58 × 53 μm, exine thick, crassinexious; calyx annular, 0.5 mm long, glabrous; style 2.9 cm long, glabrous; ovary glabrous. Drupe subglobose, dark wine-purple to black, 18 mm long, 15 mm in diam., glabrous.

Distribution. Wooded ridge and tall, moist forest with trees on the average 25–30 m tall, Estado Bolívar, Venezuela, at 1,200–1,380 m.

Paratypes. VENEZUELA. BOLIVAR: between campamento 125 and km 127, between Luepa and Cerro Venamo, 1,200 m, *Steyermark & Nilsson 177* (F, US, VEN); carretera El Dorado–Gran Sabana, La Danta, 1,250 m, *Ruiz-Terán & López-Palacios 11481* (MERF, US).

Mendoncia coriacea is perhaps most closely related to the widespread lowland Amazonian species of Colombia and Peru, *M. pedunculata* Leonard, which differs markedly by having larger (4 cm long, 1.4–1.8 cm broad), violet bracts; membranous, wider (6–10 cm broad) leaf blades; and longer, white corollas marked by reddish brown within and 5 to 6 cm long. In contrast, *M. coriacea* has coriaceous, vinaceous-lavender with green bracts 2.5–3.5 cm long and 1–1.4 cm broad; subcoriaceous to thick-coriaceous leaf blades 3.5–6 cm broad; and shorter (4.5 cm long), white, internally lavender-striped corollas.

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NEW SPECIES, NAMES, AND COMBINATIONS IN AMERICAN COMBRETACEAE

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ABSTRACT

Revision of the family Combretaceae for accounts in eight tropical American floras has revealed the following twelve novelties: *Terminalia chicharronia* subsp. *neglecta* (Bisse) Alwan & Stace, comb. nov.; *T. chicharronia* subsp. *domingensis* (Urban) Alwan & Stace, comb. nov.; *T. chicharronia* subsp. *orientensis* (Monach.) Alwan & Stace, comb. nov.; *T. ramatuella* Alwan & Stace, nom. nov.; *T. virens* (Spruce ex Eichler) Alwan & Stace, comb. nov.; *T. crispialata* (Ducke) Alwan & Stace, comb. nov.; *T. steyermarkii* Alwan & Stace, sp. nov.; *T. kuhlmannii* Alwan & Stace, sp. nov.; *T. uleana* Engl. ex Alwan & Stace, sp. nov.; *T. eichleriana* Alwan & Stace, nom. nov.; *Bucida molineti* (M. Gómez) Alwan & Stace, comb. nov.; and *Buchenavia amazonia* Alwan & Stace, sp. nov.

1. ***Terminalia chicharronia*** Wright ex Sauvalle.

Restricted to Cuba, Haiti, and the Dominican Republic, this species is very variable in the size and shape of the leaves and in the amount of indumentum on the branchlets, leaves, and inflorescence. These characters reveal four reasonably well geographically separated taxa recognized here as subspecies.

Terminalia chicharronia was based on *Chicharronia intermedia* A. Rich. (1846), which in turn was based on *Sagra 185* and *281*. The specimens at G are the best ones, but there is no evidence that Richard saw them. In P there is one sheet with three shoots—two in flower and one in fruit—which Richard did see. The label says "Herbarium Richard. No. 185, *Combretum* sp. nov., Guanabo, Marzo 1829, Coll. R. de la Sagra." The two flowering shoots are here designated as lectotype because in G there is a note from Sagra saying that no. 185 was sent first and was flowering, and no. 281 was sent later (both March 1829) and fruiting. This typification fixes subsp. *chicharronia* as the subspecies with densely pubescent to rufous tomentose leaves with strongly raised venation. It occurs most commonly in eastern Cuba (prov. Oriente), where it is sympatric with the closely related *T. eriostachya* A. Rich., which differs by having larger flowers, longer inflorescences, and glabrous styles. *Terminalia maestrensis* Bisse is here considered to be a synonym.

The other subspecies are as follows:

1a. Subsp. **neglecta** (Bisse) Alwan & Stace, comb. nov. BASIONYM: *T. neglecta* Bisse in Feddes Repert. Spec. Nov. Regni Veg. 85: 607. 1974.

Western and central Cuba (provinces Pinar de Río, Habana, and Las Villas, including Isla de Pinos).

1b. Subsp. **domingensis** (Urban) Alwan & Stace, comb. nov. BASIONYM: *T. domingensis* Urban in Symb. Antill. 7: 524. 1913.

Haiti and Dominican Republic.

1c. Subsp. **orientensis** (Monach.) Alwan & Stace, comb. nov. BASIONYM: *T. orientensis* Monach. in Caribbean Forest. 8: 79. 1974.

Synonyms: *T. nipensis* Alain, *T. aroldoi* Bisse, *T. pachystyla* Borh.

Eastern Cuba (province Oriente, mostly at higher altitude).

2. *Ramatuella* Kunth

This former genus was revised by Exell & Stace (1963), who recognized six species. Subsequent collections have shown that this should be reduced to three. Moreover, although *Ramatuella* is still recognizable by the combination of characters outlined by Exell & Stace, it seems far better reunited with *Terminalia*, as its distinction is based on only one of several combinations of characters found in *Terminalia*. Accordingly, we reduce it to sectional status.

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2a. **Terminalia** sect. **Ramatuella** (Kunth) Alwan & Stace, comb. nov. BASIONYM: *Ramatuella* Kunth, Nov. Gen. Sp. 7: 253. 1825 ("*Ramatuela*," based on misspelling of "Ramatuelle").

2b. **Terminalia ramatuella** Alwan & Stace, nom. nov. pro *Ramatuella argentea* Kunth, Nov. Gen. Sp. 7: 254, tab. 656. 1825.

The epithet *argentea* cannot be transferred to *Terminalia* as there already exists *T. argentea* C. Martius (1824), a very different species, from Brazil, Paraguay, and Bolivia.

2c. **T. virens** (Spruce ex Eichler) Alwan & Stace, comb. nov. BASIONYM: *Ramatuella virens* Spruce ex Eichler in C. Martius, Fl. Bras. 14(2): 100, tab. 26, fig. 2. 1867.
Synonyms: *R. maguirei* Exell & Stace, *R. latifolia* Maguire.

2d. **T. crispialata** (Ducke) Alwan & Stace, comb. nov. BASIONYM: *Ramatuella crispialata* Ducke, Arq. Inst. Biol. Veg. 2: 65. 1935.
Synonym: *R. obtusa* (Maguire) Exell & Stace.

3. **Terminalia steyermarkii** Alwan & Stace, sp. nov. TYPE: dwarf woody plant with branches spreading from near ground, only 0.5–1 m tall; flowers creamy-buff; leaves crowded at tip of branch, coriaceous, dull green above, gray-sericeous below, the apical youngest leaves buff-silvery sericeous; filaments greenish white; ovary and calyx gray-green; perianth pale green. Venezuela. Bolívar: Cumbre de Cerro Guaiquinima, sector nororiental, entre las brazos nororiental del Río Carapo, en una meseta arenosa pedregosa y cubierta con vegetación muy esparcida, 5°54′N, 63°25′W, 980 m, 30 May 1978, *Steyermark, Berry, G. & E. Dunsterville 117521* (holotype, LTR; isotype, VEN, not seen).

Frutex 0.5–1 m altus, ramulis dense villosis. Folia spiraliter ordinata ad ramulorum apices congesta; petiolus ca. 5–10 mm longus, dense sericeus; lamina coriacea, obovata vel elliptico-obovata, (3–)5–11 × 3–6.5 cm, apice retusa vel rotundata, basi cuneato-obtusa in petiolo decurrente, supra pubescens, subtus holosericeo argentea, venis lateralibus 7–9-paribus; venatio brochidodroma inconspicua. Inflorescentiae axillares, spicatae, pedunculus 4–5 cm longus, dense pubescens; rachis 4 cm longa, dense tomentosa. Flores 4–5-meri; receptaculum inferum 3.5 mm longum, dense villosum; receptaculum superum 2 × 4 mm, dense pubescens; calycis lobi 5 vel 4, 1.5 mm longi; stamina 8 vel 10, exserta ad 4–5 mm; stylus 5–6 mm longus, ad medium usque pilosus. Fructus ignotus.

Terminalia steyermarkii is one of those remarkable coriaceous-leaved species of sects. *Ramatuella* and *Pachyphyllum* Maguire & Exell that are confined to the vicinity of the watershed between the Río Orinoco and the northern tributaries of the Amazon. It differs from all but *T. ramatuella* by having a densely sericeous lower leaf surface, and from *T. ramatuella* by having an apparently dwarfer habit, broader and thicker leaves, and more elongated rachis.

Terminalia steyermarkii is known only from the type collection. Without fruits its precise affinities are uncertain, but the elongated rachis with bisexual flowers borne along its length suggests sect. *Pachyphyllum* rather than sect. *Ramatuella.*

4. **Terminalia kuhlmannii** Alwan & Stace, sp. nov. TYPE: Brazil. Espirito Santo: Goytacazes, Rio Doce. n.v. "Pelada," arvore frequente no mato, da madelta a provei tavel, 16 Dec. 1943, *Kuhlmann 06688* (holotype, RB 62982; isotypes, NY, RB).

Arbor. Folia spiraliter ordinata ad ramulorum apices congesta; petiolus 1–2 cm longus, glaber vel sparse pubescens, eglandulosus; lamina chartacea, 5–12 × 3–6 cm, obovata, apice subacuta vel acuminata, basi acuta, supra glabra, subtus ± glabra; venatio brochidodroma conspicua, venis secundariis subtus prominentibus 5–8 paribus, venis tertiariis subtus reticulatis, venulis conspicuis vix prominentibus. Pedunculus (in fructu) 2–3.5 cm longus, pubescens; rachis (in fructu) 2–3.5 cm longa, dense pubescens. Fructus 2-alatus, transversali oblongus, 1.2–1.7 × 3.5–4.6 cm, dense pubescens, corpore 3–4 mm lato, alis oblongis 1.4–2.1 cm latis.

Terminalia kuhlmannii belongs to sect. *Diptera* (Eichler) Engl. & Diels, which includes four other South American species. Of these, *T. januariensis* DC. and *T. guyanensis* Eichler have much larger glabrous fruits; *T. argentea* C. Martius has ovate leaves, and leaf lower surface and fruits usually tomentose at least when young; and *T. phaeocarpa* Eichler has larger leaves usually acute to rounded at apex with eucamptodromous venation, and usually glabrous fruits. *Terminalia kuhlmannii* most closely resembles *T. guyanensis*, but this is geographically remote and differs additionally in its narrower leaves with less conspicuous venation and shorter inflorescence.

A flowering specimen (*Silva 356*, LTR & CVRD) from close to the type locality probably also belongs here. It is a tree of 29 m also known as "Pelado." The flowers are densely pubescent, cream, and with styles pubescent to near the apex. Another flowering specimen (*Almeida & Santos 191*, LTR &

CEPEC), from near Ilheus, Bahia (ca. 550 km north of the former) may also be the same species; it has peduncles up to 6 cm and rachises up to 7 cm, but otherwise is very similar.

5. **Terminalia uleana** Engl. ex Alwan & Stace, sp. nov. TYPE: Brazil. St. Catarina: Baum im Ufer des Capivary, Tubarão, Jan. 1889, *E. Ule 1004* (holotype, HBG; isotypes, B (destroyed, photo F), P, US).

Arbor? Folia alternata, non congesta; petiolus 1 cm longus, pubescens vel dense pubescens, eglandulosus; lamina subcoriacea, 5–12 × 2 5 cm, obovata vel anguste obovata, apice acuminata vel acuta, basi cuneata, supra pubescens vel glabrescens, subtus pubescens; venatio eucamptodromo-brochidodroma; venae secundariae infra prominentes, 5–9 paribus; venae tertiariae fortuito reticulatae, conspicuae; areolae imperfectae. Flores ignoti. Fructus bialatus, transversali oblongus, 1.3–1.5 × (2.5–)3–4.5 cm, glaber; corpus ovato-ellipticum, 1.5 × 0.8 cm, protuberans vel parum carinatum; alae latiores quam longae, 1.3–1.7 × 1.3–2 cm, deorsum curvatae.

Engler wrote the name "*Uleana*" on the sheet at B but did not publish it. Also written on the sheet is the idea that the species is related to *T. argentea*. The new species belongs to sect. *Australes* Engl. & Diels, itself close to sect. *Diptera*, which contains *T. argentea*. Of the species in sect. *Australes*, *T. uleana* differs from *T. australis* Cambess. and *T. reitzii* Exell in fruit shape and from *T. triflora* (Griseb.) Lillo by having wider leaves and wider fruits with a differently shaped wing. The fruit wing of *T. uleana* is often curved downward (retrorsely), and this character is diagnostic; a third rudimentary wing is often present. The species has not been found since 1889.

6. **Terminalia eichleriana** Alwan & Stace, nom. nov. pro *T. punctata* Eichler in C. Martius, Fl. Bras. 14(2): 85. 1867, nom. illegit, non Roth (1821), nec Spruce ex Eichler (1867) (nom. syn. pro *Buchenavia punctata* Eichler). TYPE: Brazil. Bahia: Serra d'Acurra, *Blanchet 2794* (lectotype, BR; isolectotypes, BM, BP, BR, F, FI, G, K, LE, P, RB). The specimen chosen as lectotype was annotated by Eichler, who did not see fruits, although the isolectotype at G does bear fruits. The isolectotype at FI has the additional data: "Certão do R. S. Francesco, 1838." We know of several later collections, all from the state of Bahia.

Terminalia eichleriana belongs to sect. *Actinophyllae* Engl. & Diels and closely resembles *T. fagifolia* C. Martius in vegetative characters. The leaves usually differ in having 3–5 (vs. 5–12) pairs of lateral veins with a narrower angle of divergence. The fruits are very distinct: in *T. eichleriana* the 3(4) wings are 0.5–0.8 × 0.4–0.5 cm, while in *T. fagifolia* the 2 wings are 0.8–1.3 × 0.5–1.3 cm.

7. **Bucida molineti** (M. Gómez) Alwan & Stace, comb. nov. BASIONYM: *Terminalia molineti* M. Gómez, Anales Soc. Esp. Hist. Nat. 19: 244. 1890, nom. nov. pro *Bucida angustifolia* A. Rich., Hist. Phys. Cuba, Pl. Vasc. 521. 1846, and A. Rich. ex Griseb., Cat. Pl. Cub. 109. 1866, non DC. (1828). We have seen no (presumably Sagra) specimens connected with Richard's 1846 publication, but the specimen of *Wright 2573* at G, labeled "*Bucida angustifolia* Rich. (non DC.) ex Griseb. Cat. Cub. p. 109" is the basis for Grisebach's publication and can be selected as the lectotype of *B. molineti*. De Candolle's *Bucida angustifolia* is *Terminalia amazonia* (J. Gmel.) Exell (type: *Perrottet s.n.*, French Guiana, G).

Terminalia spinosa Northrop, Mem. Torrey Bot. Club 12: 54, tab. 13. 1902, non Engl. (1895).
Bucida spinosa (Northrop) Jennings, Ann. Carnegie Mus. 11: 201. 1917.
B. ophiticola Bisse, Feddes Repert. Spec. Nov. Regni Veg. 85(9–10): 605. 1974.
B. correlliana Wilbur, Taxon 37: 467. 1988, nom. nov. pro *Terminalia spinosa* Northrop, non Engl.

Bucida spinosa (Northrop) Jennings is illegitimate since its basionym (*Terminalia spinosa* Northrop) is a later homonym. Realizing this, Delendick (1984) proposed that *B. spinosa* Jennings be treated as a new species dating from 1917, not realizing that the earlier epithet *molineti* existed and should be used. Moreover, recently the common procedure of legitimizing names in the way that Delendick proposed has been called into question (Wilbur, 1988). Wilbur argued that the original intention of the combining author (Jennings) should not be ignored, and that names should therefore not be "rescued" in the way that Delendick proposed. Accordingly, Wilbur proposed the new name *B. correlliana*. Even if Wilbur's argument is accepted, the name *B. ophiticola* predates *B. correlliana*.

8. **Buchenavia amazonia** Alwan & Stace, sp. nov. TYPE: Colombia. Caqueta: wet tropical forest of Amazon Basin, 1 km N of Solano, 8 km southeast of Tres Esquinas, on Río Caqueta below mouth of Río Orteguaza, 200 m.

Tree 8 m high, 20 cm dbh; bark brown, smoothish; fruits green, oblong. Wet soil of old channel, near river; grass pasture of cleared lowland forest and in lowland forest. 7 Mar. 1945, *Little & Little 9626* (holotype, US; isotype, COL).

Frutex vel arbor parva, 2–8 m alta. Folia spiraliter ordinata ad ramulorum apices congesta; petiolus 0.8–2 cm longus, dense rufo-pubescens, saepe biglandulosus; lamina chartacea, (2–)3–8(–12.5) × 1.5–4(–5.5) cm, obovata vel anguste obovata vel elliptica, apice rotundato-obtusa vel acuminato-subacuta, basi cuneata, supra fere glabra, subtus fere glabra, venis primariis secundariisque sparse pubescentibus exceptis; venatio brochidodroma vel eucamptodromo-brochidodroma; costa media infra prominens; venae secundariae infra prominentes, 5–7 paribus; venae tertiariae irregulariter percurrentes, conspicuae; areolae parvae, perfecte effectae. Inflorescentiae elongato-spicatae; pedunculus gracilis, 0.5–1.5 cm longus, rufo-pubescens; rhachis 1.5–3 cm longa, pubescens. Flores 2–3(–4) × 2–3 mm; receptaculum inferum 1–2 mm longum, infime tomentosum; receptaculum superum glabrum. Fructus ellipsoideo-ovoideus, 1.3–2 × 0.7–1.2 cm, apice rotundato-obtuso vel subacuto vel breviter apiculato, basi rotundato-obtusa, sparse puberula; endocarpium in sectione transversali circulare, longitudinaliter sulcatum.

Other specimens have been seen from Colombia (Caqueta), Brazil (Amazonas), Peru (Loreto), and Ecuador (Napo), and a specimen possibly of this species from French Guiana.

This species resembles *B. oxycarpa* (C. Martius) Eichler in leaf characters, but the fruit is pubescent and not beaked. The fruit resembles that of *B. viridiflora* Ducke, but the leaves have a much closer and more conspicuous vein reticulation, and are thinner in texture and usually broader.

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SOLANUM ALLOPHYLLUM (MIERS) STANDL. AND THE GENERIC DELIMITATION OF *CYPHOMANDRA* AND *SOLANUM* (SOLANACEAE)[1]

Lynn Bohs[2]

ABSTRACT

Solanum allophyllum has previously been placed in *Cyphomandra* and in *Solanum*. This species has a number of morphological features not found in *Cyphomandra*, but has been included in the genus because it has a similar growth habit, three-leaved sympodial units with inflorescences in branch forks, and tapered anthers with an abaxial thickening. When each of these characters is closely examined, however, important differences are found between the taxa, indicating that the features they share may not be structurally homologous. New evidence derived from crossing studies and cytological investigations also supports the exclusion of *S. allophyllum* from *Cyphomandra*. *Solanum allophyllum* is self-compatible, whereas all but the single domesticated species of *Cyphomandra* are self-incompatible, and the chromosomes of *Cyphomandra* are about 2.5 to 5.5 times larger than those of *S. allophyllum*. The anther morphology, self-compatibility, and small chromosomes are all consistent with placement of this species in *Solanum*.

INTRODUCTION AND TAXONOMIC HISTORY

The generic placement of the species here known as *Solanum allophyllum* (Miers) Standl. has long been a source of confusion. Various workers have placed this species in *Solanum*, *Cyphomandra*, and *Bassovia*. It was first described as *Pionandra allophylla* by Miers (1854) in Seemann's *Botany of the Voyage of the H.M.S. Herald. Pionandra*, erected by Miers in 1845, is synonymous with Sendtner's genus *Cyphomandra*, created a few months earlier (Sendtner, 1845). Accordingly, *P. allophylla* was transferred to *Cyphomandra* by Hemsley in 1882. Standley transferred *Cyphomandra allophylla* to *Solanum* in 1927 without explanation.

Georg Bitter, unaware of Miers's species, independently described the species as *Solanum ellipsoideibaccatum* Bitt. in 1913. He noted that the tapered anthers with small terminal pores resemble those of *Solanum* subg. *Leptostemonum* (Dun.) Bitt. but surmised that his species probably represented a new section of *Solanum*. In 1914, Bitter received specimens illustrating the lobed leaves that often occur on the lower branches in this species. He emended his original description to include these lobed leaves and described a new variety, var. *ficilobum* Bitt., from a specimen exhibiting almost exclusively lobed leaves. Pittier (1947) later transferred *Solanum ellipsoideibaccatum* to the genus *Bassovia*, an error that Hunziker (1969) later corrected. *Solanum ellipsoideibaccatum* and its variety *ficilobum* are regarded here as synonyms of the earlier name *Solanum allophyllum* (Miers) Standley.

Standley's placement of the species in *Solanum* was followed in the older literature (Morton, 1944; Romero-Castañeda, 1965; Standley, 1928), but more recent workers have interpreted it as belonging in *Cyphomandra* (Bohs, 1986, 1988; Child, 1984; D'Arcy, 1973). All those who have included the species within *Cyphomandra* have noted its atypical anther structure, but placed it in *Cyphomandra* on the basis of other similarities. Child (1984) called attention to its anomalous features

[1] I thank Alan Child for sending seeds of *S. allophyllum* and several *Cyphomandra* species and for his insightful discussions on relationships in *Solanum* and *Cyphomandra*. I also thank Dave Barrington, John Sperry, and Mel Tyree for use of their lab facilities, and Greg Anderson, Dave Barrington, W. G. D'Arcy, George Rogers, and John Sperry for reading and commenting on the manuscript.

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when he erected *Cyphomandra* sect. *Allophylla* Child to accommodate this species and the allied *Cyphomandra phytolaccoides* (Rusby) Child (= *Solanum mapiriense* Bitter).

Why has the generic placement of this species been so uncertain? Though *S. allophyllum* differs from *Cyphomandra* in a number of morphological characters, it has been considered as a *Cyphomandra* because, at least superficially, this species shares with *Cyphomandra* the very features that have been used to distinguish *Cyphomandra* from *Solanum*. Both *S. allophyllum* and *Cyphomandra* have: 1) a growth habit characterized by a single erect trunk and a spreading crown of three main lateral branches, 2) three-leaved sympodial units with the inflorescences situated mainly in branch forks, and 3) tapered anthers that are thickened on the abaxial surface. Growth habit and branching pattern have been recently proposed as new characters that distinguish *Cyphomandra* from *Solanum* (Bohs, 1986). Anther structure traditionally separates the two genera (Sendtner, 1845). Herein I reexamine the morphological features of *Cyphomandra* and *S. allophyllum* with emphasis on these three proposed generic characters. New information about the breeding system and morphology of the chromosomes, pollen, and seeds of *S. allophyllum* and *Cyphomandra* is also compared. These investigations help to ascertain the generic position of this species and shed new light upon the critical characters that separate *Solanum* and *Cyphomandra*.

Materials and Methods

Morphological studies were carried out using living plants, and dried specimens from the following herbaria: A, BM, C, E, F, GH, K, M, MO, NY, P, US, and WIS. Voucher information for greenhouse material is given in the Appendix.

Growth habit is defined by reference to the architectural models of Hallé et al. (1978). This system takes into account the dynamic aspects of plant growth rather than simply considering the shape of a plant at any one time. Terminology relating to architecture and branching pattern likewise follows Hallé et al. (1978).

Compatibility studies were conducted on plants growing in pollinator-free greenhouses at Harvard University and at the University of Vermont. One to several accessions were grown of each species. Plants were either selfed or outcrossed, between accessions and between individuals of the same accession, by tapping pollen onto a clean glass slide and rubbing it across the stigma of the female parent.

For observations of meiotic chromosomes, flower buds were fixed in Farmer's solution (3 : 1 absolute ethanol : glacial acetic acid) or Carnoy's fixative (6 : 3 : 1 absolute ethanol : chloroform : glacial acetic acid) shortly after sunrise. Preparations were stained with 1–2% acetocarmine and squashed in Hoyer's solution. Root tips for mitotic chromosome observations were pretreated for up to 24 hours in a saturated solution of paradichlorobenzene at approximately 4°C, then fixed in Farmer's solution for up to 24 hours. Root tips were then stored in 70% ethanol until use, hydrolyzed in 1 N HCl for 10 minutes at 60°C, and stained as above.

Histological preparations of anthers were obtained from flowers that had been fixed in FAA, dehydrated in an alcohol series, embedded in Paraplast, sectioned, and stained with safranin/fast green.

Pollen measurements were made from fresh pollen samples obtained from greenhouse plants. The grains were shaken into a mixture of 1–2% acetocarmine and Hoyer's solution and allowed to stand for exactly 10 days before measurement. Measurements of the polar and equatorial axes on 30 grains per sample were made from a 400× camera lucida projection onto a Zeiss ZIDAS digitizer. Pollen diameter was measured on stained grains only, and was taken as the distance between the innermost layers of the pollen grain wall. Pollen volume was calculated using the formula for the volume of an ellipsoid, $V = \pi PE^2/6$, where E is the equatorial diameter and P is the polar diameter. An analysis of variance revealed no significant difference between equatorial diameter as measured in polar and equatorial views, so P and E were measured in equatorial view only.

Pollen samples for scanning electron microscope (SEM) photos were taken from dried herbarium material. The grains were mounted on the stub with double-stick tape and coated with gold-palladium. Fresh pollen from greenhouse plants that was critical-point dried and coated appeared collapsed under the SEM.

Results

Distribution, Ecology, and Morphology

Table 1 compares the morphological and ecological characteristics of *S. allophyllum* and *Cyphomandra* discussed below.

The ecological distribution, phenology, and generation time differ greatly in *S. allophyllum* and

TABLE 1. Comparison of morphological and other characters in *Cyphomandra* and *Solanum allophyllum* (details in text).

	Cyphomandra	*Solanum allophyllum*
Habitat	Mesic forest	Seasonally dry forest
Generation time	Usually > 1 yr.	< 1 yr.
Height	Up to 10 m	Up to 1.5 m
Leaf bases	Usually cordate or truncate, rarely decurrent	Subcordate to truncate, decurrent
Numer of flowers per inflorescence	> 10	4–6
Pedicel length	> 10 mm	4–6 mm
Corolla shape	Urceolate, campanulate, or stellate, not plicate	Rotate-stellate and plicate
Fruit color	Red, yellow, orange, purple, or green, never white	White to orange
Fruit shape	Not laterally compressed	Laterally compressed
Architectural model	Intermediate between Prevost's and Nozeran's models	"Fragment" of Prevost's or Nozeran's models
Sympodial units	3–4-leaved, rarely 5-leaved	3-leaved
Anthers	Tapered or not, with distinct and enlarged connective	Tapered, without enlarged connective

Cyphomandra. *Solanum allophyllum* has been collected from a single site in Honduras and is more abundant from Costa Rica and Panama through northwestern South America (Fig. 1). Although the plants are found in a variety of habitats, in Costa Rica and Panama the species seems to grow in drier sites than *Cyphomandra* species, which are almost always mesic-forest dwellers. No herbarium collections of this species from Costa Rica or Panama were made in the months of January–March, the dry season in these regions (Coen, 1983; Croat, 1978). This may indicate that *S. allophyllum* persists by losing its leaves during the dry season and perennating via its roots or larger shoots, but further field studies of this species are needed to ascertain its phenology. In the greenhouse the plants flower and fruit within five months from planting. This generation time is much shorter than most cultivated cyphomandras, which often take several years to reach reproductive age. *Solanum allophyllum* is a weakly woody shrub that rarely grows over 1.5 m tall (Fig. 2), in contrast to the majority of *Cyphomandra* species, which develop abundant secondary xylem and may reach heights of up to 10 m.

The subcordate to truncate leaf bases of *S. allophyllum* are decurrent along the petiole (Fig. 3). The leaves of *Cyphomandra* usually have cordate or less frequently truncate bases; decurrent leaf bases occur only in *C. fragilis* Bohs.

The inflorescences of *S. allophyllum* are unbranched and bear 4–6 flowers on short pedicels 4–6 mm long. Those of *Cyphomandra* can be branched or unbranched, typically bear more than 10 flowers, and have pedicels longer than 10 mm. The shape of the corolla of *S. allophyllum* can best be described as rotate-stellate (sensu Correll, 1962): fairly long corolla lobes are present, but these are connected at the base by abundant interpetalar tissue that is plicate in the bud (Fig. 4). This type of corolla is often seen in *Solanum* subg. *Potatoe* (G. Don) D'Arcy. In contrast, the corolla of *Cyphomandra* has various shapes, but never rotate-stellate or plicate.

Solanum allophyllum produces some of the most distinctive fruits in the Solanaceae. At maturity, they are glabrous and white or occasionally orange mottled with green or purplish markings. The fruits are ellipsoidal or oblong in outline, and are laterally compressed and appear elliptic in cross section (Fig. 5). Within them are many very small flattened seeds and 3–6 small stone cell aggregates. The fruits differ from those of all species of *Cyphomandra* in color and shape, and the seeds are much smaller and more numerous than those of any species of *Cyphomandra*. In the greenhouse and presumably also in the field, the fruits fall to the ground while still hard and bitter and then ripen for several weeks before becoming soft and palatable and emitting a strong sweet odor. They are most likely dispersed by ground-dwelling animals. Those of *Cyphomandra* are held on the tree and

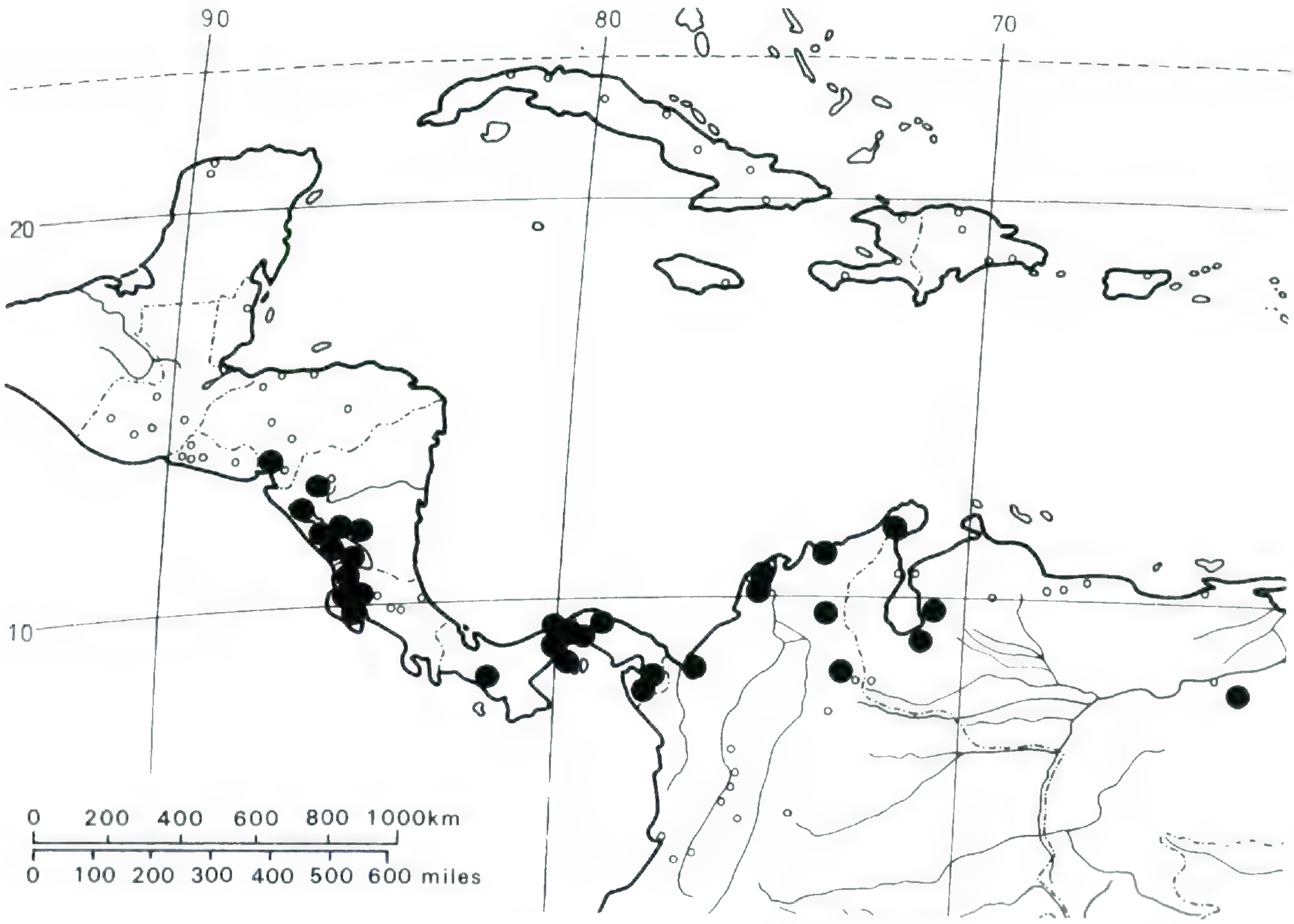


FIGURE 1. Distribution of *Solanum allophyllum*. (Base map copyright 1979 by the University of Utrecht.)

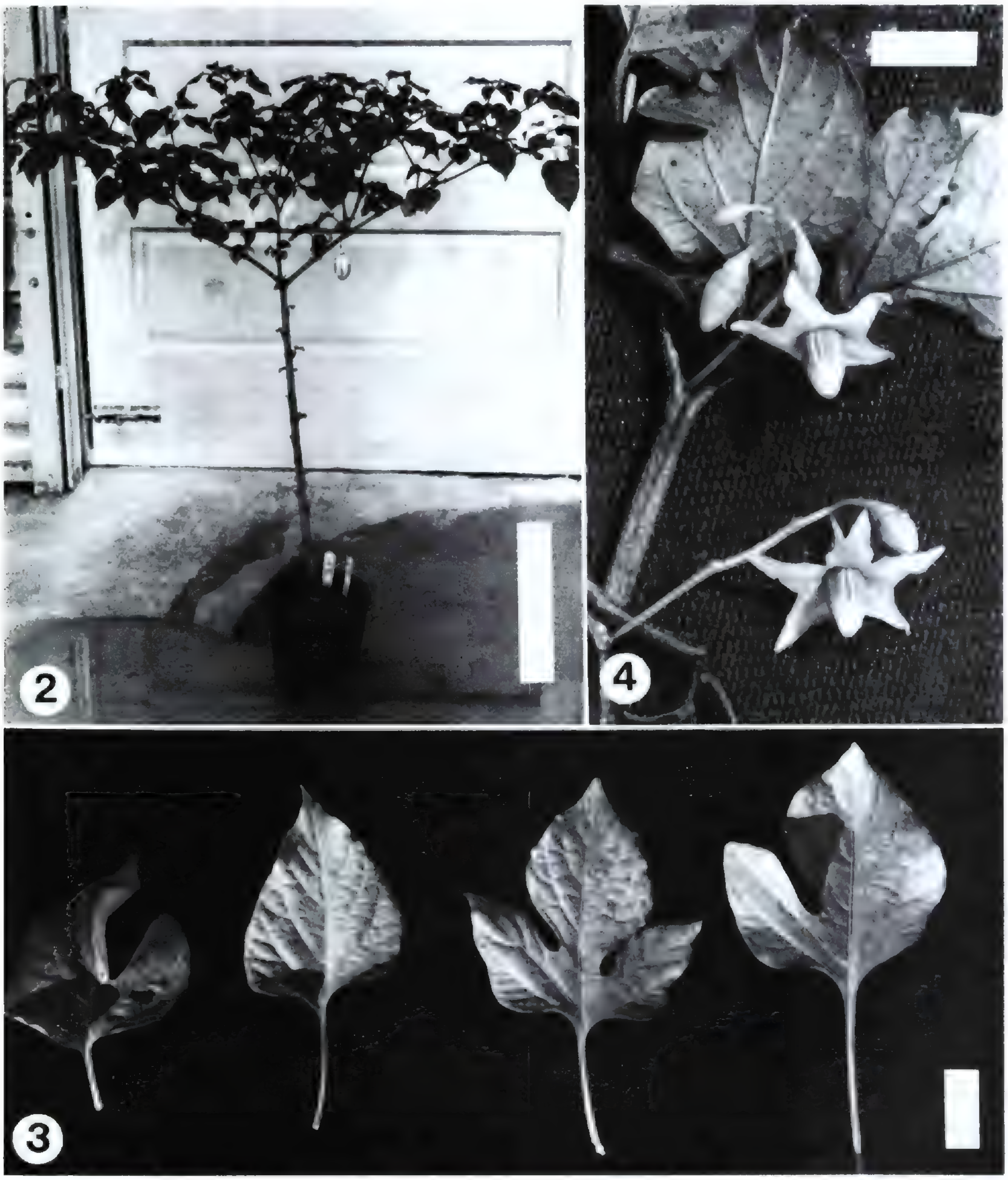
only fall after they are completely ripe. Their dispersal agents are unknown, but they may be attractive to birds or bats.

ARCHITECTURE

The distinctive growth habit or shape of *S. allophyllum* and many species of *Cyphomandra* is a conspicuous feature that allows the plants to be recognized easily in the field. In terms of architecture, however, *Cyphomandra* and *S. allophyllum* are similar only in the initial phase of their growth (Fig. 6). In both, the seedling axis produces a single orthotropic, or upright, trunk with the leaves spirally arranged in a 2/5 phyllotaxis. This trunk ends with the production of a terminal inflorescence. Usually three plagiotropic, or horizontal, shoots then elongate from axillary buds located just below the inflorescence to produce a spreading crown (Fig. 6A, D). Further branching within the crown occurs by sylleptic elongation of axillary shoots immediately below the successive terminal inflorescences; thus the crown is composed of a series of sympodial units where all the flowers and fruits are borne. Beyond this, *Cyphomandra* and *S. allophyllum* diverge in their architecture.

In *Cyphomandra*, after continued sympodial growth and numerous episodes of flowering and fruiting, the plagiotropic branches begin to senesce. A new trunk then arises proleptically from an axillary bud on the old trunk below the branch tier and continues orthotropic growth until another terminal inflorescence and branch tier is produced. In this way, the main axis is composed of successive sympodial trunk modules bearing spatially and temporally separated reproductive crowns (Fig. 6B, C). I have seen this architecture in at least six species of *Cyphomandra*, and it is probably widespread in the genus. In contrast to *Cyphomandra*, *S. allophyllum* does not produce successive trunk modules. The whole plant in *S. allophyllum* is therefore equivalent to a single structural unit of the *Cyphomandra* growth form.

The architecture of *Cyphomandra* described above occupies an intermediate position between Prevost's and Nozeran's models in the scheme of Hallé et al. (1978). Both models have an orthotropic sympodial trunk and tiered plagiotropic



FIGURES 2–4. *Solanum allophyllum*. —2. Greenhouse-grown plant. Scale bar = 0.25 m. —3. Leaves from trunk. Scale bar = 2 cm. —4. Flowers. Scale bar = 1 cm.

branches. In Prevost's model both the trunk and plagiotropic branches generally have spirally arranged leaves, whereas in Nozeran's model the orthotropic and plagiotropic branches have highly contrasting leaf arrangements, usually with spiral phyllotaxis on the trunk and distichous phyllotaxy on the branches. Plagiotropy of the branches in Nozeran's model is perpetuated if a crown branch is independently propagated, whereas in Prevost's model the plagiotropy of the crown branches is usually lost when they are separated from the trunk. The leaf arrangement of the crown branches in *Cyphomandra* is affected by pronounced twisting of the axes and differential elongation of branch internodes (see section on branching pattern below for a more detailed description of leaf arrangement, and Danert, 1958, 1967, for comparative morphology of the shoot systems in Solanaceae). Therefore, although the leaf arrangement on the plagiotropic shoots is not distichous, the crown branches show pronounced dorsiventral symmetry in contrast to the radial symmetry of the spirally arranged trunk leaves. Cuttings taken from the crown region of *C. betacea*, *C. diploconos*, and *C. diversifolia* produce lower, bushier plants than those taken from the upright axes (Fletcher, 1979; pers. obs.),

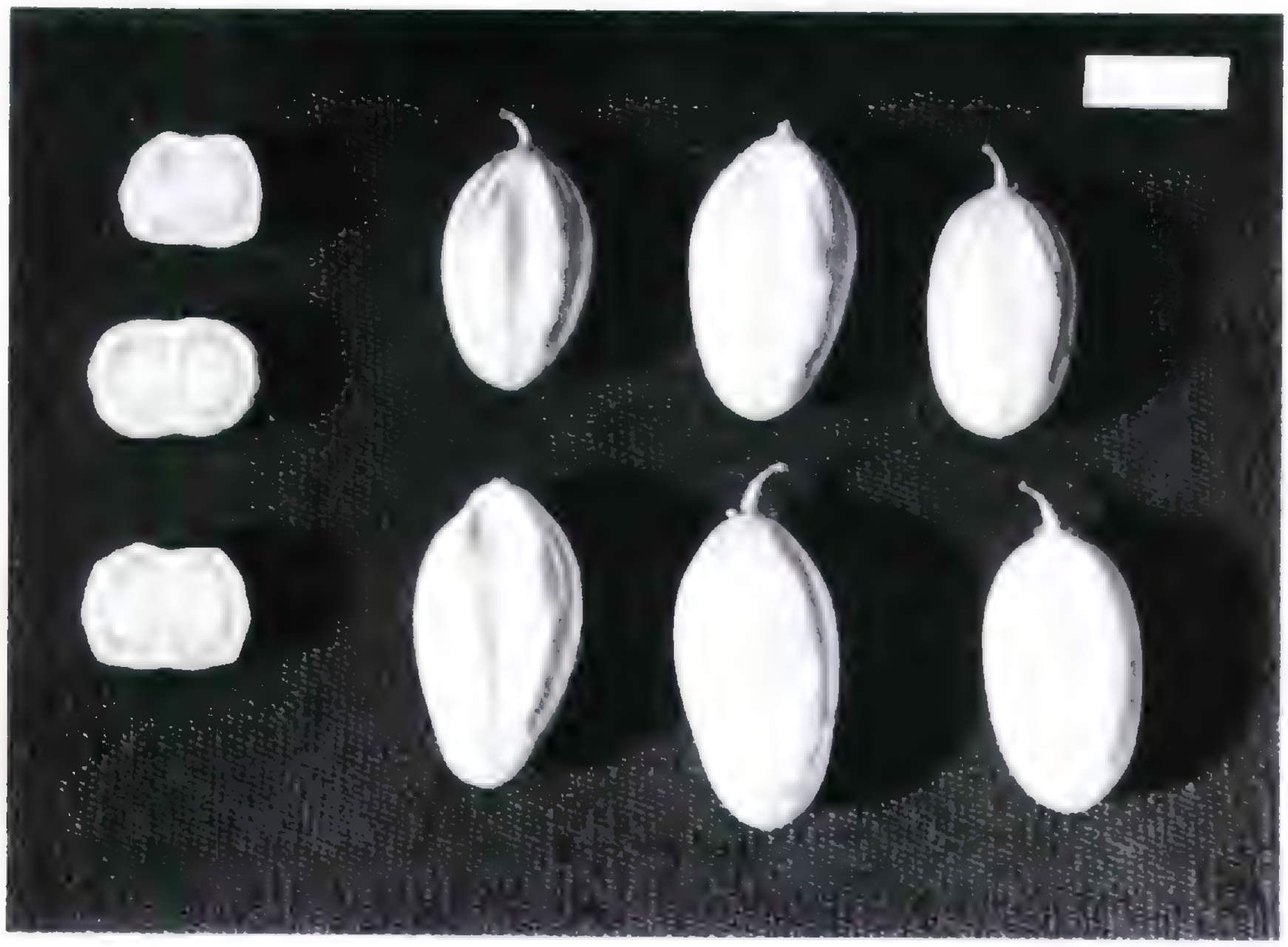


FIGURE 5. Fruits of *Solanum allophyllum*. Scale bar = 2 cm.

so these species apparently exhibit the inherent nature of plagiotropy in the crown branches characteristic of Nozeran's model. At least until an accurate interpretation of leaf arrangement on the plagiotropic shoots is available, it is probably best to consider *Cyphomandra* as being intermediate between Prevost's and Nozeran's model.

The architecture of *S. allophyllum* does not strictly conform to any of the models defined in Hallé et al. (1978). It most closely resembles Leeuwenberg's model, which is exhibited by several species of *Solanum* and *Capsicum* (Hallé et al., 1978). However, in Leeuwenberg's model, all the axes are orthotropic and equivalent, whereas in *S. allophyllum* there is evident differentiation between the trunk and crown branches. Perhaps the best way to characterize the architectural form of *S. allophyllum* is to consider that it may have been derived by "fragmentation" from more woody counterparts with multiple trunk modules, such as those seen in *Cyphomandra*. Fragmentation occurs when only a portion of the original tree model is expressed, and is commonly seen in herbaceous relatives of woody plants with more strongly developed trunk modules. Should it indeed be the case that the architectural form of *S. allophyllum* is related in this way to more extensive tree models, it may argue that this relatively herbaceous species has been derived by reduction and fragmentation from woody ancestors.

BRANCHING PATTERN

Three- to four-leaved sympodial units are the rule within the crown of nearly all species of *Cyphomandra* (Fig. 7); the only known exception is *C. corymbiflora*, which frequently has five-leaved sympodia. Three-leaved sympodial units are also characteristic of *S. allophyllum*. Commonly, the leaf subtending the renewal shoot is carried up to a point nearly opposite that of the first leaf produced on the axillary shoot so that the seemingly opposite leaves are actually members of successive sympodial shoot generations. In *S. allophyllum* and in many species of *Cyphomandra*, two renewal shoots grow out from below the terminal inflorescence, thus situating it in a branch fork. This shoot structure was previously thought to be peculiar to *Cyphomandra* (Bohs, 1986), and its presence in *S. allophyllum* was evidence supporting the inclusion of the species within *Cyphomandra*. Members of *Solanum* may have one- to many-leaved sympodial units, and the inflorescences may be axillary, extraaxillary, opposite a leaf or leaf cluster, or rarely in branch forks.

Subtle differences exist in leaf and shoot arrangement within the crown branches of *Cyphomandra* and *S. allophyllum* apart from the leaves and branches making up the sympodial shoot structure. In *S. allophyllum*, nearly all the axillary buds of the crown expand into short shoots, giving the

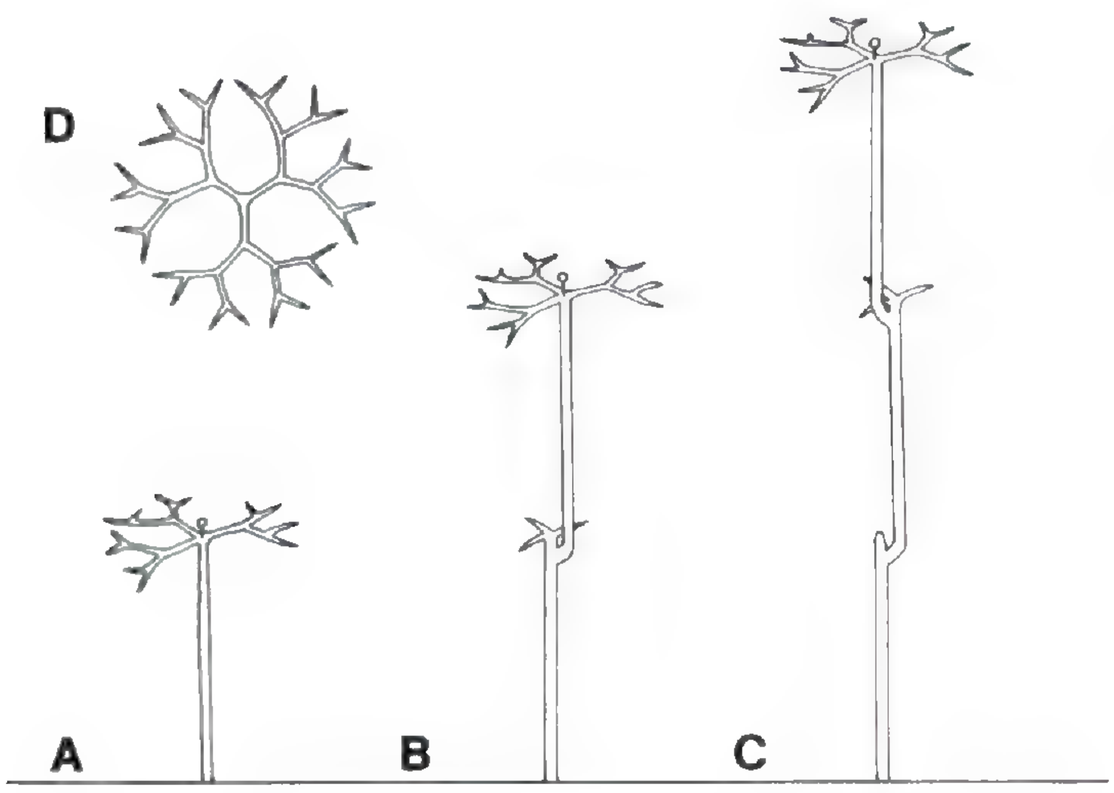


FIGURE 6. Architecture of *Cyphomandra* and *Solanum allophyllum*. —A, B, C. Successive growth stages in *Cyphomandra*, showing the sympodial nature of the trunk and the plagiotropic orientation of the crown branches. *Solanum allophyllum* does not develop beyond stage A. —D. Top view of crown, showing three main plagiotropic branches.

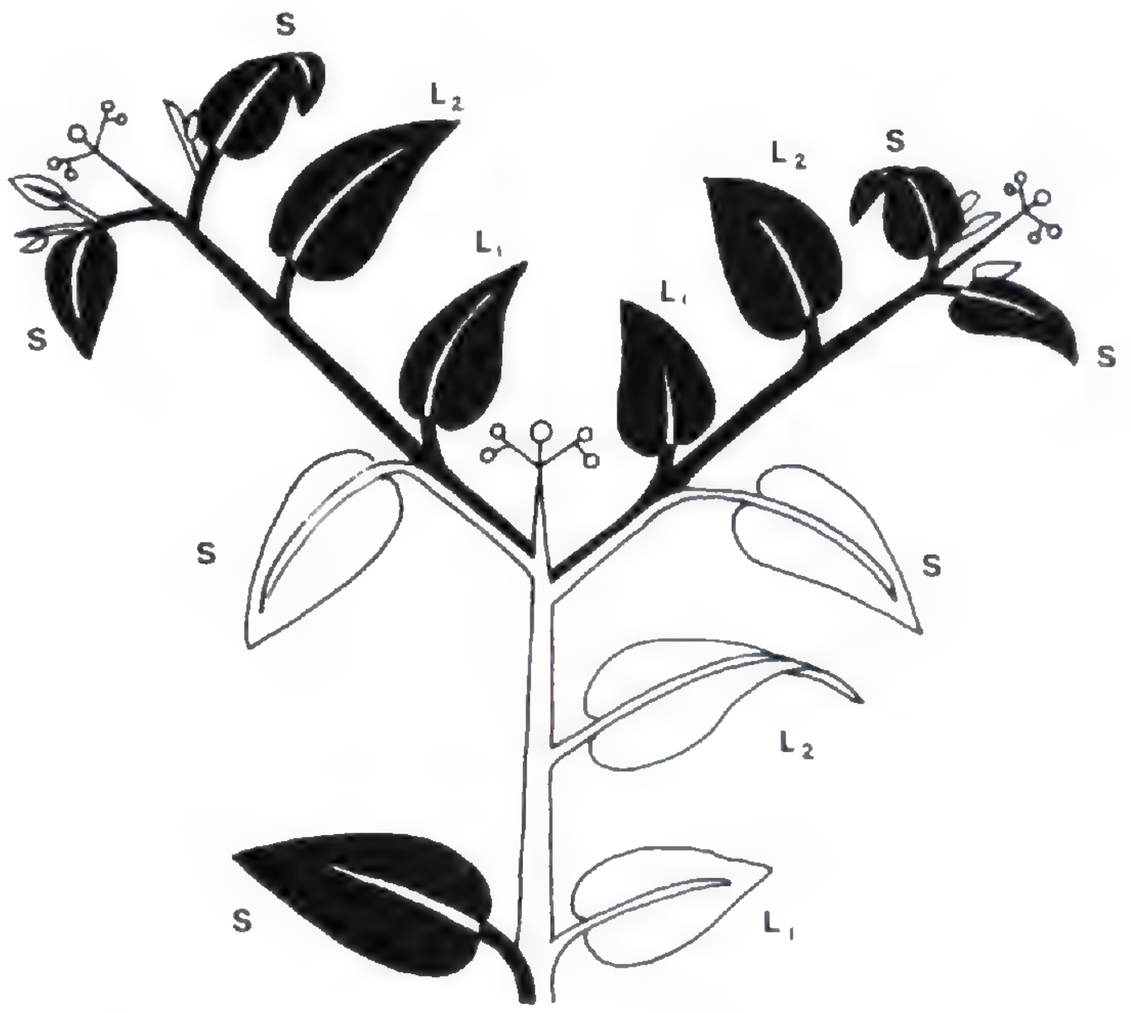


FIGURE 7. Diagram of branching pattern in the crown of *Cyphomandra* and *Solanum allophyllum*. Black and white shading denotes successive sympodial units. The subtending leaf (S) of the axillary shoot has been carried up to a level subopposite the first leaf on this shoot (L_1). The diagram shows a species with four-leaved sympodia; in three-leaved sympodia, the leaf L_2 is absent.

crown a dense leafy appearance. In *Cyphomandra*, sylleptic growth is restricted to the axillary buds immediately subtending the terminal inflorescences of the sympodial units, the rest of the buds remaining dormant unless released by pruning or breaking the tip of the branch. In the greenhouse, *S. allophyllum* also undergoes pronounced seasonal reiteration, with expansion of many buds on the trunk by prolepsis and elongation of the short shoots of the crown. It is not known whether *S. allophyllum* reiterates in this way under natural conditions; as already mentioned, it may die back to the main stem each year and produce a new plant conforming to the initial model at the beginning of the rainy season.

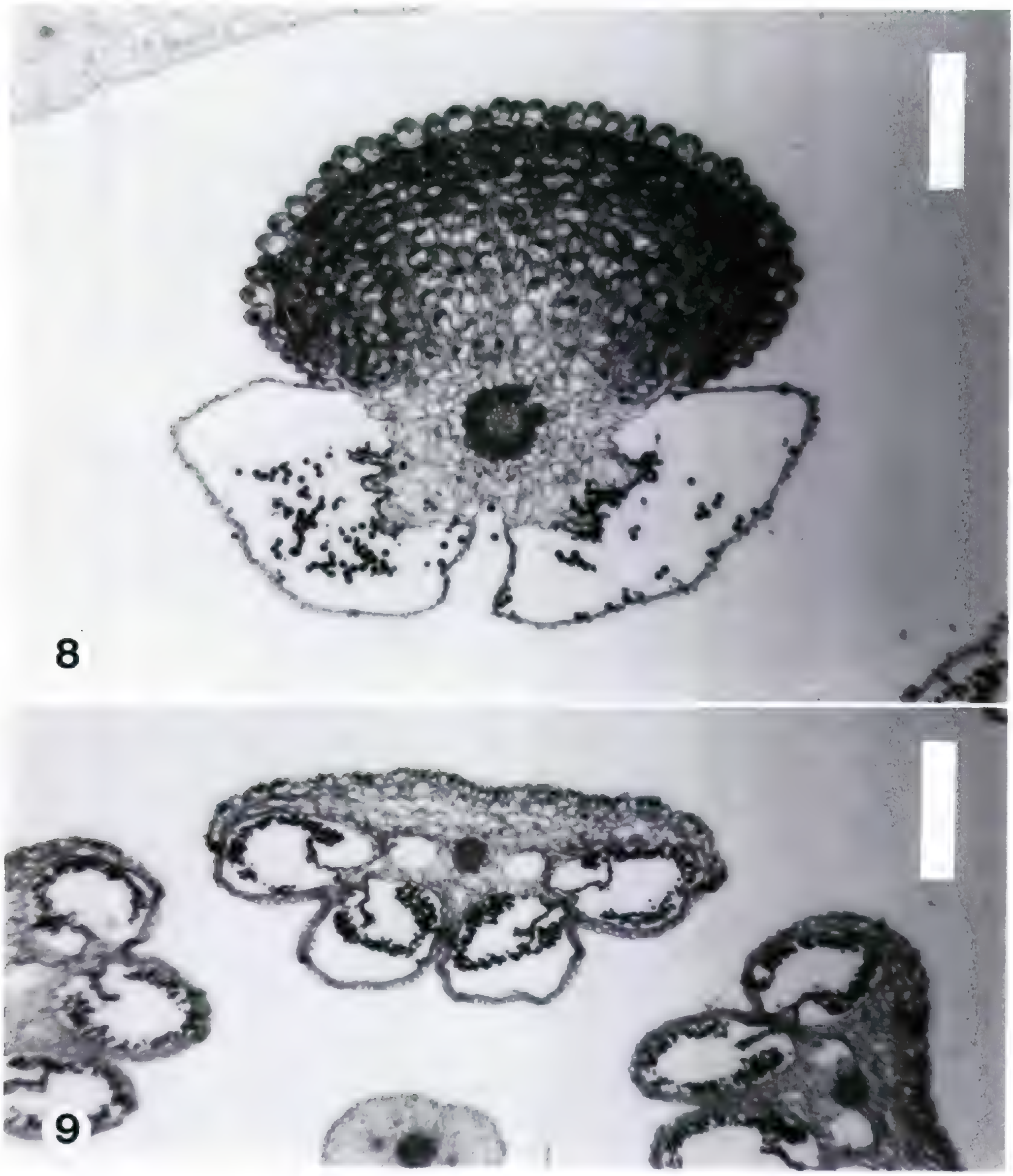
ANTHER MORPHOLOGY

Tapered anthers with an abaxial thickening occur in *Cyphomandra* and *S. allophyllum* (Figs. 8, 9). Anther shape is not a definitive characteristic of either genus, however; tapered anthers occur in other species of *Solanum* (e.g., in subg. *Leptostemonum* (Dun.) Bitt., subg. *Potatoe* (G. Don) D'Arcy, and sect. *Herposolanum* Bitt.), and although they are common in *Cyphomandra*, they are not exhibited in all of its species. There is no present evidence to indicate that tapered anthers are homologous within or among these groups. A more important criterion for distinguishing *Cyphomandra* from *Solanum* is found in the enlarged anther connective. In *Cyphomandra*, the anther connective is usually very thickened and prominent abaxially and is sharply delimited from the thinwalled anther thecae. Anthers of *Solanum* can be thickened in various ways, but they never have a distinct and abaxially prominent connective.

Solanum allophyllum has a thickened area on the abaxial side of the anther that has been interpreted as an enlarged connective like that of *Cyphomandra*, and has led to the inclusion of *S. allophyllum* within *Cyphomandra*. Microscopic cross sections through the anther region of *S. allophyllum* and a representative of *Cyphomandra*, *C. diversifolia* (Dun.) Bitt., show that anther structure is very different in the two taxa. In *Cyphomandra* (Fig. 8), the thickened portion is expanded

TABLE 2. Compatibility studies in *Cyphomandra* and *Solanum*.

	Selfed		Outcrossed	
Taxon	N	% Successful crosses	N	% Successful crosses
C. betacea	20	55%	36	36%
C. diversifolia	77	0%	152	6%
C. diploconos	108	0%	117	66%
C. hartwegii	38	0%	19	32%
C. uniloba	33	0%	11	55%
C. acuminata	60	0%	-	
C. corymbiflora	32	0%	30	93%
Solanum allophyllum	21	48%	52	31%



FIGURES 8, 9. Transverse sections through anthers.—8. *Cyphomandra diversifolia*.—9. *Solanum allophyllum*. Scale bars = 0.5 mm.

abaxially, the thecal walls are free and do not contribute to the thickening, and there is a sharp demarcation between the swollen connective and the thin-walled anther thecae. In contrast, the thickened area in *S. allophyllum* is not expanded abaxially and is contiguous with the walls of the anther thecae (Fig. 9). There is a gradual rather than abrupt transition from the thickened area on the abaxial surface to the thin-walled anther thecae. This type of anther structure conforms to that of many other species of *Solanum*. These differences are evident in transverse sections through fully mature anthers; similar studies on developing stages in these species may further emphasize these differences and may also reveal the derivation of the tissue involved in the anther thickening in both taxa.

COMPATIBILITY

Table 2 illustrates the results of controlled pollinations in the greenhouse of flowers of *S. allophyllum* and various species of *Cyphomandra*. The results show that of the seven species of *Cy-*

FIGURE 10. Camera lucida drawings of meiotic chromosomes in microsporangia.—A. *Cyphomandra diversifolia*.—B. *Solanum allophyllum*. A and B at same magnification.

phomandra tested, all are self-incompatible with the exception of the cultivated tree tomato, *C. betacea* (Cav.) Sendtn. In contrast, *S. allophyllum* appears to be self-compatible. Neither *S. allophyllum* nor *C. betacea* sets fruits in pollinator-free greenhouses without deliberate pollination. This indicates that these two species may not be autogamous and require a pollinator to transmit self pollen, or that they may be apomictic and pseudogamous. The style in *S. allophyllum* is not visible directly after anthesis, but elongates and emerges through the anther cone after the anthers dehisce. Thus, protandry may prevent selfing in this species.

CYTOLOGY

The most compelling evidence for the exclusion of *S. allophyllum* from *Cyphomandra* comes from chromosome studies. *Solanum allophyllum* and nine species of *Cyphomandra* that have been examined so far have $n = 12$ chromosomes (Bohs, unpublished data; Pringle & Murray, in press). This chromosome number is common in *Solanum* and the Solanaceae in general. However, chromosomes of the two taxa differ markedly in size (Figs. 10, 11). Investigations of seven species of *Cyphomandra* have revealed that the chromosomes in this genus are very large, averaging about 8 μm in length with a range of approximately 3 to 14 μm (Bohs, unpublished data). DNA amounts as measured by flow cytometry were among the largest yet known in the Solanaceae (Pringle & Murray, in press). In contrast, both the mitotic and meiotic chromosomes of *S. allophyllum* range between 1 and 2.5 μm in length and are thus on the order of 2.5 to 5.5 times smaller than those of *Cyphomandra*.

POLLEN

Pollen grains of *S. allophyllum* and *Cyphomandra* were examined for potential taxonomic characters. The grains of *S. allophyllum* are tricolporate and have exine sculpturing consisting of very small rounded granules best observed with SEM (Figs. 12–14). *Cyphomandra* pollen is also tricolporate, and most species have granular exine sculpturing like that of *S. allophyllum*, although several *Cyphomandra* species (e.g., *C. pendula* (R. & P.) Sendtn. and *C. pilosa* Bohs) lack such granules and have a psilate exine.

Although the aperture type and exine sculpturing show few taxonomically useful differences, the grains of *Cyphomandra* and *S. allophyllum* do differ somewhat in size and shape. Table 3 compares the pollen dimensions and volume of *S. allophyllum* and seven species of *Cyphomandra*. In the terminology of Erdtman (1952, 1969), all species of *Cyphomandra* have spheroidal or prolate spheroidal grains, whereas those of *S. allophyllum* are more elliptic in equatorial view and fall into the subprolate shape class. All taxa ex-

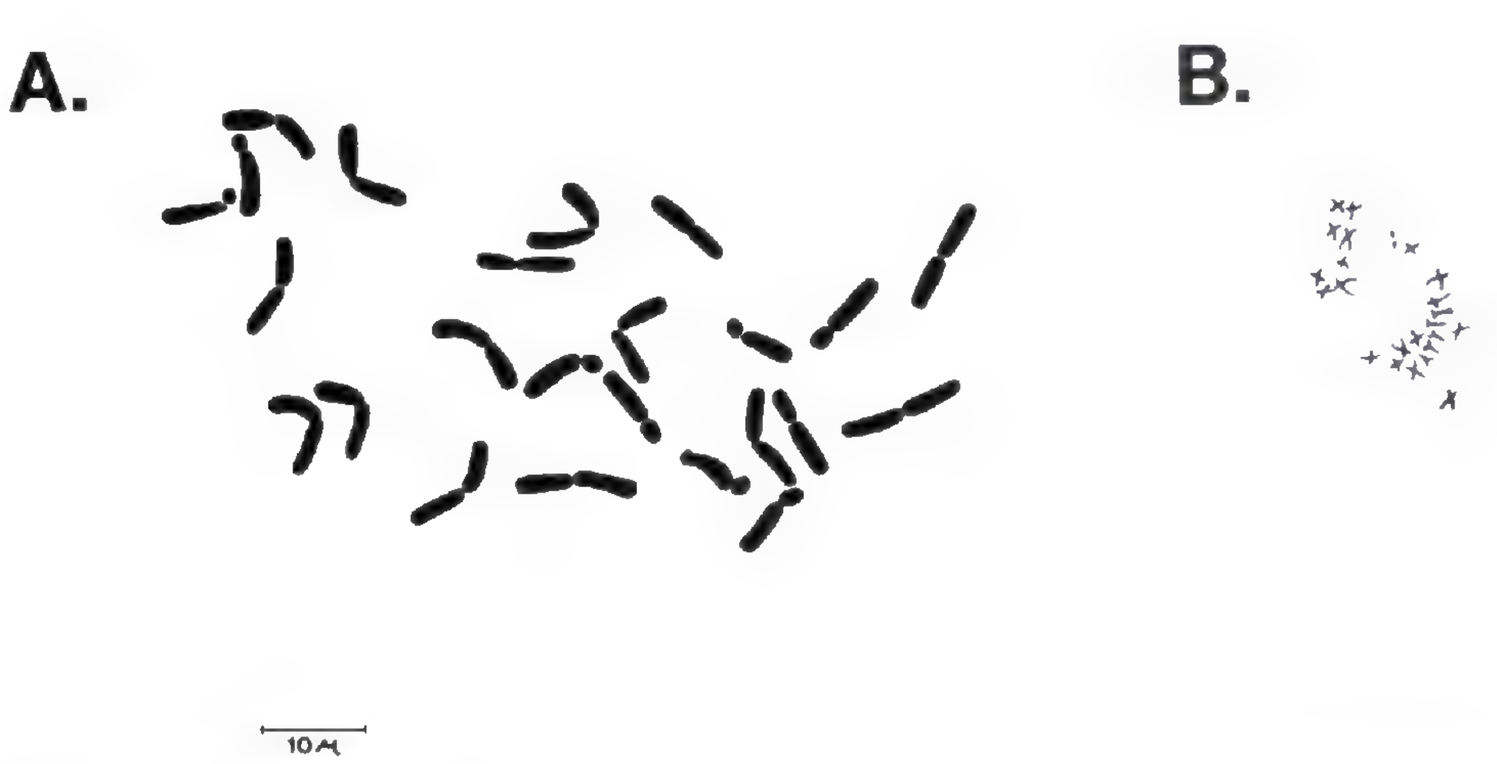
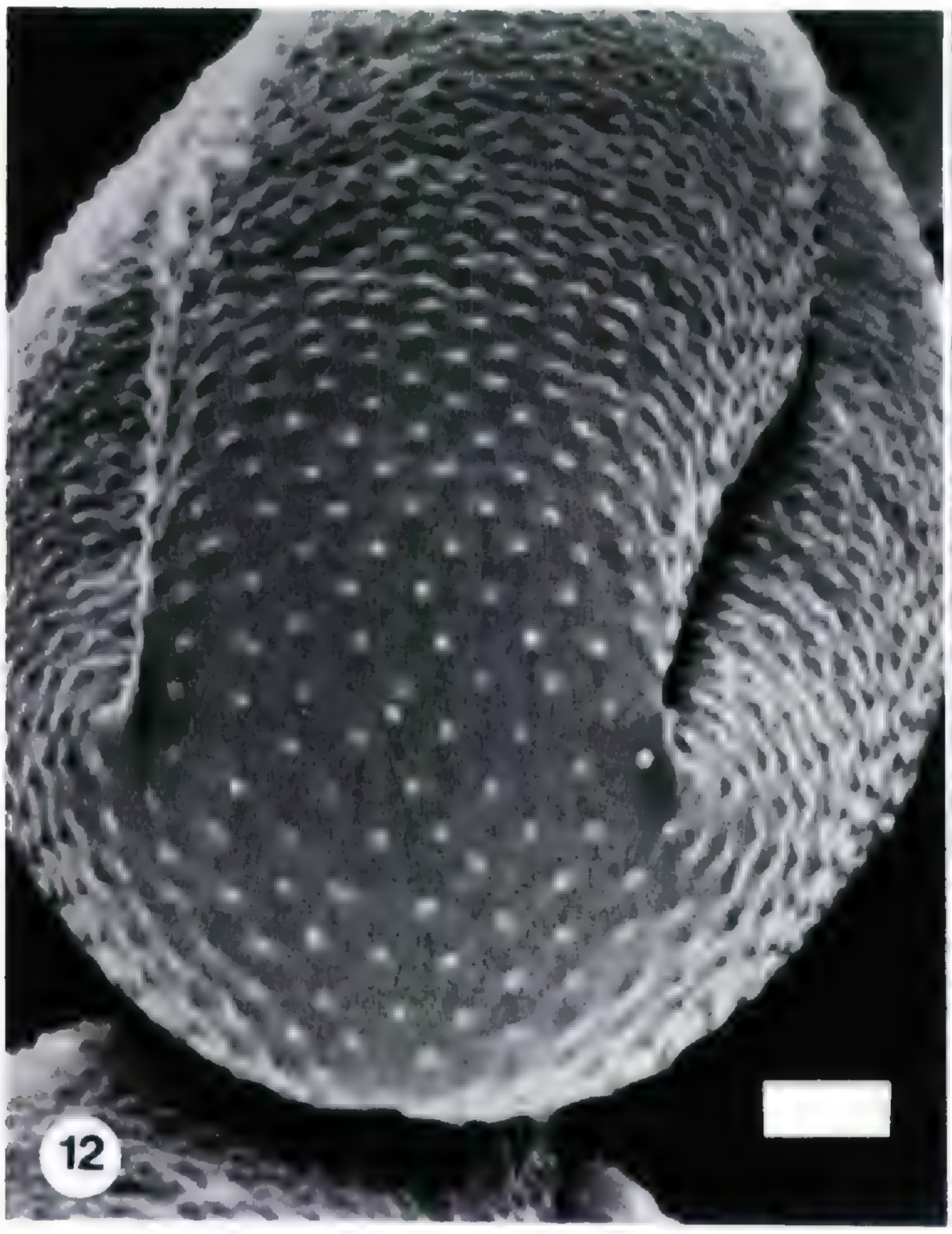
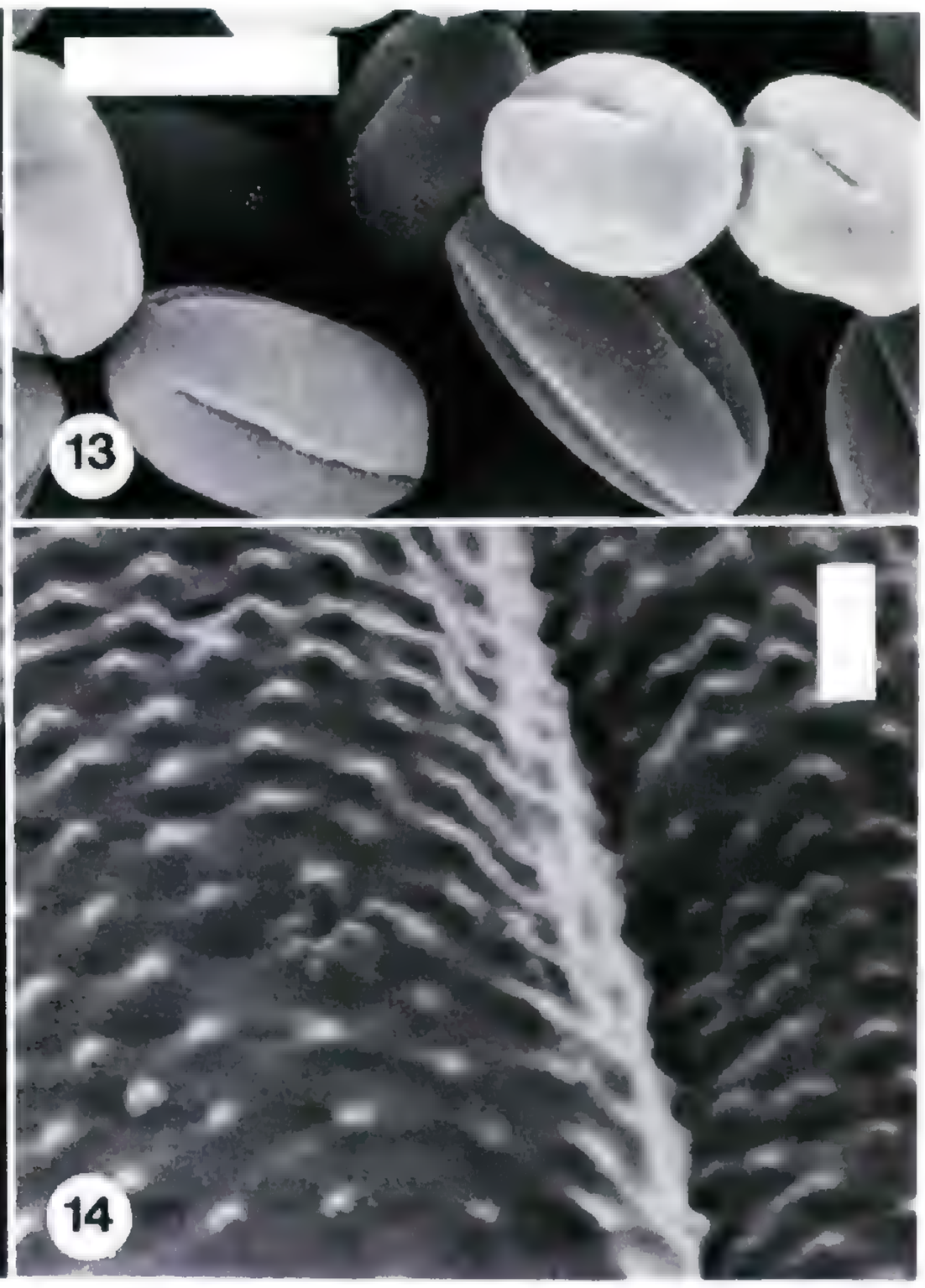


FIGURE 11. Camera lucida drawings of mitotic chromosomes in root tips.—A. *Cyphomandra acuminata*.—B. *Solanum allophyllum*. A and B at same magnification.





FIGURES 12–14. Pollen grains of *Solanum allophyllum*. — 12. Scale bar = 1 μm. — 13. Scale bar = 10 μm. 14. Scale bar = 0.5 μm.

amined have small- to medium-sized grains (again using Erdtman's terminology), but those of *S. allophyllum* are much smaller than any species of *Cyphomandra*. *Cyphomandra* grains have volumes about 2.5 to more than 10 times larger than those of *S. allophyllum*.

SEED SIZE

The seeds of *S. allophyllum* are substantially smaller than those of any of the *Cyphomandra* species examined (Table 3), ranging from about $\frac{1}{35}$ to $\frac{2}{5}$ the size of *Cyphomandra* seeds.

DISCUSSION

There are numerous differences in ecology, phenology, and morphology between *S. allophyllum* and *Cyphomandra*, but these alone do not permit an unequivocal placement of the species in either *Solanum* or *Cyphomandra*. Architecture and some aspects of the branching pattern further differentiate *S. allophyllum* from *Cyphomandra*, but again not enough to place the former definitively in either genus. A problem with the use of these characters is the wide range in architecture and branching pattern seen in *Solanum*. It looks as if these two characters cannot be as useful in distinguishing *Cyphomandra* and *Solanum* as was previously thought.

In contrast, a consideration of anther morphology shows that *S. allophyllum* does not have a distinct and enlarged anther connective like that of *Cyphomandra*. The anther structure formerly interpreted as a similarity between it and *Cyphomandra* is now revealed to be a difference that separates the two taxa. It appears that the presence of an enlarged anther connective is the most reliable morphological criterion for distinguishing *Cyphomandra* from *Solanum*.

The fact that *S. allophyllum* is self-compatible (SC), whereas the majority of *Cyphomandra* species are self-incompatible (SI), is at least an implication that *S. allophyllum* is not a *Cyphomandra*. Both SC and SI are known in *Solanum*, so the inclusion of *S. allophyllum* in *Solanum* is consistent on the basis of this character.

Self-compatibility in *C. betacea* could be an indication of its relatively recent origin. SC is considered to be a derived character in the Solanaceae (de Nettancourt, 1977; Whalen & Anderson, 1981). If this applies equally well to *Cyphomandra*, then the self-compatibility of the cultivated

TABLE 3. Pollen size and seed weight in *Cyphomandra* and *Solanum allophyllum*. Thirty grains/taxon measured for pollen size. Three measurements of 10 seeds averaged for seed weight. Standard deviations given in parentheses after measurements.

Taxon	Pollen polar diameter (μm)	Pollen equatorial diameter (μm)	Pollen volume (μm^3)	Seed weight (10 seeds) (g $\times 10^{-2}$)
C. diversifolia	33.66 (1.89)	31.92 (1.48)	18,068 (2,628)	3.97 (0.064)
C. uniloba	31.28 (1.63)	30.58 (1.42)	15,414 (2,182)	3.44 (0.276)
C. diploconos	29.24 (1.26)	27.73 (1.02)	12,043 (1,801)	1.84 (0.080)
C. acuminata	29.16 (1.09)	26.87 (0.92)	11,057 (1,108)	—
C. betacea	22.47 (1.21)	21.93 (0.76)	5,678 (637)	5.10 (0.127)
C. hartwegii	21.61 (0.96)	20.35 (0.95)	4,706 (587)	24.44 (0.706)
C. corymbiflora	21.45 (1.16)	19.97 (1.32)	4,520 (780)	4.03 (0.682)
S. allophyllum	16.54 (0.75)	14.21 (0.75)	1,756 (232)	0.70 (0.025)

C. betacea would be considered derived, perhaps in response to selection pressures relating to its domestication.

The small chromosomes of *S. allophyllum* conform to the size reported for species of *Solanum* from several different subgenera (Roe, 1967) and are the best indication that this species belongs in *Solanum*. The present study shows that there is a tendency toward large chromosomes in *Cyphomandra*. This appears to be a very useful character distinguishing *Cyphomandra* from *Solanum*. Further studies of chromosome size in the Solanaceae are needed to determine if this character is consistent in other species. Comparison of genome sizes between putatively primitive and derived members of many different plant groups demonstrates that changes in genome size can occur in either direction (Ohri & Khoshoo, 1986). Additional chromosome studies coupled with morphological data may eventually allow us to determine trends in the evolution of genome size in *Cyphomandra*, *Solanum*, and other solanaceous genera.

The exine sculpturing of *S. allophyllum* pollen also resembles that of *Solanum*. Anderson & Gensel (1976) and Edmonds (1984) reported similar granular exine sculpturing in *Solanum* sects. *Basarthrum* (Bitt.) Bitt. and *Solanum*, respectively. The occurrence of the same type of exine sculpturing in *Cyphomandra*, however, argues against the use of this character to distinguish *Cyphomandra* from *Solanum*. This same type of sculpturing also has been reported for other genera related to *Solanum* (Basak, 1967) and is probably the general pollen type of the tribe Solaneae.

The pollen grains and seeds of *S. allophyllum* are much smaller than those of any species of *Cyphomandra*. The pollen dimensions of *S. allophyllum* are comparable to some of the smaller grains reported for *Solanum* (Anderson & Gensel, 1976; Basak, 1967; Murry & Eshbaugh, 1971), and the size of the seeds falls within the range for *Solanum* (pers. obs.). Pollen or seed size has not been critically examined as a taxonomic character separating *Cyphomandra* and *Solanum*.

The small pollen and seeds of *S. allophyllum* may be connected with its small chromosome size. Bennett (1972) observed that genome size was correlated with pollen volume, seed weight, and minimum generation time in various species of herbaceous plants. The association of small chromosome size with small pollen volume, seed weight, and short generation time in *S. allophyllum* may indicate that this correlation also holds in this species. Further observations are needed to ascertain whether these characteristics are correlated in other solanaceous species, and whether pollen and seed size may be used as indicators of chromosome size.

Affinities of *S. allophyllum* within *Solanum* are problematic. This species is allied with two others, *S. mapiriense* Bitter from Bolivia and an undescribed species from Amazonian Peru (Bohs, in prep.). At present I know of no existing section of *Solanum* that accommodates these three species. They are perhaps best regarded as a new section of *Solanum*, as Bitter (1913) suggested. A taxonomic treatment of these three species and a consideration of their placement within *Solanum* will appear in a later paper.

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Appendix. Voucher information.

Solanum allophyllum (Miers) Standley
Seed from *D'Arcy 9472*, collected in Panama, Prov. San Blas, in front of Ustupo. Vouchers: *Bohs 2339* (GH, VT).

Cyphomandra acuminata Rusby
Seed from *Solomon & Escobar 12458*, collected in Bolivia, Prov. Nor Yungas, 8.7 km below Chuspipata on road to Yolosa. Vouchers: *Bohs 2338* (GH, VT).

Cyphomandra betacea (Cav.) Sendtn.
Seed collected by C. Sperling in market, Quito, Ecuador. Vouchers: *Bohs 2274* (GH), *2275* (VT).

Cyphomandra corymbiflora Sendtn.
Seed collected in southeastern Brazil, sent by G. Pringle, D.S.I.R., New Zealand. Vouchers: *Bohs 2343* (GH, VT).

Cyphomandra diploconos (Mart.) Sendtn.
Seed collected in Brazil, Prov. Paraná, city of Curitiba. Vouchers: *Bohs 2335* (GH, VT).

Cyphomandra diversifolia (H. & B. ex Dunal) Bitter
Seed from *Benitez de Rojas 2744*, collected in Venezuela, Estado Aragua, Parque Nacional Henri Pittier. Vouchers: *Bohs 2341* (GH, VT).

Cyphomandra hartwegii (Miers) Sendtn. ex Walp.
Seed collected in Colombia, Dept. Huila, Fundación Merenberg. Voucher: *Bohs 1644* (GH).

Cyphomandra uniloba Rusby
Seed from *Sperling & King 5500*, collected in Bolivia, Prov. La Paz, Dept. Larecaja, between Consata and Mapiri. Vouchers: *Bohs 2283* (VT), *2284* (GH).

NOVELTIES IN SOUTH AMERICAN *MALOUETIA* (APOCYNACEAE)[1]

Mary E. Endress[2]

ABSTRACT

Three new species of *Malouetia* (*M. bubalina*, *M. molongo*, and *M. naias*) and one new variety (*M. pubescens* var. *glabra*) are described. All new taxa are from northwestern South America.

The following novelties have accumulated during studies of the genus *Malouetia*, for the most part in connection with the *Flora of the Venezuelan Guayana*.

1. **Malouetia bubalina** M. E. Endress, sp. nov. TYPE: Colombia. Amazonas: Río Caquetá, Monochoa, 25–30 km en amont de Araracuara, Sabana de Mosco, 30 Dec. 1976, *Sastre & Raichel 5062* (holotype, P). Figure 1.

Arbor lactescens. Folia decussata, lamina late elliptica vel obovata apice breviter et abrupte caudata 8–9.5 cm longa, 4–4.5 cm lata, basi anguste cuneata vel attenuata, coriacea vel subcoriacea, glabra, subtus ad nervorum axillas domatiis conspicuis instructa, nervis lateralibus ca. 6 utroque latere; petioli 3–5 mm longi. Inflorescentiae terminales e fasciculis 12–20-floris compositae. Calyx extus puberulus. Corolla flavida, hypocraterimorpha, tubo 6–6.5 mm longo; lobis ovatis acutis 6–7.5 mm longis, 2.5–3.5 mm latis utrinque dense puberulis; antherae basi faucis tubularis insertae sessiles fere ½ exsertae anguste lanceolatae dorso pilosae; ovarium dense pubescens. Folliculi 2 plus minusve crassi fusiformes 8–10 cm longi, 1 cm diametro versus medium fer 180° usque divergentes; semina 2 cm longa lineari-oblonga pilis longissimis retrorsis comatum basi obtusata.

Medium to large trees up to 30 m tall with abundant white latex; branches rather slender, angled and flattened at the nodes, with a glossy blackish sheen in the younger parts, becoming gray and conspicuously lenticellate with age. Leaves decussate, 8–9.5 cm long, 4–4.5 cm wide, the blades coriaceous to subcoriaceous, broadly elliptic to obovate-elliptic, shortly and bluntly acuminate at the apex, narrowly cuneate to attenuate at the base, the margins revolute, glabrous on both surfaces, the upper surface nitidulous, drying dark brown, the lower surface opaque, paler, with conspicuous domatia in the axils of the midvein; secondary veins ca. 6 on each side, arcuate-ascending, anastomosing before the margin, impressed on the upper surface, prominulent and darkened on the lower surface; tertiary veins inconspicuous on both surfaces; petioles 3–5 mm long, canaliculate, glabrous. Inflorescences 12–20-flowered, in terminal clusters; peduncle 1–2 mm long, glabrous, blackened, glossy; bracteoles ca. 1 mm long, broadly ovate, acute, coriaceous, subglabrous to sparsely puberulent outside, glabrous inside. Flowers pedicellate, pedicels 4–6 mm long, glabrous; calyx 2 mm diam., puberulent on the outer surface, glabrous on the inner surface with 5 small, flattened glands near the base alternating with the lobes, the lobes ca. 1.8 mm long, ovate, tapering to a rather blunt apex, the margins minutely ciliolate; corolla salverform, yellowish, glabrous on both surfaces, the tube proper 4.5–5 mm long, 1–1.3 mm diam., cylindrical, the upper cupular part 1.5 mm long, 1.5 mm diam., the orifice constricted by 5 rudimentary coronal scales, emphasizing the 5 nectar channels, the lobes 6–7 mm long, 2.5–3.5 mm wide, ovate, acute, densely puberulent on both surfaces; anthers inserted at the base of the cupular part of the corolla tube, about ½ exserted, sessile, narrowly lanceolate, sagittate, 2 mm long, dorsally barbellate in the upper half, the side wings glabrous, acuminate, incurving at the base; ovary ovoid, apocarpous, bilocular, ca. 0.5 mm high, densely pubescent, surrounded at the base by a glabrous, regularly 5-lobed disc nectary. Fruit apocarpous, glabrous, brown-black, composed of 2 stout, thick-walled, woody, fusiform follicles, 8–10 cm long, 1 cm diam. at the broadest point, diverging at ca.

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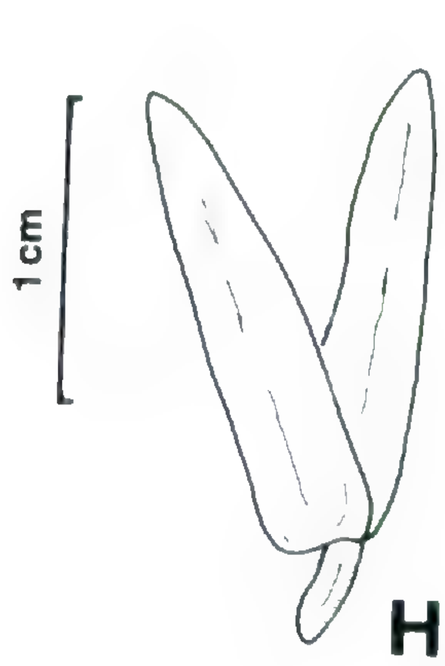

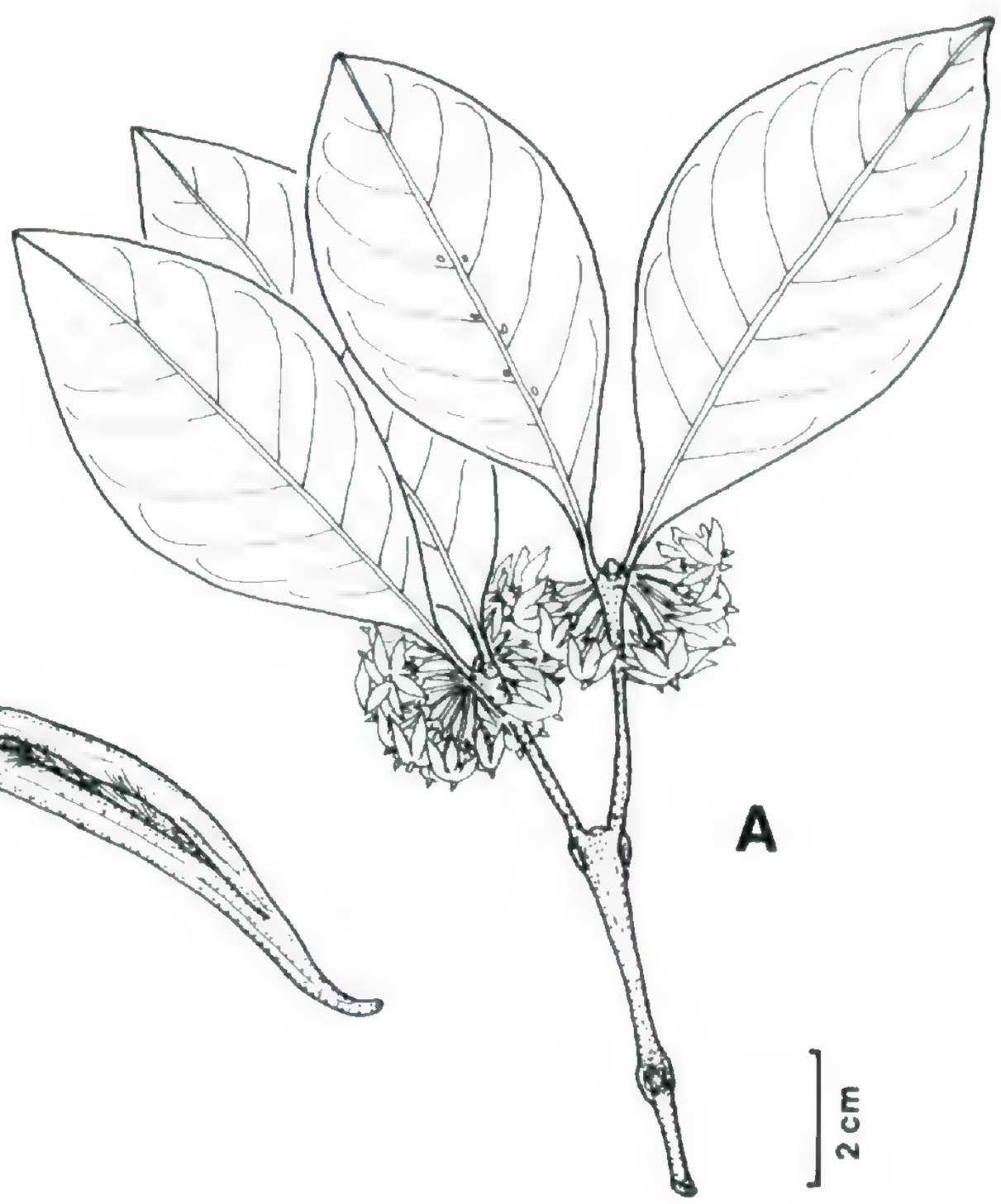

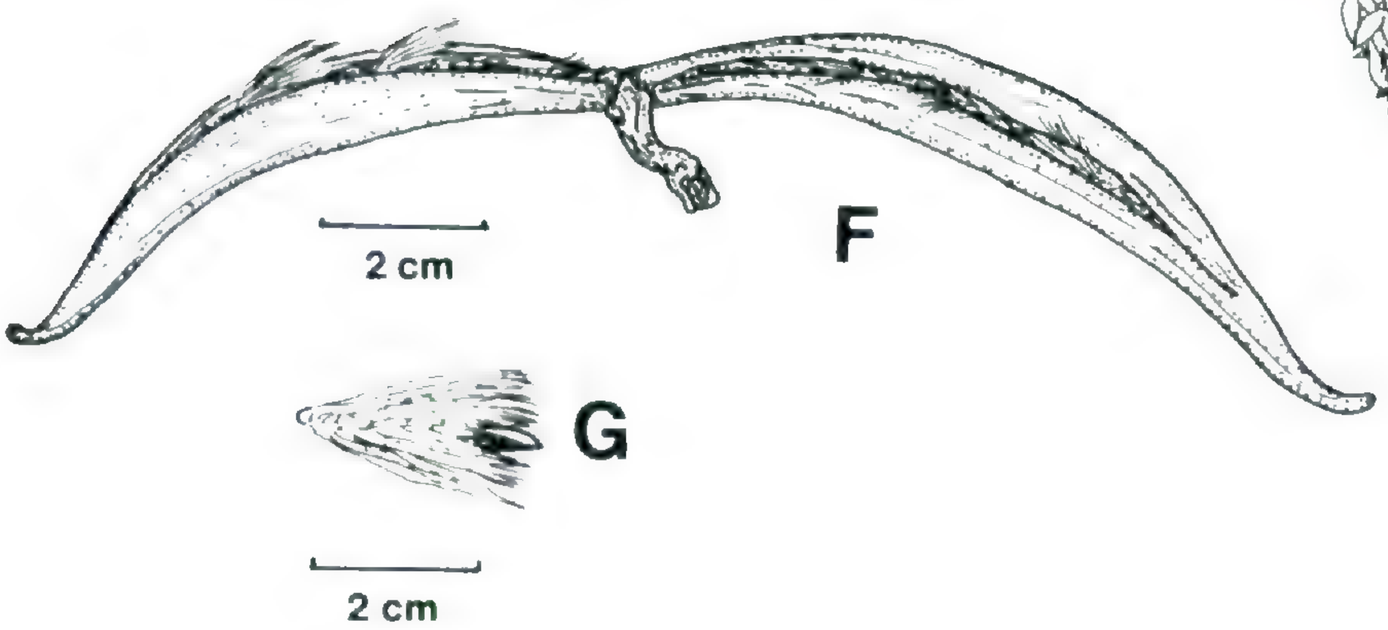

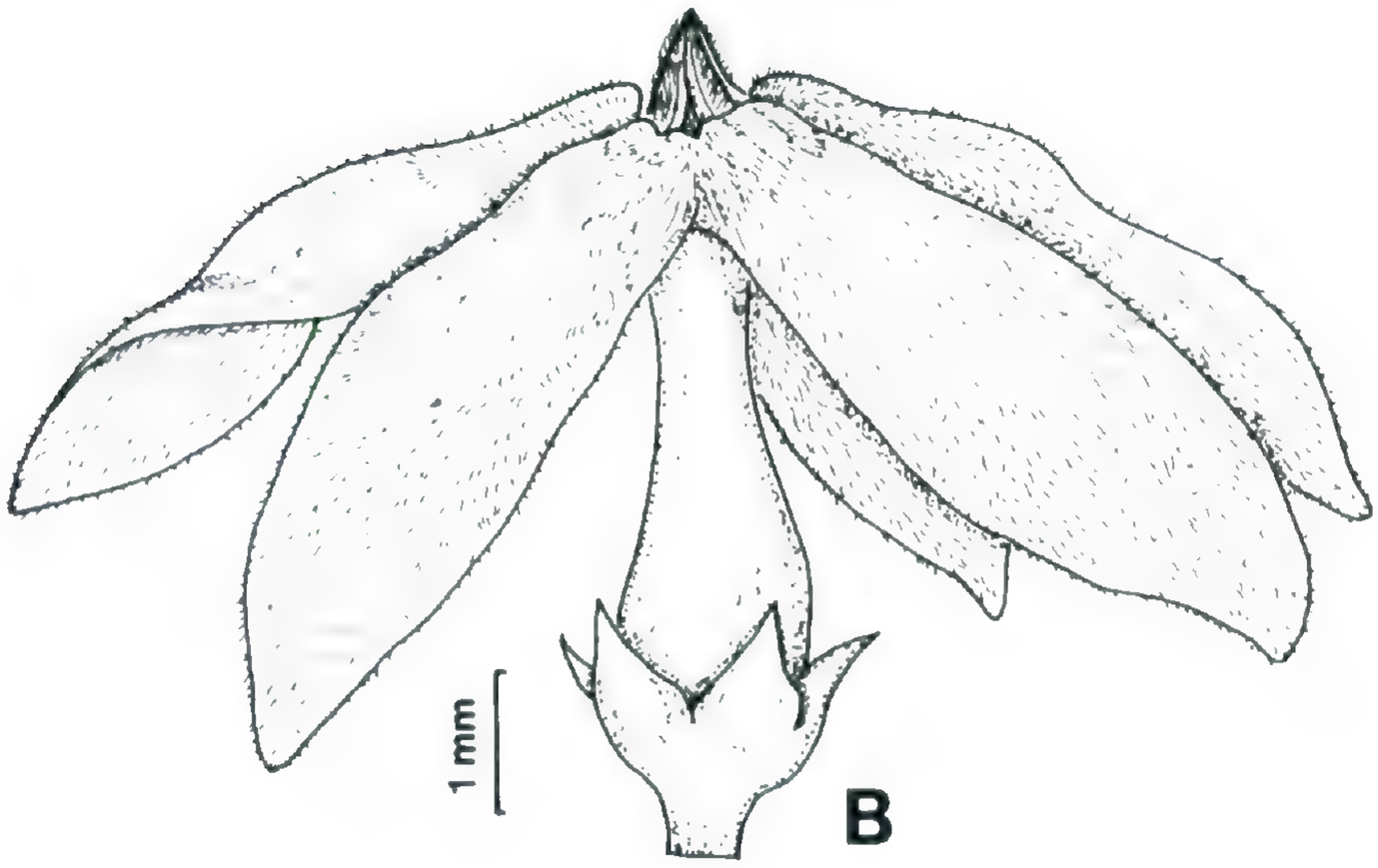

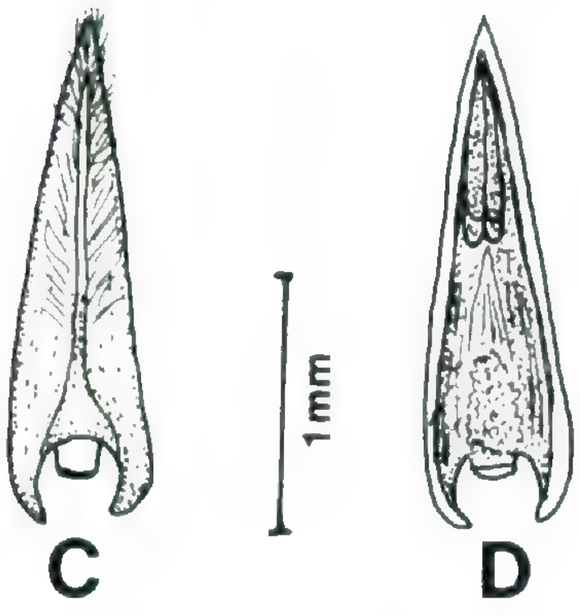

FIGURE 1. *Malouetia bubalina*.—A. Habit.—B. Flower.—C. Anther, dorsal view.—D. Anther, ventral view.—E. Embryo.—F. Fruit.—G. Seed.—H. Embryo. Based on the holotype.

180° then curving downward; seeds 2 cm long, slender, fusiform, laterally flattened, slightly convex on one side, the ventral surface longitudinally sulcate, the apical end (i.e., toward the fruit apex) abruptly converging into a rounded tip 1 mm long, proximally tapering to a rather blunt end, the apical tip embedded in a dense mat of long tan hairs, these attached to the apical half of the seed and directed toward the base of the follicle. Beneath the hairs the testa very thin, stiffly papery, smooth, glossy, yellowish tan, longitudinally striate; the endosperm forming a leathery case around the embryo; embryo 1.8 cm long, straight, the cotyledons rather fleshly, ca. 3½ times as long as the radicle, this thick, bent slightly.

Distribution. Colombia, known only from high forest over white sand at the type locality on the Río Caquetá.

The specific epithet refers to the bifid, stout, curving fruit reminiscent of buffalo horns.

Malouetia bubalina is most closely related to *M. arborea* (Vell.) Miers of eastern coastal Brazil, which also has stout fruits and seeds with an indumentum. But whereas the hairs on the seeds of *M. arborea* (Vell.) Miers are woolly and extend in all directions, those of *M. bubalina* are straight and directed toward the base of the follicle. The new species also differs by having much shorter pedicels and more ovate corolla lobes.

2. Malouetia molongo M. E. Endress, sp. nov. TYPE: Venezuela. T.F. Amazonas: Santa Cruz, margen del Río Atabapo, cerca del boca del Río Atacavi, *Foldats 3653* (holotype, NY). Figure 2.

Frutex vel arbuscula lactescens usque 2 m alta. Folia opposita obovata vel elliptica 4.5–7.5 cm longa, 1.5–2.5 cm lata, opaca subtus pallidiora margine revoluta nervis lateralibus 5 7 utroque latere; petioli 2–5 mm longi. Inflorescentiae terminales et axillares e fasciculis 2–3-floris compositae; calyx 2 mm longus, extus glaber; corolla alba hypocraterimorpha tubo 15.5–17 mm longo, lobis ovatis obtusis 8–9 mm longis, 4–5 mm latis, extus glabris intus prope basin granulato-papillatis; antherae inclusae paullo supra medium corollae tubum insertae; ovarium glabrum; ovula in utroque carpello ca. 12 3–4-seriatim affixa. Fructus ignoti.

Shrubs or small trees up to 2 m tall with white latex; branches blackish, glossy and angled in the younger parts, becoming terete and grayish with age. Leaves opposite, 4.5–7.5 cm long, 1.5–2.5 cm wide, the blades coriaceous, obovate to elliptic, obtuse to rounded at the apex, cuneate at the base, the margins revolute, glabrous on both surfaces, opaque, slightly paler on the lower surface, domatia absent; secondary veins 5–7 on each side, arcuate-ascending, anastomosing before the margin, obscure on both surfaces; tertiary venation inconspicuous on both surfaces; petioles 2–5 mm long, glabrous. Inflorescences 2–3-flowered, in terminal and axillary clusters; peduncle 1–2 mm long, glabrous; bracteoles broadly triangular, glabrous, ca. 1 mm long. Flowers pedicellate, pedicels 5–10 mm long, glabrous; calyx 2 mm long, 2–2.5 mm diam., glabrous without, glabrous within with pale, rather irregularly shaped toothlike glands alternating with the lobes, the lobes 1.5–2 mm long, glabrous, fleshy; corolla salverform, white, the tube 13–14 mm long, the upper cupular part 2.5–3 mm diam., glabrous without, glabrous within except for a short region of pilose hairs directly below the anthers and in the cupular part near the orifice, the orifice constricted by 5 weltlike rudimentary coronal scales, the lobes 8–9 mm long, 4–5 mm wide, ovate, obtuse at the apex, the outer surface glabrous, the inner surface papillose-puberulent and becoming more densely puberulent at the base; anthers inserted somewhat above midway in the corolla tube, completely included, 3 mm long, oblong, apiculate at the apex, the dorsal side glabrous, the side wings straight, the bases short and blunt; style-head cylindrical; ovary ovoid, apocarpous, bilocular, ca. 0.8 mm high, glabrous, surrounded at the base by a low, glabrous, 5-lobed disc nectary, the lobes truncate at the apex, basally connate for more than ½ their length; ovules ca. 12 per carpel, arranged in 3–4 rows. Fruit unknown.

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Santa Cruz, margen del Río Atabapo, cerca del boca del Río Atacavi, *Foldats 3654* (NY, VEN).

Distribution. Known only from the type locality in Amazonian Venezuela near the confluence of the Río Atacavi with the Río Atabapo, on flooded river banks.

The name comes from *molongó* a frequent local name for various Apocynaceae of inundated habitats.

This species most closely resembles *Malouetia gracilis* (Benth.) A. DC. from Guyana but differs by having five cleft weltlike scales constricting the mouth of the corolla tube. In *M. gracilis* (Benth.) A. DC. coronal scales are lacking.

3. Malouetia naias M. E. Endress, sp. nov. TYPE: Colombia. Vaupés: Mitú and vicinity, along Río Vaupés between Río Yí and Río Kubiyú, inundated margin of river, 9 July

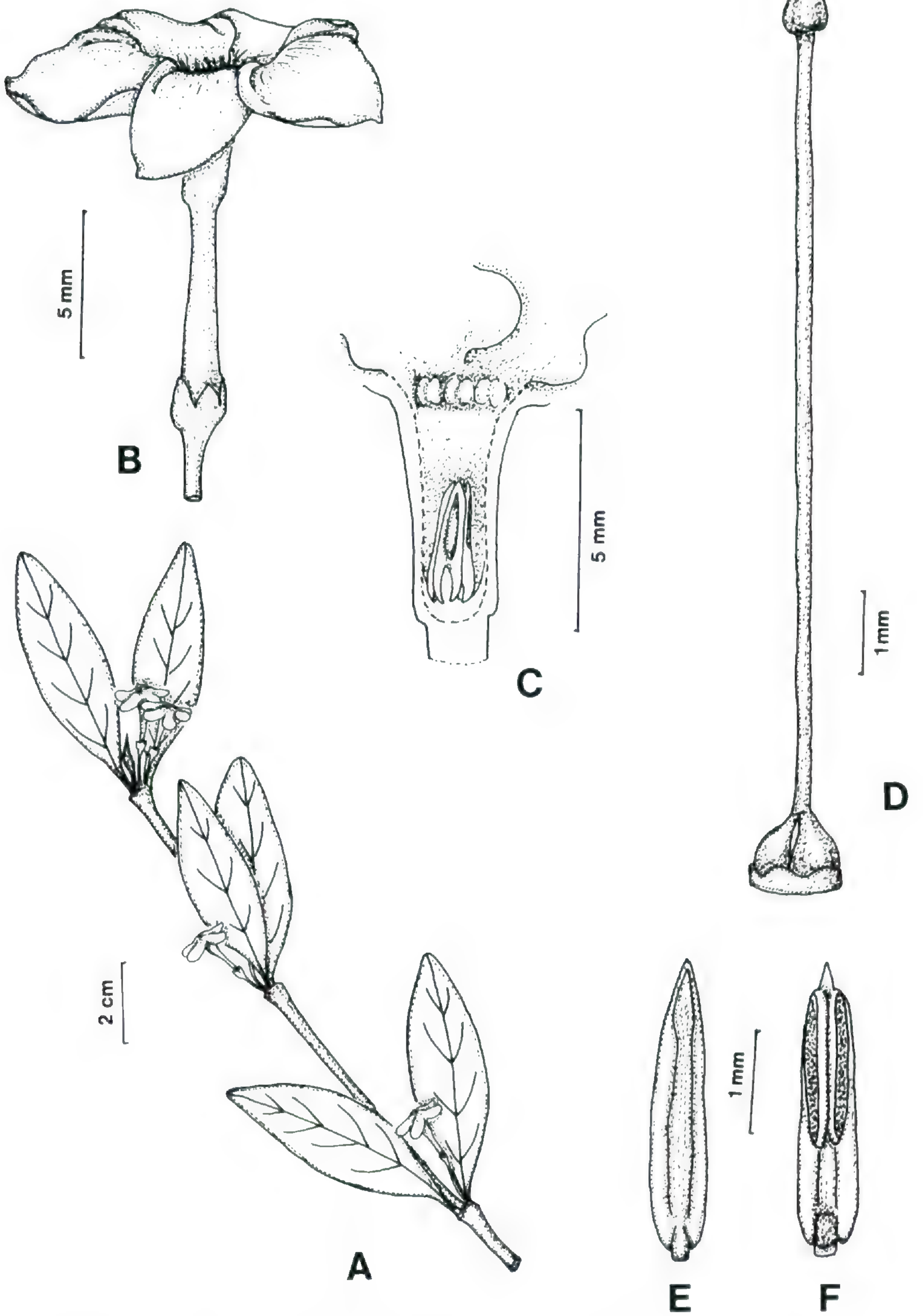

FIGURE 2. *Malouetia molongo*.—A. Habit. B. Flower.—C. Longitudinal section through upper portion of corolla showing coronal scales and positions of anthers. D. Gynoecium.—E. Anther, dorsal view.—F. Anther, ventral view. Based on the holotype.

1976, *Zarucchi et al. 1825* (holotype, US; isotypes, COL (n.v.), GH (n.v.), HBG, MO, USF). Figure 3.

Frutex vel arbuscula lactescens. Folia lamina lanceolata , apice caudata acumine 1–2 cm longa basi rotundata vel cuneata, utrinque glaberrima, in axillis nervi mediani interdum domatiis instructa, 5–10 cm longa, 1–3 cm lata; petioli 1–3 mm longi. Inflorescentiae axillares et (sub?)terminales e fasciculis (1–)2–4-floris compositae; calyx profunde lobatus intus extusque glaber, lobis anguste lanceolatis acuminatis; corolla viridi-alba vel flavida hypocraterimorpha, tubo 4–7 mm longo, 0.7–1.1 mm dia-

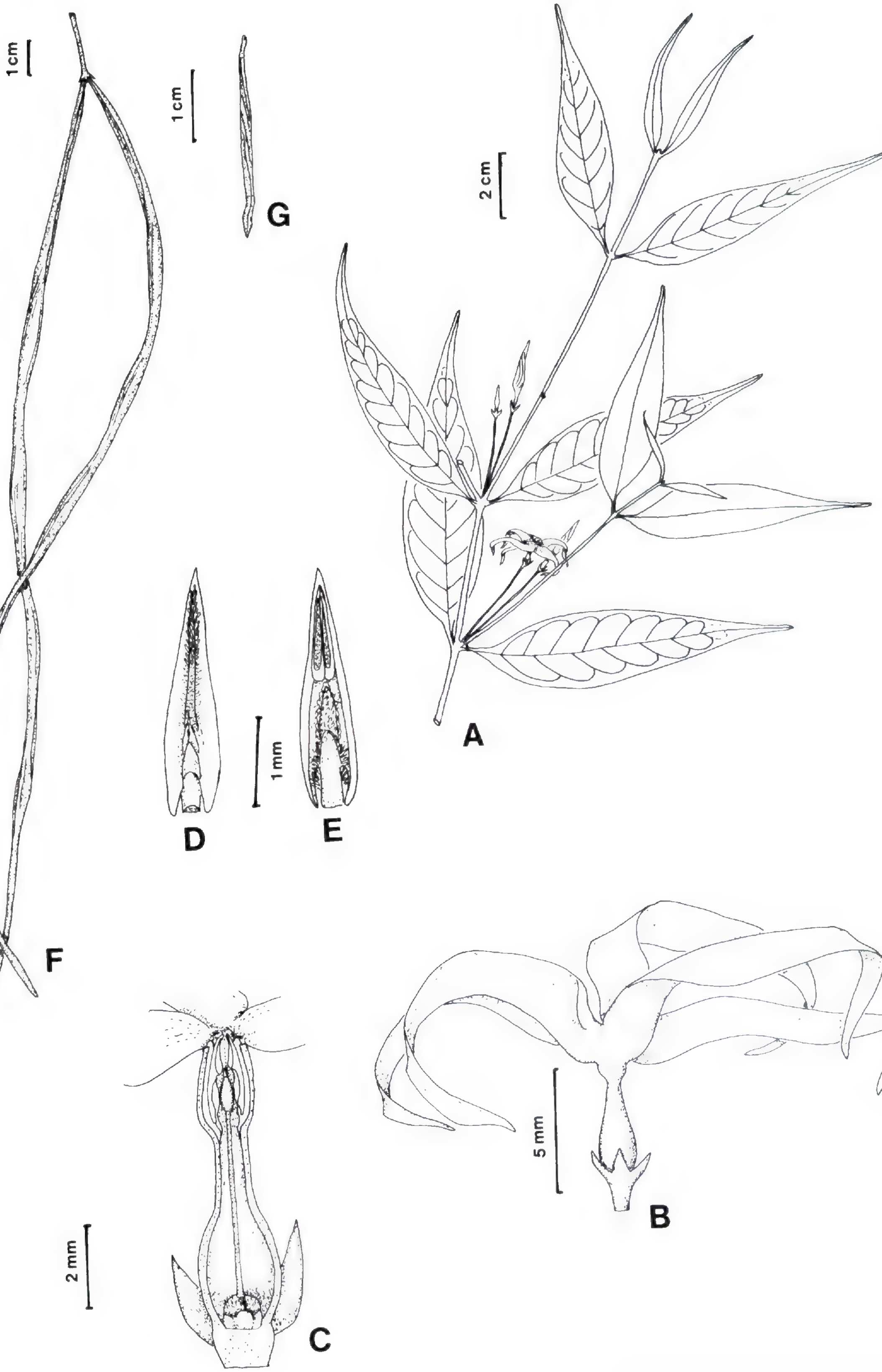

FIGURE 3. *Malouetia naias*.—A. Habit.—B. Flower.—C. Longitudinal section through flower showing positions of anthers.—D. Anther, dorsal view.—E. Anther, ventral view.—F. Fruit.—G. Seed. Based on the holotype.

metro basi inflato 1.2–2 mm diametro, lobis lanceolatis extus glabris intus prope basin granulato-puberulis vel villosulis 8 23 mm longis 1.8-3.5 mm latis; antherae basi faucis tubularis insertae, inclusae, tantum apice exsertae, dorso sparse pilosae; ovarium dense puberulum; ovula in utroque carpello 8 10 biseriatim affixa. Folliculi 2 graciles teretes glabri 25-28 cm longi, 3 mm diametro; semina lineari-cylindrica indumento microscopico denso et pilis dispersis 1–1.5 mm longis obtecta.

Shrubs or small trees 2–4(–8) m tall with sticky white latex; branchlets slender, glabrous, glossy reddish brown and flattened toward the nodes in younger portions, becoming gray and lenticellate with age. Leaves opposite, the blades thinly to firmly chartaceous, (5–)8–10 cm long, (1–)1.5–3 cm wide, lanceolate, the apex with acumen (1–) 1.5–2 cm long, rounded to cuneate at the base, completely glabrous on both surfaces, the upper surface often drying matte dark olive-brown to gray-green, the lower surface paler, with or without domatia in some of the axils of secondary veins with the midvein; secondary veins 8–9(–10) on each side, arcuate-ascending, anastomosing before the margin, impressed on the upper surface, prominulous on the lower surface; petioles 1–3 mm long, glabrous, reddish brown, with reddish brown pectinate glands at the base on each side. Inflorescences axillary or subterminal clusters of (1–)2–4 flowers; peduncle 1–2 mm long, glabrous, reddish brown; bracteoles ca. 1 mm long, narrowly ovate-triangular, glabrous, ciliolate at the margin. Flowers pedicellate, pedicels (1.3–)2–2.5 cm long, gracile to filiform, glabrous; calyx split almost to the base, glabrous on both surfaces, sometimes minutely puberulent near the apex on the inside, with 5 small flattened glands on the inside, the lobes narrowly lanceolate, acuminate, somewhat spreading, (1.5–)2–2.5 mm long, 0.3–0.8 mm wide, the margins densely and minutely ciliolate; corolla salverform, greenish white to cream or pale yellowish, the tube inflated at the base, the mouth occluded by 5 rudimentary coronal scales, the upper cupular part 1–1.5 mm long, 1–1.5 mm diam., the tube proper (3–)4.5–5.5 mm long, 0.7–1 mm diam. at the orifice, 1.2–2 mm diam. at the base, glabrous without, sparsely pilose within just below the level of stamen insertion, otherwise glabrous; lobes lanceolate (8–)10–15(–23) mm long, (1.8–)2–3.5 (–5) mm wide, glabrous on the lower surface, glabrous on the upper surface except near the base, this granular-pubescent to villosulous; stamens inserted near the orifice of the corolla tube, only the very tips exserted, narrowly lanceolate, 2.5–2.8 mm long, dorsally sparsely pilose, the side wings glabrous, acuminate and curving inward at the base; style-head cylindrical, 1–1.2 mm long, style filiform; ovary ovoid, apocarpous, bilocular, 1 mm high, densely puberulent, disc nectary glabrous, ca. half as long as the ovary, 5-lobed, the lobes connate for ca. ⅔ their length; ovules 8–10 per carpel, arranged biserially. Fruit apocarpous, glabrous, longitudinally finely striate, medium brown, composed of 2 slender, terete follicles 25–28 cm long, ca. 3 mm diam.; seeds linear-cylindric, 3 cm long, 1 mm diam., the ventral face longitudinally sulcate, the entire surface covered by a dense indument of microscopic hairs interspersed with a sparse scattering of thin, whitish to pale gold pilose hairs 1–1.5 mm long.

Additional specimens examined. COLOMBIA. VAUPES: Mitú and vicinity, *Zarucchi et al. 1810* (COL, GH, US, USF), *1847* (COL, GH, HBG, MO, US, USF). VENEZUELA. AMAZONAS: Caño de Cholo, 15 km NE of San Carlos de Río Negro, 4 km SW of Solano, *Liesner 4059* (MO, Z), *8560* (MO, VEN, WAG), *8879* (MO, WAG), *Gentry et al. 46425* (HBG). PERU. LORETO: Maynas, Mishana, Río Nanay, Estación Biológia Callicebus, *Vásquez & Jaramillo 3280* (MO, Z), *6108* (MO, Z).

Distribution. Colombia, Amazonian Venezuela, and Peru, in primary, secondary, and seasonally inundated lowland rainforest.

The specific epithet refers to the resemblance to the delicate water nymph.

This new species is most closely related to *Malouetia flavescens* (Willd. in R. & S.) Müll.-Arg. and *M. nitida* Spruce ex Müll.-Arg. However, *M. naias* is more delicate in all aspects than either of the above species. The following key is provided as an aid to identification.

KEY TO THE *MALOUETIA FLAVESCENS* SPECIES GROUP

1a. Leaves 9–18 cm long, 3–7 cm wide; corolla tube 6–10 cm long; seeds 3 mm diam. 2
2a. Anthers exserted ..... *M. flavescens*
2b. Anthers included ..... *M. nitida*
1b. Leaves 8–10 cm long, 1.5–3 cm wide; corolla tube 5.5–7.5 cm long; seeds 1 mm diam. ..... *M. naias*

4. **Malouetia pubescens** Markgraf var. **glabra** M. E. Endress, var. nov. TYPE: Venezuela. Apure: Rómulo Gallegos, Río Capanaparo, near Hato Carabali, *Davidse & Gonzales 16028* (holotype, MO; isotypes, NY, VEN).

A var. *pubescens* lamina foliorum subtus glabra et petiolis glabris differt.

Small trees up to 12 m tall with white latex; branches glabrous with a glossy blackish varnish. Leaves decussate, 8–15 cm long, 1.8–6.5 cm wide, the blades membranous, oblong-elliptic, the apex

acuminate, cuneate to obtuse at the base, glabrous and drying intense green on both surfaces; domatia usually present in some of the axils of the secondary veins with midvein; secondary veins 6–9 on each side, slightly impressed on the upper surface, prominulous on the lower surface; tertiary venation rather obscure on the upper surface, distinctly reticulate on the lower surface; petioles 2–4 mm long, glabrous. Inflorescences (10–)20–30-flowered, in terminal and axillary clusters; peduncle 1–2 mm long, glabrous. Flowers pedicellate, pedicels 2.5–5.5 mm long, glabrous; calyx 1–2 mm long, 1–2 mm diam., minutely puberulent on the outer surface, the inner surface with 5 small glands near the base of the lobes, the lobes 0.5–1 mm long, ovate, acute, the margins minutely ciliolate; corolla salverform, white to yellowish white, the tube 3–3.5 mm long, 0.5–0.8 mm diam., enlarged at the base, constricted at the orifice by 5 bilobed rudimentary coronal scales, glabrous on both surfaces, the lobes 4–5.5 mm long, 1.2–2 mm wide, oblong-ovate, acute, spreading or slightly reflexed, minutely puberulent on both surfaces; anthers inserted near the orifice of the corolla tube, almost completely exserted, 1.5 mm long, sagittate, the dorsal side barbellate, the side wings glabrous, basal appendages fused to the connective, slightly incurved, the ends blunt; style-head conical; ovary apocarpous, bilocular, 1 mm high, ovoid, sparsely puberulent at the apex, surrounded at the base by a 5-lobed disc nectary; ovules 10–12 in each carpel, arranged biserially. Fruit apocarpous, glabrous, dark brown, longitudinally striate, composed of 2 slender, thinly woody follicles, 11–19 cm long, 4–4.5 mm diam.; seeds linear-fusiform, compressed, plicate, the ends acuminate, tapering diagonally, 2 cm long, 2.5 mm diam., with a dense indument of pale tan to ochre lanate hairs ca. 1.5 cm long; embryo straight, 1 cm long, the cotyledons about 4 times as long as the radicle.

Additional specimens examined. COLOMBIA. VICHADA: Parque Nacional Natural "El Tuparro," ca. 7 km NE of El Tapón, *Zarucchi & Barbosa 3764* (FMB, MO, Z), *3766* (FMB, MO, Z). VENEZUELA. BOLIVAR: Río Parguaza, near Pilon, *Wurdack & Monachino 41116* (F, NY, S, US).

Distribution. Apure and Bolívar, Venezuela, and Vichada, Colombia, in gallery forest.

The new variety differs from var. *pubescens* in having leaves completely glabrous on both surfaces. The two varieties, which occur sympatrically in Vichada, Colombia, show no habitat differences.

TICODENDRON: A NEW TREE FROM CENTRAL AMERICA

Jorge Gómez-Laurito[1] *and Luis D. Gómez P.*[2]

ABSTRACT

Ticodendron incognitum is named as a new genus and species, and the taxonomic position of this tree is discussed.

Despite many years of floristic research in various Central American countries, new findings still surprise botanists. Such is the case of a tree, here described as a new genus and species, which has puzzled many scientists in the field and in herbaria and which has produced much correspondence and discussion. Based on studies of embryology, palynology, wood anatomy, and other features, a new family of dicots will be published soon for this genus.

Ticodendron incognitum Gómez-Laurito & Gómez P., gen. et sp. nov. TYPE: Costa Rica. Alajuela: Reserva Forestal de San Ramón, ca. Colonia Palmareña, 900–1,200 m, 10°10′N, 84°35′W, 30 Mar. 1987, male and female tree, *G. Herrera, I. Chacón & A. Solís 515* (holotype, CR; isotypes, F, K, MO). Figures 1–5, 6.

Arbor dioicus vel polygamo-dioicus, 7–20 m altus, 40–80 cm diametro ad pectoris. Germinationis hypogaeus. Cortex exfolians; interna facies nonnulla aliquanda caeruleopurpurascens. Lignum spadiceum, durissimum. Ramulis teretis, 3–5 mm crassis, nodosis, sulcatis, griseis, versus apicem complanatis, juvenis pilosis, pilibus unicellulatis simplicibus vel raro apicem furcatis, pallide ambarinis, cicatricibus stipulorum delapsorum notatis. Stipulae subulatae, usque 15 mm longae, circumdatae, caducae. Petiolis 10–15 mm longis, supra sulcatis, juvenis hirsutis (vide supra), demum lenticellatis. Foliae alternae, lamina elliptico-ovata, 8–13 cm longa, 4–8 cm lata, subcoriacea, margine in parte superiore serrata, base cuneata, apicem acuminata supra glaberrima, infra glabrescente, juvenis utrinque lanatis, pilibus longioris, rigidis, acutis, nervis secundaris 8–13 paribus, regulariter arquatis, subopositis, paralellis, infra elevatis, supra canaliculatis, ceteri nervis sub lente reticulatis, flavislucem transmissa. Inflorescentiae secundatae. "Amenta" 1.5–4 cm longa, simple vel ramificata, aliquando flos feminea coronatis. Axis leviter fractiflexis, pilosis. Stamina numerosae, 2–4 verticillatae dispositae; (verticillum 8–12 mm diametrum) bracteae 3, latae ovatae vel deltoideae, 5 mm longae, 5 mm latae basae, mox deciduae; filamenta 2–3 mm longa, teretes, pilosa; antherae oblongae, 2 mm longae, basifixae; thecae geminatae, longitudinaliter dehiscentibus, connectivo subulato producto. Granula pollinis ca. 2 μm crassa, subglobosa, leviter. Flos feminea solitariae extremitatis surculorum dispositae. Pedicelis 3 mm longis, adpresopilosis. "Bracteae involucratae" 3, ovatae, 2.5–3 mm longae, adpreso-pilosae, mox deciduae. Perianthium tubus adpresso-pilosus, carnosus, viridis. Ovarium inferum, biloculare in perianthium tubus inclusum, placentatio axilis. Ovula 4 (ut videtur abortu 1), hemitropa. Stigmata 2, pilosa, 5–12 mm longa. Fructus asymetricus, unilateraliter inflatus, ovatis, basim rotundatis, apicem acutis, drupaceis, vix 7 cm longis, 4 cm crassis, viridis, mucilaginosis; in siccitatem putamen avellaneum, lignossimum, longistrorsum sulcatus.

Dioecious or polygamodioecious trees, 7–20 m tall, 40–80 cm dbh. Germination hypogeal. Inner bark reddish or purplish. Wood yellowish, very hard. Twigs 3–5 mm thick, flattened toward the tips, pilose when young. Stipules subulate, to 15 mm long, caducous. Petioles 10–15 mm long. Leaves alternate, blades elliptic-ovate, 8–13 cm long, 4–8 cm wide, subcoriaceous, the margins serrate in the upper part. The base cuneate, the apex acuminate. Glabrous above, glabrescent beneath, woolly in early stages, with 8–13 secondary veins. Male flowers arranged in amentlike inflorescences 1.5–4 cm long, these simple or branched, sometimes crowned by a solitary female flower. Stamens many, verticillate, surrounded by 3 bracts, these broadly ovate to deltoid, 5 mm long, 5 mm wide at base, early deciduous. Filaments 2–3 mm long, pilose; anthers oblong, 2 mm long, geminate. Female flowers surrounded by bracts, solitary on pedicels 3 mm long, these appressed-pilose. Bracts ovate, 2.5–3 mm long, appressed-pilose. Ovary inferior, bicarpellate, 4-locular, included in the

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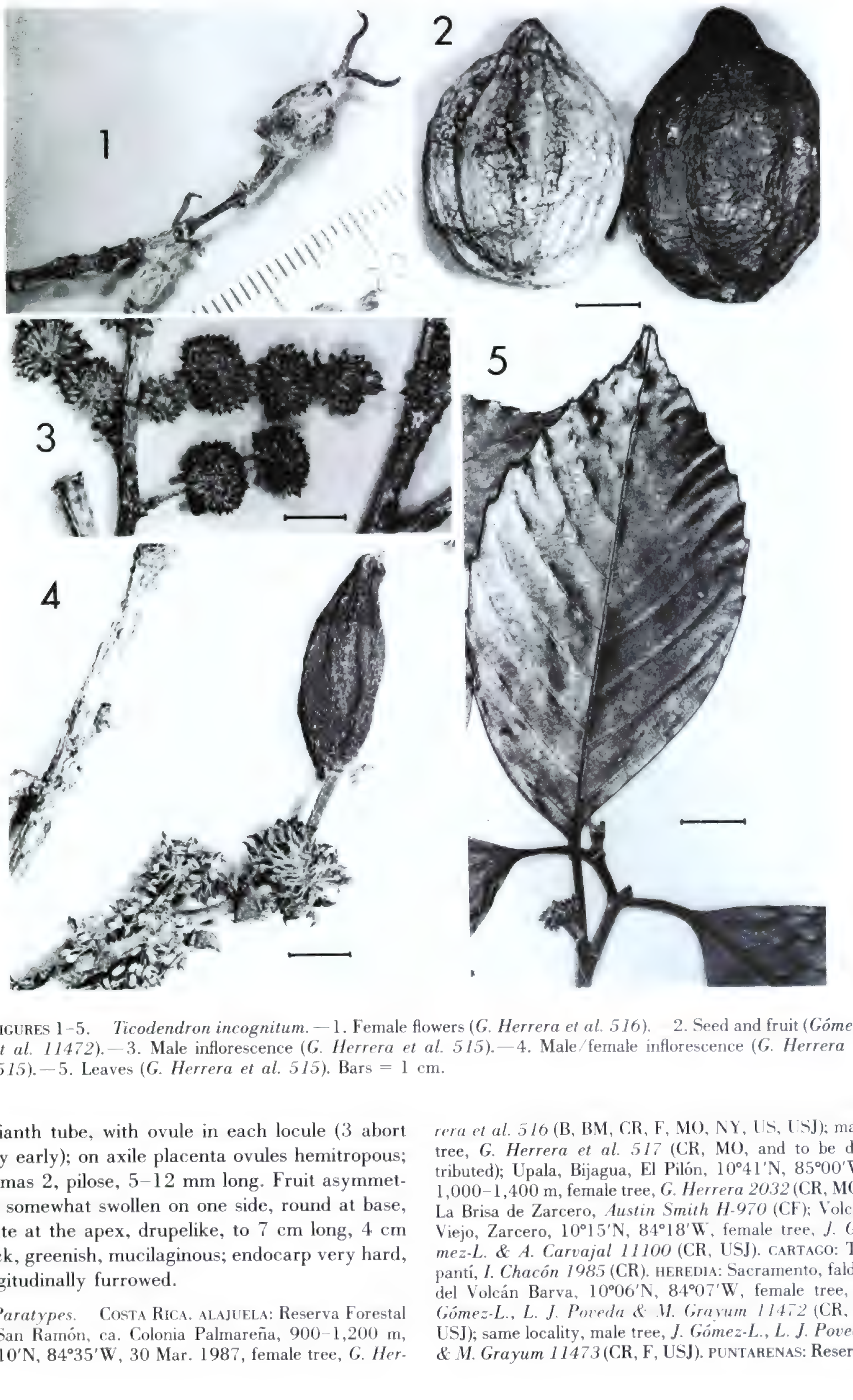

FIGURES 1–5. *Ticodendron incognitum.*—1. Female flowers (*G. Herrera et al. 516*).—2. Seed and fruit (*Gómez-L. et al. 11472*).—3. Male inflorescence (*G. Herrera et al. 515*).—4. Male/female inflorescence (*G. Herrera et al. 515*).—5. Leaves (*G. Herrera et al. 515*). Bars = 1 cm.

perianth tube, with ovule in each locule (3 abort very early); on axile placenta ovules hemitropous; stigmas 2, pilose, 5–12 mm long. Fruit asymmetric, somewhat swollen on one side, round at base, acute at the apex, drupelike, to 7 cm long, 4 cm thick, greenish, mucilaginous; endocarp very hard, longitudinally furrowed.

Paratypes. COSTA RICA. ALAJUELA: Reserva Forestal de San Ramón, ca. Colonia Palmareña, 900–1,200 m, 10°10′N, 84°35′W, 30 Mar. 1987, female tree, *G. Herrera et al. 516* (B, BM, CR, F, MO, NY, US, USJ); male tree, *G. Herrera et al. 517* (CR, MO, and to be distributed); Upala, Bijagua, El Pilón, 10°41′N, 85°00′W, 1,000–1,400 m, female tree, *G. Herrera 2032* (CR, MO); La Brisa de Zarcero, *Austin Smith H-970* (CF); Volcán Viejo, Zarcero, 10°15′N, 84°18′W, female tree, *J. Gómez-L. & A. Carvajal 11100* (CR, USJ). CARTAGO: Tapantí, *I. Chacón 1985* (CR). HEREDIA: Sacramento, faldas del Volcán Barva, 10°06′N, 84°07′W, female tree, *J. Gómez-L., L. J. Poveda & M. Grayum 11472* (CR, F, USJ); same locality, male tree, *J. Gómez-L., L. J. Poveda & M. Grayum 11473* (CR, F, USJ). PUNTARENAS: Reserva

FIGURE 6. *Ticodendron incognitum*. —A. Portion of stem of flowering staminate plant. —B. Staminate inflorescence. —C. Stamen. —D. Staminate flower. —E. Bracts subtending staminate flower. —F. Pistillate inflorescence. —G, H. Pistillate flower. —I. Endocarp, front view. —J. Endocarp, cross section. —K. Stipules. —L. Leaf apex (A, K, L from *McPherson 12493*; B–E from *Haber 7072*; F–H from *Haber 6840*; J from *McPherson 8401*.)

Natural de Monteverde, *W. Haber & E. Bello 2058* (CR, MO); same locality, *Haber et al. 6840, 6868, 7071, 7072, 7286* (CR, MO, and to be distributed); same locality, sterile tree, *Hammel et al. 15385* (MO), female tree, *15396* (MO). SAN JOSÉ: Bajo de La Hondura, *L. J. Poveda 864* (CR). PANAMA. BOCAS DEL TORO: Fortuna Dam region, near trail along continental divide, 8°45′N, 82°15′W, 1,250 m, sterile branches with fruits from ground, *McPherson & Hammel 8401* (MO, C, KYO, PMA). CHIRIQUÍ: vicinity of Fortuna Dam, S of reservoir, 8°45′N, 82°15′W, 1,100–1,300 m, sterile tree, *McPherson 11659* (MO); same locality, male and female tree, *McPherson 12493* (MO, PMA, and to be distributed). COCLÉ, N of El Copé, 8°38′N, 80°35′W, 750 m, sterile tree, *McPherson 12615* (MO). NICARAGUA. ZELAYA: Cerro La Pimienta number 1 and 2, E range, summit of 2 peaks, northernmost and central, ca. 13°45′N, 84°59′W, 900–1,600 m, sterile tree, *Pipoly 5233* (MO).

Etymology. *Tico*, a Costa Rican diminutive, and *dendron*, Greek for tree. Its unusual characters were first noticed by Costa Rican botanists.

The first known collection was made in this country at the beginning of the century by C. Wercklé (*s.n.*, US No. 1010451) near San Cristóbal. The specific epithet refers to its Hamamelidean relationships.

The new genus and species of Hamamelidean affinities (Gómez-Laurito & Gómez, 1989) has prompted much discussion: a possible relationship to Urticales (e.g., Ulmaceae or Cecropiaceae) has been suggested. Dilleniales (Wolfe, 1989) and Rosales have also been proposed as possible orders for *Ticodendron*. For some time, placement in the Ulmaceae was favored and our genus does resemble genera of this family (e.g., *Aphananthe* Planchon), but its morphology excludes *Ticodendron* from subfamilies Ulmoideae or Celtidoideae. As in the Ulmaceous genus *Zelkova* Spach, *Ticodendron* has drupaceous fruits and somewhat distichous, pinnately veined leaves, but has four hemitropous ovules, three of which abort very early in development. Leaf characteristics suggested to W. Burger (pers. comm.) a relationship to the Cecropiaceae, but our observations revealed a bicarpellate ovary and two well-differentiated and free stigmas, among other differences. The dry, hardened fruits bear a faint resemblance to those of *Corylus* L., and, when we first saw a vegetative specimen, we thought of *Carpinus* L., which reaches northern Nicaragua.

Several genera of Hamamelidales (e.g., *Tetracentron* Oliver, *Sinowilsonia* Hemsley, *Altingia* Noronha, and others) show many of the morphological characteristics of the new plant and suggest that its true affinities lie within this order, although its precise placement requires further study.

The venation and marginal teeth of *Ticodendron* leaves have been compared and found somewhat similar to those of fossil Juglandaceae (Hickey, fide Raven, pers. comm.). Some botanists initially proposed Flacourtiaceae as the proper family.

A possible relationship between *Ticodendron* and the Antillean *Picrodendron* Planchon, based on the similar appearance of the pistillate flowers, has been suggested (M. Grayum, pers. comm., 1987) but *Ticodendron* has simple leaves and strongly asymmetrical fruits. Further, its pollen grains are unusually small and not of the *Olfieldia*-type, which occurs in the Euphorbiaceae, where most modern authors place *Picrodendron* (Hakki, 1985; Hayden et al., 1984; Webster, 1975). Wood anatomy (Carlquist, in press) and reproductive morphology (Tobe, in press) point to Fagales.

Ticodendron incognitum forms sparse stands or is found isolated in the montane evergreen forest of Central America. In Costa Rica, it usually grows from 900 to 2,300 m elevation associated with *Aiouea costaricensis* (Mez) Kostermans, *Phoebe hammeliana* W. Burger, *Cedrela salvadorensis* Standley, *Eugenia lepidota* Berg, and other species. The common names given to this tree are *jaúl macho* and *jaúl nazareno* (male alder, purplish alder). Both names recall the alderlike habit of *Ticodendron* and the purplish tinge of fresh cuts in most of the trees. Also, it is called *duraznillo* and *candelillo morado*. The wood is used as firewood. It is fine-grained, dries a pale rosy-brown, takes a high polish, and is harder than that of *Alnus*.

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A SECOND SPECIES OF THE AMPHI-ATLANTIC GENUS *ALONSOA* (SCROPHULARIACEAE) IN SOUTH AFRICA[1]

Kim E. Steiner[2,3]

ABSTRACT

A second species of the predominantly South American genus *Alonsoa* has been found to occur in South Africa, having been incorrectly classified previously as *Diascia unilabiata* (Linn. f.) Benth. Its correct combination in *Alonsoa* already exists and is here resurrected, along with a full description and synonymy. *Alonsoa unilabiata* differs from South American species in having oil-secreting trichomes in shallow corolla sacs and from the other South African species in its annual habit, dilated filaments, and acuminate, bilobed stigma. Flowers of *Alonsoa unilabiata* are self-compatible, but are usually out-crossed by *Rediviva* (Melittidae) oil-collecting bees. Differences between *Alonsoa* and *Diascia* are discussed.

Alonsoa Ruiz & Pavón is a small genus of approximately 16 species that until recently was believed to be restricted to the New World (Edwin, 1971; Hilliard & Burtt, 1984; Roux, 1986). It is concentrated primarily in the Peruvian Andes of South America but ranges north through Central America to Mexico and south to Chile and Bolivia; it also occurs in the Cape floristic region of South Africa.

Alonsoa is one of seven genera that Bentham (1876) placed in the Hemimeridae, the others being *Diascia*, *Nemesia*, *Diclis*, *Hemimeris*, *Colpias*, and *Angelonia*. Since the American genus *Angelonia* is now placed in its own tribe Angelonieae (Pennell, 1920; Barringer, 1983, 1985), the Hemimeridae, with the exception of most species of *Alonsoa*, are basically restricted to southern Africa.

The first *Alonsoa* (*A. peduncularis* (Kunze) Wettstein) species discovered in Africa was collected by Zeyher (*3485*) in the late 1830s from woody gorges around Uitenhage in the eastern Cape. The original description (Kunze, 1842) was prepared from cultivated plants at the Leipzig botanical garden. The source of that seed was Lehmann of Hamburg who obtained it from someone in South Africa. The original source is uncertain, but, due to the rarity of this plant, it may well have come from Zeyher's collection. No subsequent collections of this taxon were made until its discovery at a second locality in 1985 (Roux, 1986). Since this second site is far removed from areas of past or present cultivation, and since no known South American species have corolla sacs, Bentham's (1876) suggestion that the original specimen collected by Zeyher was naturalized from South America is highly unlikely. Evidently Bentham's reluctance to accept *Alonsoa* as indigenous to South Africa was due to the unusual amphi-Atlantic distribution that this would represent.

Out of a combined total of about 4,500 genera occurring in Africa (including Madagascar) and South America, approximately 115 (2.6%), including *Alonsoa*, are restricted to these subcontinents (Thorne, 1973; Hilliard & Burtt, 1984). Of these, only seven (0.2% of the full total) occur in the Cape flora of South Africa. Among genera shared between South Africa and America, *Alonsoa* is the only genus presently centered in the Andes. Except for a few widespread genera (e.g.,

[1] I thank J. P. Rourke for nomenclatural assistance, and D. Snijman and several anonymous reviewers for commenting on earlier versions of the manuscript. Peter Goldblatt kindly checked and provided photocopies of some early publications by Ruiz & Pavón; F. Astholm identified *Alonsoa meridionalis* var. *lactea*; and J. Manning drew Figure 5. The assistance of V. B. Whitehead in the study of *Alonsoa* pollination has been invaluable.

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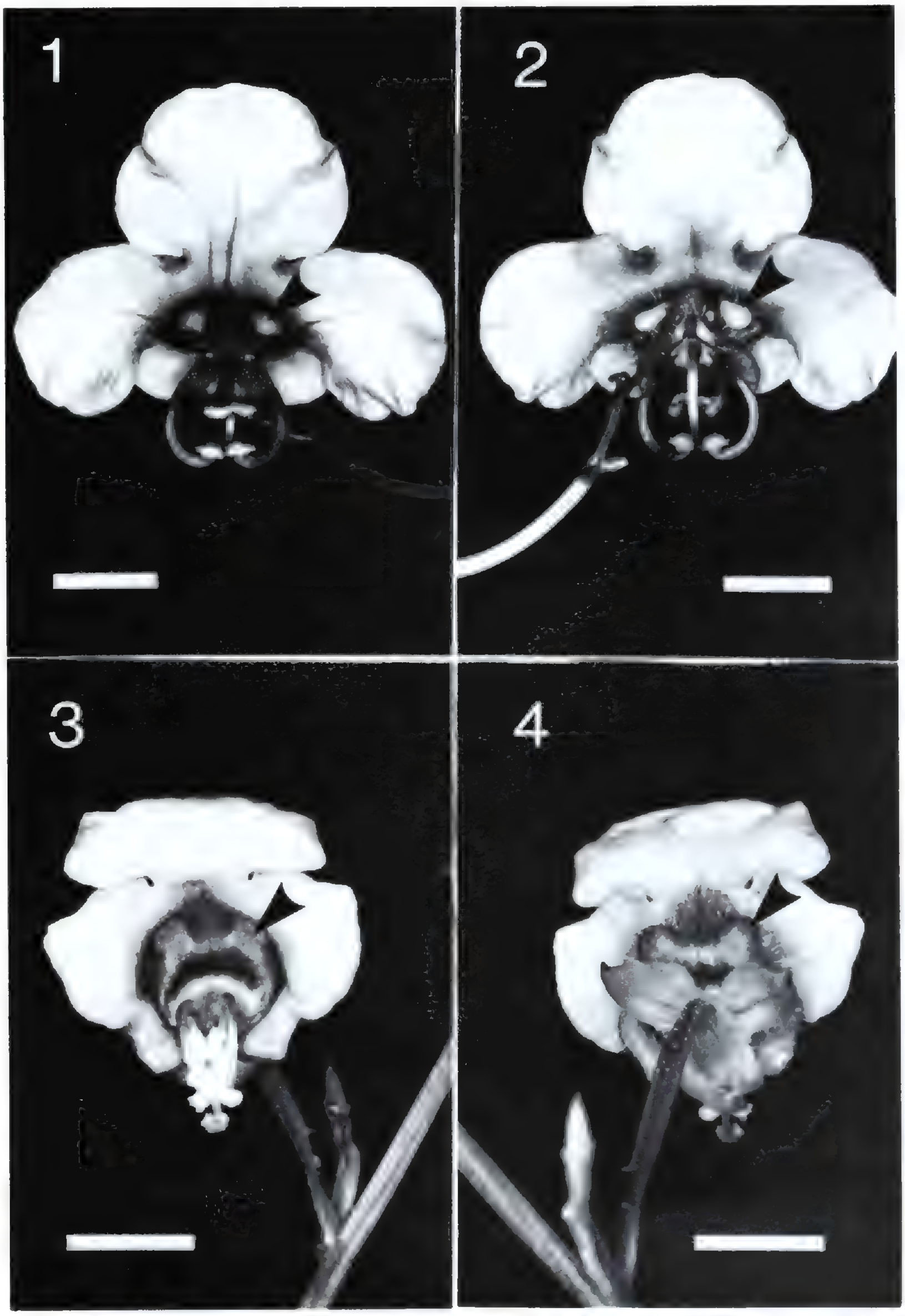


FIGURES 1–4. *Alonsoa* flowers.—1. *A. unilabiata*, front view.—2. *A. unilabiata*, rear view.—3. *A. peduncularis*, front view.—4. *A. peduncularis*, rear view. Arrowheads indicate sacs containing oil-secreting trichomes. Scale lines = 0.5 cm.

Limosella, *Lindernia*, and *Ilysanthes*) and the parasitic genera *Melasma* and *Alectra* with tiny easily dispersed seeds, *Alonsoa* is the only connection between South American and African Scrophulariaceae. This and other evidence led Raven & Axelrod (1974) to suggest that the Scrophulariaceae probably did not exist when the two subcontinents were close together. Thus, *Alonsoa* must have reached Africa subsequently by long distance dispersal.

In America, *Alonsoa* is characterized by racemose inflorescences, resupinate flowers with the corolla tube split to the base between the lower (morphologically upper) lobes, and oblong to elliptic, usually longitudinally furrowed seeds (Edwin, 1971; Hilliard & Burtt, 1984). South African members of the genus are additionally characterized by two shallow yellow sacs in the gamopetalous portion of the corolla at the base of the lateral corolla lobes (Figs. 1–4, 5A, B). These sacs are densely packed with oil-secreting trichomes (Hilliard & Burtt, 1984; Roux, 1986; Steiner, pers. obs.).

My current research on the annual *Diascia*

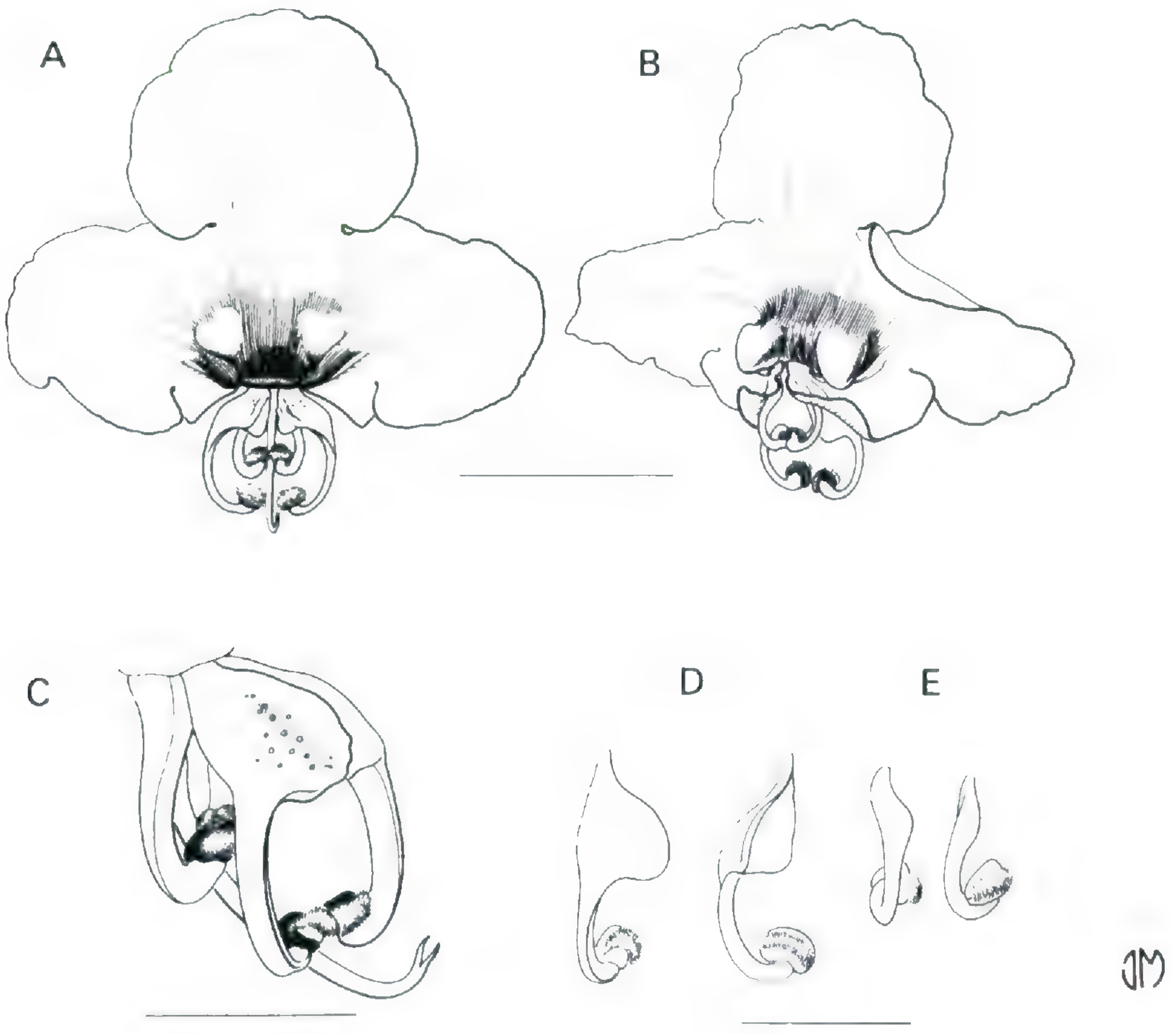


FIGURE 5. *Alonsoa unilabiata*—A. Front view of flower.—B. Rear view of flower.—C. Stamens, style, and stigmas. D. Anterior stamens.—E. Posterior stamens. Scale line for A and B = 1 cm. Scale lines for C–E = 0.5 cm.

species from the western Cape has revealed that a second species of *Alonsoa* has been incorrectly classified as *Diascia unilabiata* (Linn. f.) Benth. The presence of a second *Alonsoa* species in South Africa strengthens the unusual amphi-Atlantic connection within the genus and warrants an examination of the distinction between *Alonsoa* and *Diascia* in general, and the taxonomic history, variation, and reproductive biology of *Alonsoa unilabiata* (Linn. f.) Steudel in particular.

HABIT AND HABITAT

Alonsoa unilabiata is a winter-flowering (July–October) annual herb with simple to dissected leaves and pink to orangish pink resupinate flowers with dark purple-maroon centers. Contrasting with the dark center is a yellow translucent window or sac at the base of each lateral corolla lobe.

Alonsoa unilabiata occurs from near the west coast of South Africa (Elands Bay and Lamberts Bay), where it is found in loose sands of old stabilized dunes at about 100–200 m, northeast to the escarpment of the Bokkeveld Mountains (Nieuwoudtville area), and along the Roggeveld escarpment from Calvinia south to the northwestern edge of the Little Karoo (Konstabel and Tweeside) (Fig. 6). On the escarpments of the Bokkeveld and Roggeveld, these plants grow primarily in sandy to clay loam soils derived from shales, except around Nieuwoudtville where they occur on heavy doleritic clays. Drège collected *A. unilabiata* from the southwestern Cape near Cape Town in 1836, but no recent collections have been made from this area. *Alonsoa peduncularis*, in contrast, is known from only two localities in the southern and eastern Cape floristic region (Fig. 6).

There appear to be three fairly recognizable ecotypes of *A. unilabiata* associated primarily with different soil types. The differences between the ecotypes, involving mainly extent of leaf dissection and corolla sac shape, are not, however, great enough to warrant taxonomic recognition.

DISTINCTIONS BETWEEN *DIASCIA* AND *ALONSOA*

Corolla morphology of South American and South African species of *Alonsoa* is remarkably similar (Figs. 1–5A, 7). Most obvious is the resupination which places the enlarged morphologically lower lip in an upright position. Resupination was overlooked for *A. unilabiata* by Linnaeus f. (1781) and all subsequent botanists except Diels (1897), presumably because this character is obscured in

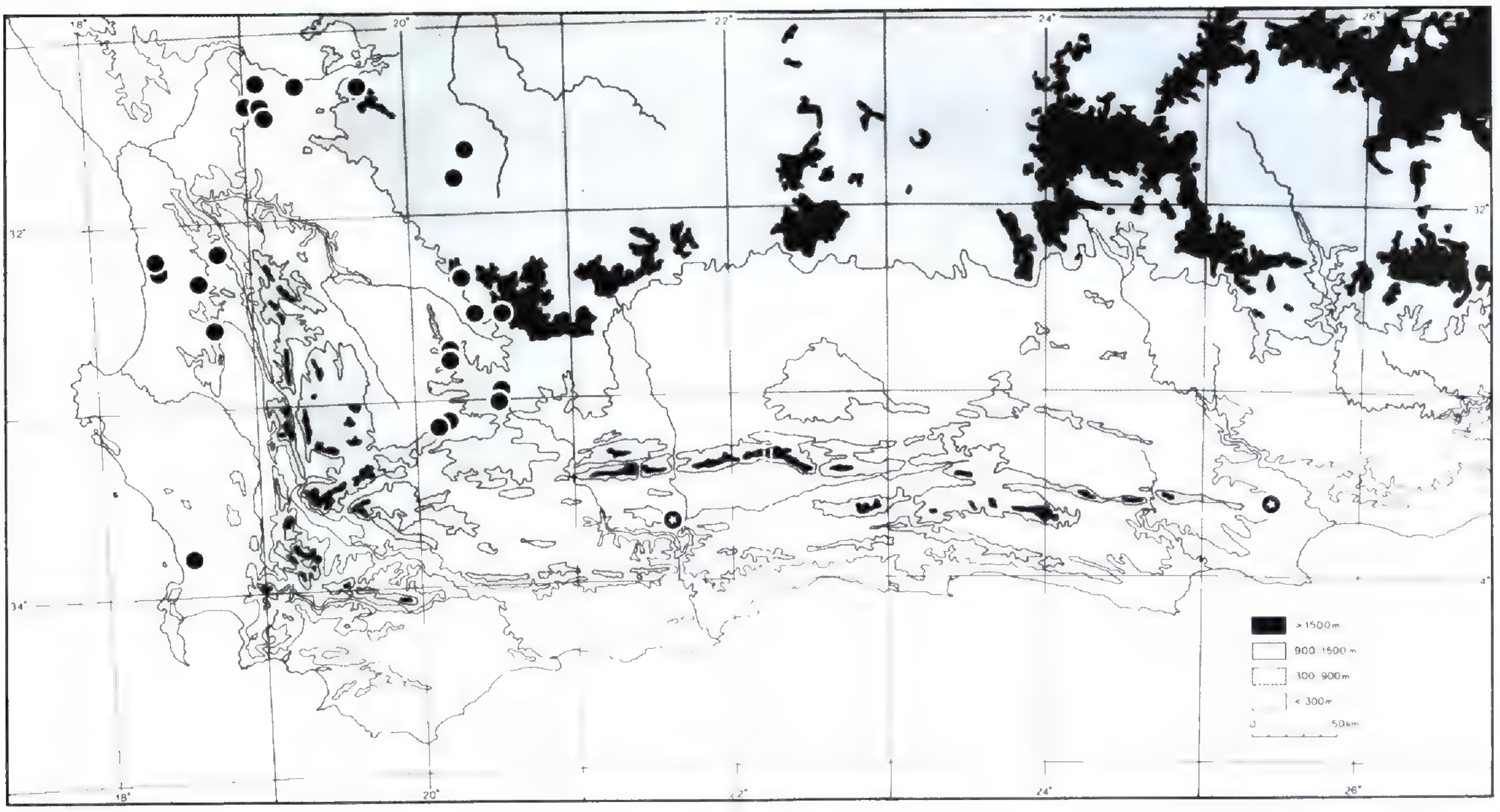


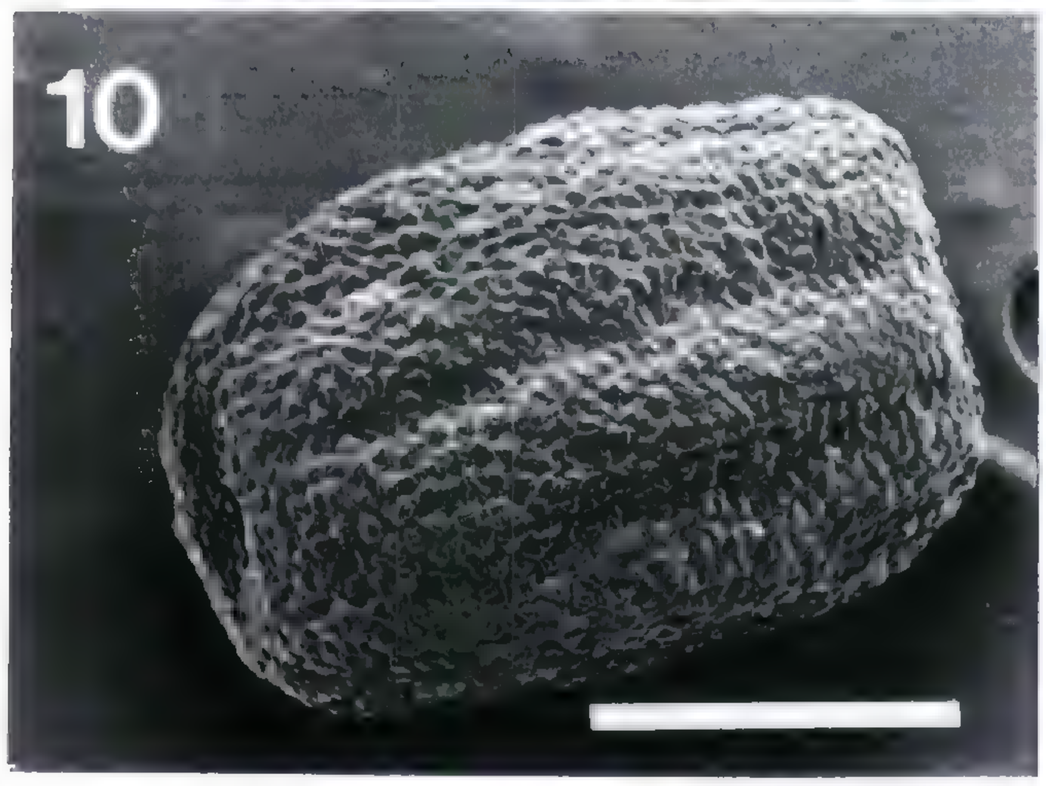
FIGURE 6. Distribution of *Alonsoa unilabiata* (solid circles) and *Alonsoa peduncularis* (star circles) in South Africa.

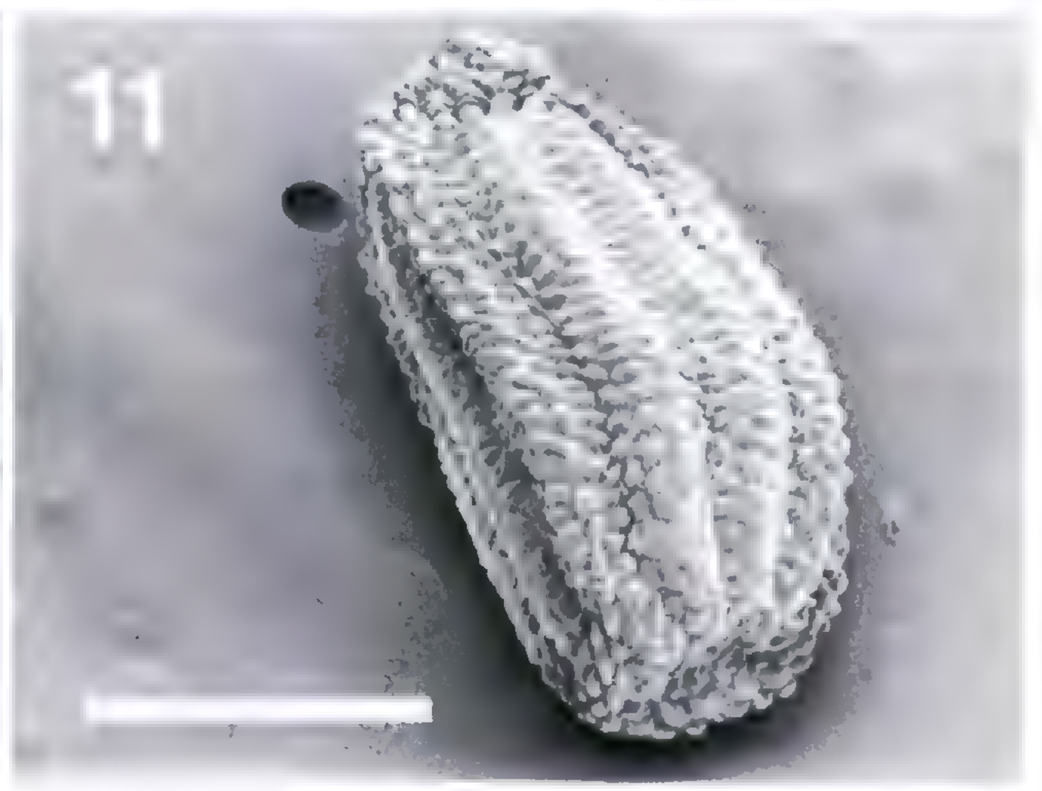
pressed material. *Diascia* species do not have resupinate flowers. Coupled with the rather strange appearance of the corolla caused by resupination in *Alonsoa* is the complete split in the corolla between the lower (morphologically upper) lobes (Fig. 5B), a character that Kunze (1842; in Hilliard & Burtt, 1984) erroneously attributed solely to *Alonsoa peduncularis* (as *Schistanthe peduncularis*). This condition is also found in *A. unilabiata*, as well as New World species *A. meridionalis* (L.f.) Kunze and others (pers. obs.; Edwin, 1971). The *Diascia* corolla always has a short but distinct tube (i.e., gamopetalous portion) without a split.

Another distinction between *Alonsoa* and *Diascia* is the form of the androecium. In *Diascia* (and in the related *Nemesia* and *Diclis*) the anterior (lower) filaments twist around the base of the posterior (upper) filaments, causing the upper part of the anterior stamens to be placed in a posterior position and the posterior stamens to appear in the anterior position (Hilliard & Burtt, 1984). No such twisting of the filaments occurs in *Alonsoa*, although a similar result without twisting is achieved in *A. peduncularis*, where the anthers of the lower (morphologically upper) stamens are situated above the anthers of the upper (morphologically lower) stamens. In *A. meridionalis*, the stamens are upright; in *A. unilabiata* (Fig. 5C) and *A. peduncularis* they project downward. This downward orientation in *A. unilabiata* is caused by the turning under of the lower (morphologically upper) rim of the corolla just above the point of filament attachment. *Alonsoa unilabiata* is set apart from all other *Alonsoa* species by its strongly dilated filaments (Fig. 5C–E).

FIGURE 7. Flower close-up of *Alonsoa meridionalis* subsp. *lactea* from El Angel, Ecuador.

Seed morphology further distinguishes *Alonsoa* from *Diascia*. As shown in Figures 8–11, *A. unilabiata*, *A. peduncularis*, and other *Alonsoa* species have wingless, oblong to elliptic seeds, usually with longitudinal straight (or undulate in *A. unilabiata*) furrows (Edwin, 1971). *Diascia* species have dorsiventrally flattened embryos and usually have elaborate wings or cuplike extensions on the seed coats. The pollen of *A. unilabiata* and *A. peduncularis* is tricolpate in contrast with the hexa-





FIGURES 8–11. Scanning electron micrographs of *Alonsoa* seeds.—8. *A. unilabiata* from Elands Bay.—9. *A. unilabiata* from Calvinia District.—10. *A. peduncularis*.—11. *A. meridionalis* from Peru. Scale lines = 0.5 mm.

to octacolpate grains of all examined *Diascia* species. *Diascia* and *Alonsoa* are distinguished in Table 1.

POLLINATION AND BREEDING SYSTEM

The major difference between South African and South American *Alonsoa* species is the presence in the former of a pair of shallow corolla sacs (Figs. 1–4, 5A, B) containing a dense patch of oil-secreting trichomes (trichome elaiophores). These trichomes consist of a two-celled stalk, bearing two or three secretory cells (Fig. 12).

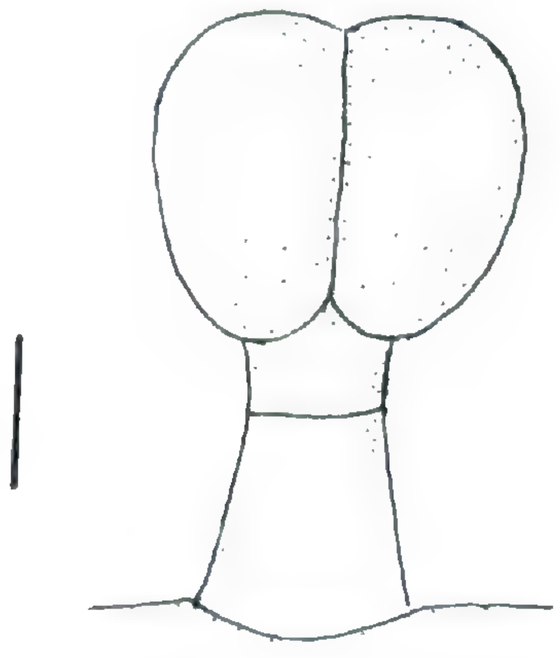


FIGURE 12. Trichome elaiophore from the corolla sac of *Alonsoa unilabiata*. Scale line = 15 μm.

The presence of elaiophores has a direct bearing on the manner in which these species are pollinated. *Alonsoa unilabiata* is pollinated by female oil-collecting bees in the genus *Rediviva*. Plants grow-

TABLE 1. Characters distinguishing *Alonsoa* from *Diascia*.

Alonsoa	*Diascia*
Flowers resupinate	Flowers never resupinate
Corolla split to the base between the morphologically upper lobes	Corolla with a short distinct tube, never split
Bases of filaments straight	Bases of filaments twisted placing anterior stamens in a posterior position
Pollen tricolpate	Pollen hexa- to octacolpate
Seeds oblong with longitudinal furrows and no wings	Seeds usually dorsiventrally flattened and with wings or with extensions of the testa fused into a cup

ing in the sandveld near Elands Bay are pollinated by two small (ca. 10 mm long) undescribed black species (*Rediviva* "*ruficornis*" and *R.* "*nigra*"), while plants on the Roggeveld escarpment from Grasberg to Sutherland (with the exception of Nieuwoudtville) are pollinated by a different undescribed species *R.* "*alonsoae*" and rarely by *R.* "*racemosae.*" At Nieuwoudtville, plants are visited by *R.* "*macgregori*" and *R.* "*racemosae.*" In all cases, bees place their heads at the base of the upper (morphologically lower) corolla lobe while inserting their forelegs into the oil-containing sacs. The dark central portion of the corolla as well as the yellow sacs are ultraviolet absorptive and contrast with the UV reflective corolla lobes (Steiner, pers. obs.). The presence of an ultraviolet absorptive region is common in oil-secreting species of *Diascia* and *Hemimeris* and appears to help orient the bee on the flower (Steiner, in press, pers. obs.).

Specialized scraping and absorptive setae on the forelegs of the *Rediviva* pollinators facilitate extraction of the oil, which is transferred to the hind legs and carried back to the nest (Whitehead & Steiner, 1985; Steiner & Whitehead, 1988; Buchmann, 1988). While probing for oil with its forelegs, the bee's abdomen curls into the cradle formed by the filaments, causing the anthers to rub against and deposit pollen on the upper tergites. Pollen is deposited from the abdomen onto the stigma of the next flower as the bee repeats this process.

The two *Rediviva* species at Elands Bay do not depend solely on *A. unilabiata* for oil, but also visit at least three other oil-producing species including *Hemimeris sabulosa* L.f. and two undescribed *Diascia* species. On the Roggeveld escarpment, with the exception of the Nieuwoudtville area, *A. unilabiata* is pollinated almost exclusively by *Rediviva* "*alonsoae.*" Even more unusual, however, is the apparent restriction of this bee to the flowers of *A. unilabiata* for oil, despite the cooccurrence of other oil-producing species at each site. This bee is the only one of 16 western Cape *Rediviva* species that is restricted to a single oil host plant (Steiner & Whitehead, pers. obs.).

Pollinator observations on other *Alonsoa* species are lacking. *Alonsoa peduncularis* occurs sympatrically with *Diascia patens* (Thunb.) Fourcade and may share the same *Rediviva* "*lepidos*" pollinator that collects oil from and pollinates that species, while New World species of *Alonsoa*, all of which lack oil-secreting trichomes, are probably pollinated by pollen-collecting bees. Many of the American species have large sturdy apically dehiscing anthers that form a cone around the style similar to that found in *Solanum*. These species are probably "buzz" pollinated (Buchmann, 1983) by large *Bombus* (Apidae) or *Centris* (Anthophoridae) bees.

The presence of shallow yellow corolla sacs in some annual *Diascia* species (*D. capensis* (L.) Britten, *D. diffusa* (Thunb.) Benth., *D. cardiosepala* Hiern, *D. elongata* Benth. et al.) probably accounts for the past confusion between *Alonsoa unilabiata* and *Diascia*. It is unlikely, however, that the presence of these sacs is indicative of a close relationship between *Diascia* and *Alonsoa* (Steiner, unpublished). Instead, it probably indicates a convergence based on adaptation to pollination by oil-collecting bees (Whitehead & Steiner, 1985; Steiner & Whitehead, 1988). Such unrelated parallel evolution of oil secretion has occurred numerous times in families as disparate as Orchidaceae, Iridaceae, Malphighiaceae, Krameriaceae, Scrophulariaceae, and Primulaceae; in unrelated orchid genera such as *Oncidium* and *Disperis*; and among unrelated Scrophulariaceae, such as *Calceolaria*, *Bowkeria*, and *Diascia* (Vogel, 1974, 1986; Simpson & Neff, 1981, 1983; Steiner, 1987).

Alonsoa unilabiata is self-compatible, as are other species in the genus, including *A. peduncularis* (Roux, 1986) and *A. meridionalis* (pers. obs.). Both of these last-mentioned species readily self-pollinate, and *A. peduncularis* can produce cleistogamous flowers under certain circumstances (pers. obs.). Flowers of *Alonsoa unilabiata*, however, self-pollinate only occasionally because of the spatial separation between anthers and stigma.

Alonsoa unilabiata is most closely allied to *Alonsoa peduncularis*, with which it shares the presence of corolla sacs containing trichome elaiophores, characters that must have evolved in Africa in conjunction with *Rediviva* oil-collecting bees. The annual habit, curved and dilated filaments, and acuminate two-lobed stigma, however, are all specialized features that set *A. unilabiata* apart from *A. peduncularis* and the South American species.

Synonymy and Description

Linnaeus f. (1781), Thunberg (1784), and Bentham (1846, 1876) all failed to realize that *Alonsoa unilabiata* (Linn. f.) Steudel has resupinate flowers. As a result, Diels (1897) described a new species (*Diascia nutans* Diels) for a collection of *A. unilabiata* from the Hantam Mountains near Calvinia. Discussing the resupinate corolla in his species, Diels stated that "evidently this development led to the same result as resupination of the *Alonsoa*

corolla, in fact the convergence developed so far that without the pits in the throat of the corolla, our species [*D. nutans*] would have to be placed in *Alonsoa*." The type of *D. nutans* was destroyed in Berlin, but the description and recent collections from the same locality (*Steiner 759*) suggest that Diel's plant must have been *A. unilabiata* (Linn. f.) Steudel.

When Bentham (1836) described *D. heterandra* he had not seen the type of *Alonsoa unilabiata* nor did he see it prior to his treatment of *Diascia* in De Candolle's *Prodromus* (p. 17, 1846). This may explain why he described Drège's collection as a new species in the first instance and why he retained it in his later publication. One of the characters used by Bentham to distinguish *D. heterandra* was the presence of sterile filaments. Judging from the poor preservation of the type as well as the relative ease with which anthers become detached in fresh material, it is likely that the missing anthers fell off during preparation and subsequent handling, since the specimen matches *A. unilabiata* in all other respects.

The type location for *Diascia heterandra* Benth., between Blouberg and Tygerberg, is considerably south of the main west coast distribution of *A. unilabiata*. Habitats near the type locality, however, are similar to those found around Elands Bay, where *Alonsoa unilabiata* can be locally common. The area between Blouberg and Tygerberg has been dramatically altered by the spread of urbanization and alien acacias, hence *A. unilabiata* is probably no longer there.

Diascia dissecta Hiern is simply a variant of *A. unilabiata* related to growth conditions. Its tall and spindly habit and more narrowly dissected leaves are typical of plants along the Roggeveld escarpment that grow up through shrubs.

Alonsoa unilabiata (Linn. f.) Steudel, Nomencl. Bot. ed. 2. 61. 1840. *Antirrhinum unilabiatum* Linn. f., Suppl. Pl. 279. 1781. *Hemimeris unilabiata* (Linn. f.) Thunb., Nov. Gen. Plant. 4: 78. 1784. *Diascia unilabiata* (Linn. f.) Benth. in DC., Prodromus 10: 257. 1846. TYPE: South Africa: e. Cap. b. spei, *Thunberg s.n.* (sheet 14207) (lectotype, here designated, UPS, microfiche at BOL).

Diascia heterandra Benth. in Hook., Comp. Bot. Mag. 2: 16. 1836. TYPE: South Africa: Cape Flats, between Blauw Berg and Tyger Berg, below 500 ft., *Drège 7887* (holotype, K).

Diascia nutans Diels, Bot. Jahrb. Syst. 23: 472. 1897. TYPE: South Africa: Hantam Mountains, *Meyer s.n.* (holotype, B, destroyed), ex char. only.

Diascia dissecta Hiern, in Fl. Capensis 4: 153. 1904. TYPE: South Africa: Gerrit Snyman's farm in the Roggeveld Karoo, *Burchell 1289* (holotype, K).

Annual herb, erect, simple or branching; main stem 30–400 mm high, up to 2 × 2 mm in cross section, quadrangular, green to reddish purple, glabrous to glandular-villous or hirsute, more densely so towards base. Leaves simple, opposite, subopposite or upper stem leaves alternate, in up to 5 pairs per branch, 4–55(–60) × 3–25 mm, lanceolate to ovate, dentate to pinnatifid, upper surface glabrous, lower surface glabrous to glandular-villous-hirsute with translucent hairs, apex acute, base obtuse or attenuate; lobes 1.5–9 × 1.0–5.0 mm, linear to ovate, occasionally secondarily lobed or divided, the apex acute; petioles 2–20 mm long, glabrous to glandular-villous-hirsute. Flowers 1–4 in a loose terminal raceme, alternate; bracts 4–31 × 1–6 mm, becoming smaller upwards, linear to ovate, entire to pinnatifid, glabrous to glandular-villous-hirsute; pedicels 5– 18 mm long, ascending, resupinate, slightly longer in fruit, glabrous to glandular-villous-hirsute. Calyx segments 2.5–3.0 × 1.0 mm, narrowly elliptic, entire, lowermost (morphologically uppermost) slightly narrower and shorter, ca. 2 mm long, obtuse, entire, hirsute with minutely glandular translucent hairs. Corolla bilabiate, 12–24 × 13–26 mm; upper lip (actually lower lip in upper position due to resupination) of 3 lobes, upper lobe (morphologically lower lobe) ca. 6–11 × 7–13 mm, very widely ovate, sparsely glandular-villous-hirsute outside, glabrous inside; 2 lateral lobes 5–10 × 6–11 mm, depressed ovate, bases oblique, pink to orangish pink; gamopetalous portion below the 3 lobes 3–5 × 5–9 mm, very dark purple, bisaccate; sacs 2.2–3.3 mm long, openings 1.5–2.0 × 1.3–2.1 mm, cordate to transversely elliptic in outline, sacs projecting back and downward, yellow, inner surface densely covered with oil-secreting trichomes; lower lip completely split to the base; lower lobes (morphological upper lobes) ca. 2–4 × 4–7 mm, transversely elliptic and partly folded under, bases oblique; pink to orangish pink. Stamens didynamous, projecting downward and involute to form 2 concentric cordate rings, with outer ring 4.0–4.5 mm diam. and inner ring ca. 2.5 mm diam.; posticous filament 6–8 mm long, broadly dilated in the lower half into a kneelike projection and in upper half involute; anticous filament 4–5 mm long, lacking a broad dilation, involute; both deep purple, glandular-puberulent; anthers ca. 1 mm long, bearded with light blue hairs; thecae yellowish blue, opening outward; pollen tricolpate. Ovary 1.2–1.5 × 1.2–1.5 mm, widely ovate in outline, obtuse, glandular-puberulent; ovules 20–30; style 5.5–8 mm, involute, su-

bulate, persistent; stigma minutely bifid, with acute lobes; capsule 6.0–8.5 × 4–6 mm, pyriform, apex emarginate; seeds 1.4–1.9 mm, oblong to elliptic in outline, with shallow undulating longitudinal furrows, dark reddish brown.

Additional specimens examined. South Africa: **31.19** (CALVINIA): ca. 10 mi. from Nieuwoudtville on road to Kareebooms, *Lewis 5868* (NBG); near Grasberg, N of Nieuwoudtville (AC), *Barker 9348* (NBG); Van Rhyns Pass, *Bond 1156* (NBG), *Esterhuysen 6142* (BOL); top of Van Rhyns Pass, *Lewis 5461* (NBG); Van Rhyns Pass on S-facing side of W-facing slope, *Steiner 901* (NBG); Klip Koppies, Nieuwoudtville, *Lewis 5854* (NBG); between Oorlogs Kloof and Papkuilsfontein, *Leipoldt 3454* (NBG); Farm Glen Lyon, S of Nieuwoudtville, *Oliver 46* (PRE); Matjesfontein, *Schlechter 10919* (SAM); road to Theunissedrift, 0.5 km NE of junction with Grasberg road, *Steiner 1355* (NBG); Farm Klipbok (AD), *Lewis 5882* (NBG); Farm Toren, 2 km E of Klipwerf road, 16.4 km N of Calvinia–Loeriesfontein road (BC), *Steiner 759* (NBG); near Augustfontein Mtn., S of Calvinia (CB), *Barker 9301* (NBG). **31.20** (WILLISTON): Blomfontein, E of Middelpos (CC), *Barker 10781* (NBG, STE); near Elandsfontein farm on road from Calvinia to Middelpos, *Grant & Theiler 4898* (BOL); 21.7 km N of Ceres turnoff on Middelpos Calvinia road (via Rooiwal), *Steiner 817* (NBG); Farms Bloomfontein/Hartbeesfontein, NW of Middelpos, *Steiner 822* (NBG). **32.18** (CLANWILLIAM): Zuurfontein, near Lambert's Bay (AB), *R. Schlechter 8556* (BOL); Vensterklip, N of Verloren Vlei (AD), *Boucher 2832* (STE); road between Lamberts Bay and Elands Bay, 7 km S of junction with Road 365, *Steiner 1546* (NBG); road to Lambert's Bay, 1.5 km N of junction with Elandsbaai–Redlinghuys road (R366), *Steiner 772* (NBG); road between Lamberts Bay and Elands Bay, 5 km S of junction with Road 365, *Steiner 1543* (NBG); between Clanwilliam and Graafwater (BB), *L. Bolus 23172* (NBG, BOL); in arenosis near Alexander's Hoek (BC), *R. Schlechter 5124* (BOL); Het Kruis (DA), *Stephens & Glover 8770* (BOL). **32.20** (SUTHERLAND): Klipfontein, SW of Sutherland escarpment edge (AD), *Oliver 4402* (STE, PRE); Houthoek, Sutherland (CA), *Hanekom 1068* (STE, PRE); Klipbanksrivier (N.W.) (CB), *Acocks 16961* (PRE); Farm Thyskraal, 86.7 km NE of road 355 (CC), *Steiner 792* (NBG); Verlatekloof (DA), *Steiner 794* (NBG); 23 mi. (36.8 km) SSW of foot of Komsberg Pass, *Leistner 260* (PRE); Road 354, 31.2 km N of junction with National Road (N1) (DC), *Steiner 1061* (NBG); below road to Sutherland (R354), 45.1 km N of junction with National Road (N1) at Matjiesfontein, *Steiner 1051* (NBG). **33.20** (MONTAGU): Tweedside (AB), *Compton 3014* (BOL); Konstabel (AD), *Compton 3754* (NBG, BOL); 20 mi. N of Matjiesfontein (BA), *Hall 3262* (NBG). WITHOUT PRECISE LOCALITY: Cape Flats, between Blauw Berg and Tyger Berg, below 500 ft., *Drège 7887* (K); between Elandskloof and Clanwilliam, *Leipoldt s.n.* (BOL 21270).

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NOTES

A NEW SPECIES OF *ISOËTES* FROM TERRITORIO FEDERAL AMAZONAS, VENEZUELA

While preparing a treatment of the genus *Isoëtes* for the *Flora of the Venezuelan Guayana*, several specimens from Territorio Federal Amazonas in Venezuela were found to represent an undescribed and distinctive species. This species is described and compared with other species of the northern Andes.

The various terms for organs and their character states follow Hickey (1985, 1986a); terminology for spore morphology follows Hickey (1986b). Two-dimensional shape characterizations for the ligule, labium and sporangium follow Radford et al. (1972).

Isoëtes vermiculata Hickey, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Atabapo, Cerro Marahuaca, submerged in small rivulet, 03°37′N, 65°23′W, 2,520–2,650 m, 26–27 Feb. 1985, *Steyermark & Holst 130758* (holotype, MO; isotypes, MU, Ven n.v.). Figures 1–3.

Ab aliis speciebus neotropicis differt subula triquetra, velo fere completo, ligula habenti pulvino depresso-ovato, auriculato, et macrosporis rugulatis vel subretatis.

Corm globose, 20–35 mm diam., bilobed; roots arising synchronously from the circumbasal fossa. Leaves numerous, stiff, erect to strongly recurved, to 85 mm long, 8–19 mm wide at the base, 1.3–2.0 mm wide at mid-length; alae chartaceous to submembranaceous, hyaline proximally, castaneous to blackish brown or dark green distally, 1.5–2.5 mm wide at the sporangium, 10–20 mm long (24–29% of the total leaf length), the apices on outer leaves acute to free, those on inner leaves attenuate; subula triquetrous, dark green, the apex acute to attenuate, corneous; fibrous bundles absent; scales and phyllopodia not seen. Sporangia obovate to widely depressed-obovate in surface view, hyaline, unspotted, 4.0–4.5 mm long, 2.5–4.0 mm wide, basal. Velum complete to incomplete, covering 66–100% of the sporangium. Ligule margins delicate, ephemeral; the cushion dark, persistent, depressed-ovate, 0.23–0.40 mm high, 1.1–1.4 mm wide, auriculate. Labium absent or only poorly developed. Megaspores white, slightly shiny, rugulate to subretate, often with a weakly developed, smooth girdle, 880–990 ($\bar{x}$ = 943) μm diam.; proximal ridges straight, broadly rounded, the equatorial ridges straight or scalloped, broadly rounded. Microspores pale reddish brown, scabrate, 35.5–45.8 ($\bar{x}$ = 40.1) μm long, 25.2–34.4 ($\bar{x}$ = 29.5) μm wide.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Atabapo, summit, Cerro Marahuaca, 03°50′N, 65°28′W, 2,580–2,600 m, 30 Mar.–1 Apr. 1983, *Steyermark & Delascio 129259* (VEN); submerged in stream, attached to margin in shallow water, 03°40′30″N, 65°26′20″W, 2,560 m, 10–12 Oct. 1983, *Steyermark 129586* (MO, UC).

Isoëtes vermiculata is known only from streambanks on the summit of Cerro Marahuaca of the Territorio Federal Amazonas in southern Venezuela. The species is named for the distinctive wormlike markings on the proximal and distal faces of the megaspores.

Isoëtes vermiculata is a distinctive element of the *Isoëtes* flora of northern South America. When fertile, it is most easily identified by its large, rugulate to subretate megaspores and depressed-obovate sporangia with nearly complete vela. It can be identified vegetatively by a combination of the triquetrous (three-sided, with rounded angles) subula, depressed-ovate, auriculate ligular cushion, and absence of a well-developed labium. The only other species of *Isoëtes* known from this region of Venezuela is *I. triangula*, a lowland, seasonal species having a trigonal (three-sided with sharp angles) subula, large labium, and pustulate megaspores, and not having a velum.

Not enough is known about *I. vermiculata* to judge affinities with other species in the genus. The triquetrous subulae and rugulate to subretate megaspores of *I. vermiculata* are, however, similar to

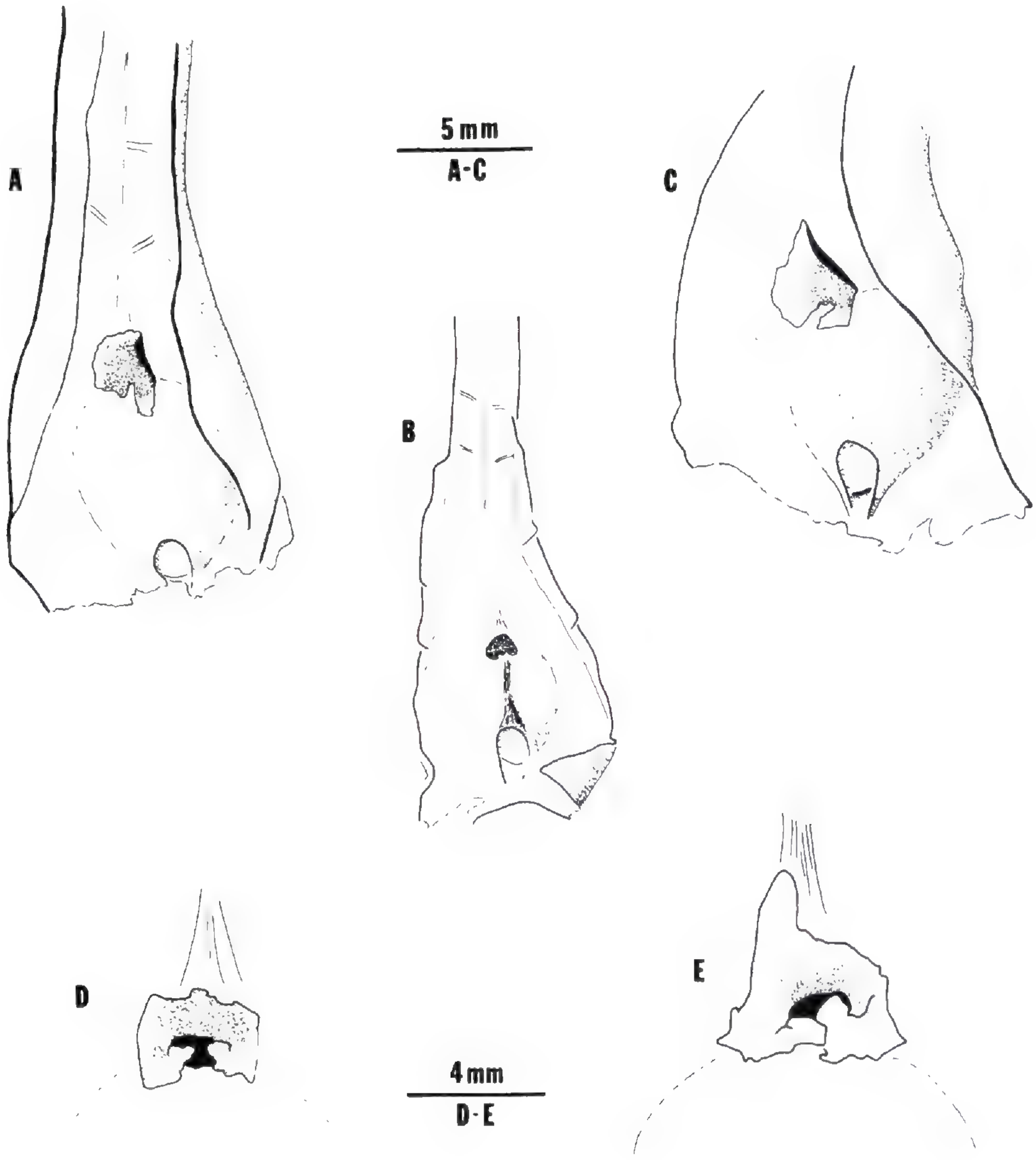
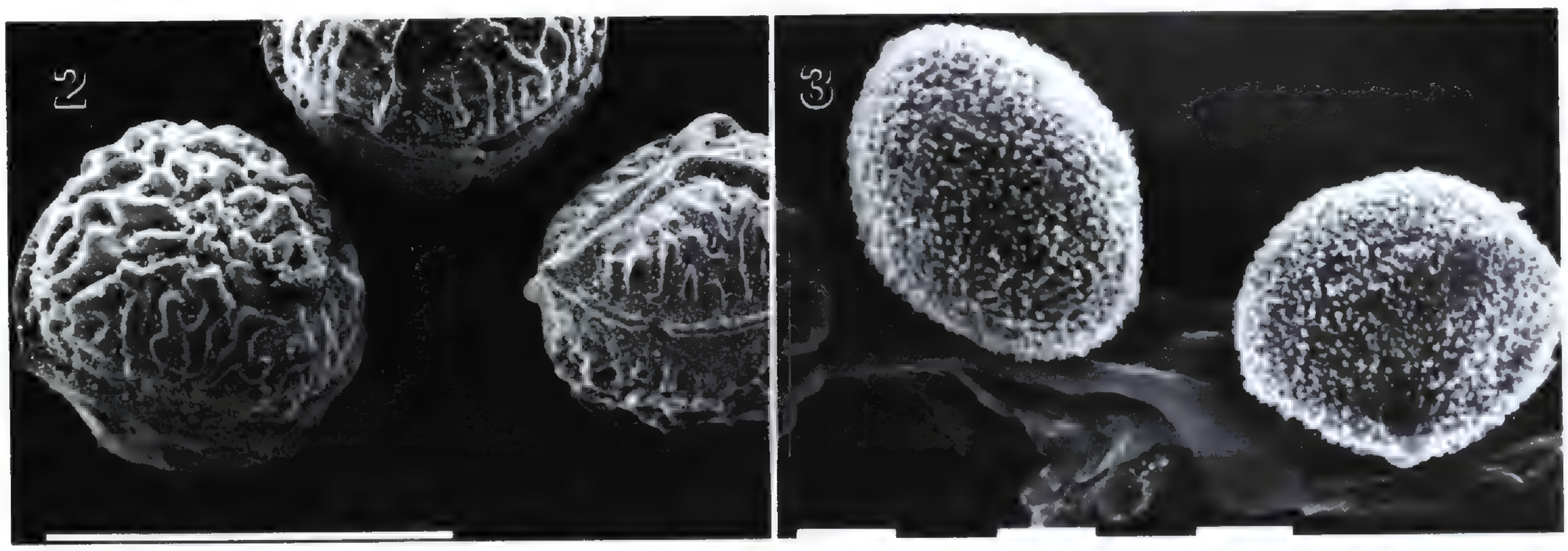


FIGURE 1. Leaf base morphology of *Isoëtes vermiculata*.—A. Microsporophyll showing nearly complete velum and partially eroded ligule, *Steyermark & Holst 130758* (MU).—B. Megasporophyll with a nearly complete velum and an entire ligule, *Steyermark 129586* (UC).—C. Microsporophyll on which only the ligular cushion remains, *Steyermark & Holst 130758* (MU). D, E. Variation in ligule form, *Steyermark & Delascio 129259* (VEN).—D. Ligule cushion with all of the ligular margin eroded.—E. Same as D but with portions of the upper ligular margin and marginal auriculate base remaining (black = foveola; stippled = cushion).



FIGURES 2, 3. Spores of *Isoëtes vermiculata*. —2. Distal and equatorial views of rugulate megaspores showing a nearly smooth girdle distal to the equatorial ridge, *Steyermark & Holst 130758* (MU). Bar = 1 mm.—3. Distal and equatorial views of scabrate microspores, *Steyermark & Holst 130758* (MO). Bars = 10 μm.

those of *I. novogranadensis*, *I. andina*, and *I. killipii*. Both *I. novogranadensis* and *I. killipii* are distinctive in having levigate microspores, whereas those of *I. andina* have the plesiomorphic echinate condition. The large spores of *I. vermiculata* suggest a hybrid of high ploidy level, perhaps $10x$ or $12x$. Whether this hybridization event took place when other taxa inhabited the area (perhaps during the Pleistocene) or whether it represents a morphologically and geographically distinct segregate population of a more widespread hybrid is open to question.

This research was supported by NSF Grant BSR 860672.

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—R. James Hickey, Botany Department, Miami University, Oxford, Ohio 45056, U.S.A.

A NEW VENEZUELAN *VIROLA* (MYRISTICACEAE)

This note describes and illustrates a new species of *Virola* from Cerro Sarisariñama in the Venezuelan Guayana.

Virola is a genus endemic to the American continent with its center of diversity and greatest species richness in the western Amazon region. With this

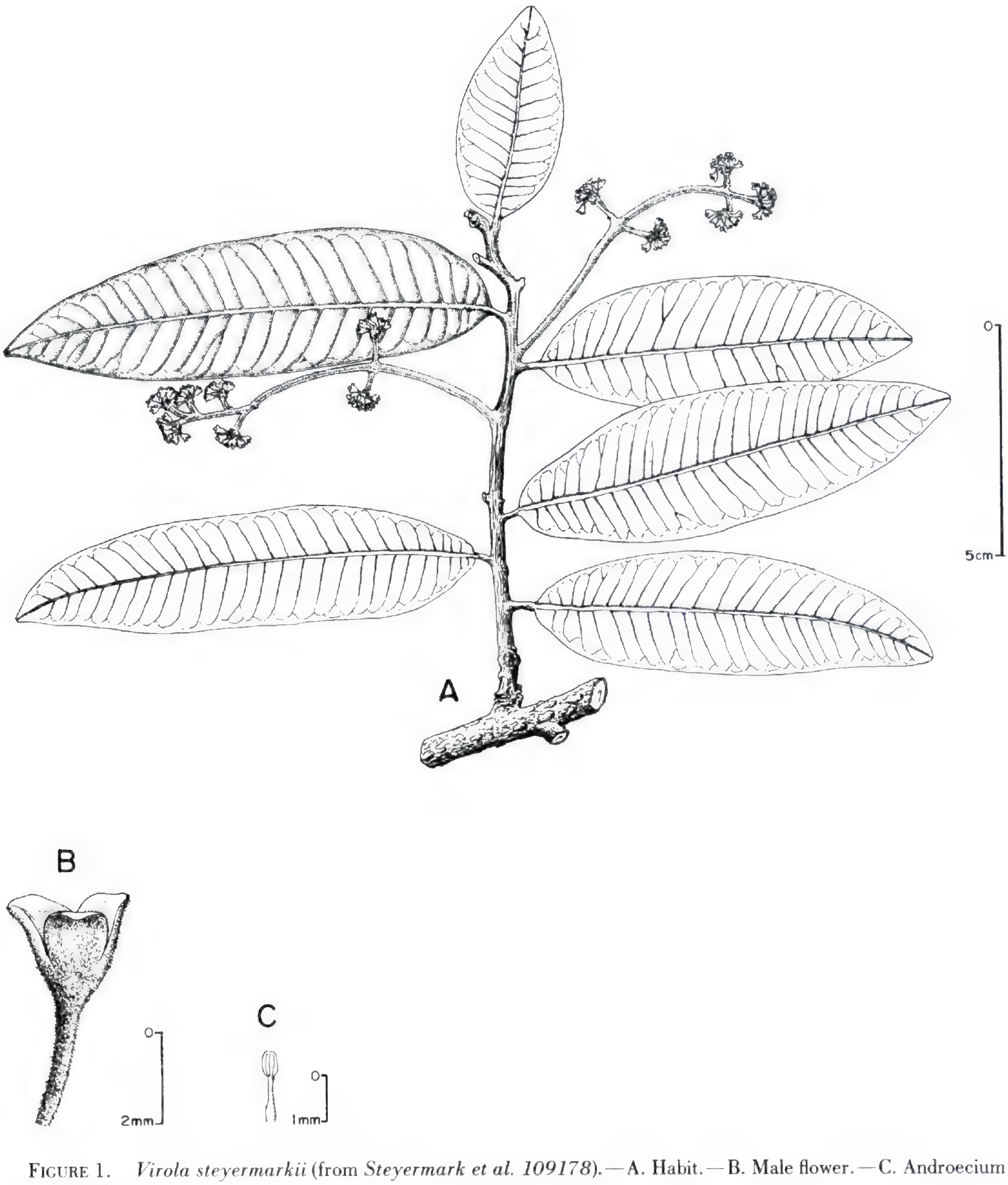

FIGURE 1. *Virola steyermarkii* (from *Steyermark et al. 109178*).—A. Habit.—B. Male flower.—C. Androecium from male flower.

ANN. MISSOURI BOT. GARD. 76: 1163–1164. 1989.

new species of *Virola*, there are now 13 Venezuelan species in this genus of 48 species.

Virola steyermarkii W. Rodrigues, sp. nov. TYPE: Venezuela. Bolívar: Meseta del Jaua, Cerro Sarisariñama, cumbre, porción nor-este, 04°41′40″N, 64°13′20″W, quebrada baja en selva más alta de promedio de 15–20 cm de alto, 1,400 m, 16–18 Feb. 1974 (fl), *J. A. Steyermark, V. Carreño-Espinhoza & C. Brewer-Carias 109178* (holotype, VEN; isotype, INPA). Figure 1.

A *V. officinali* Warb. maxime similis nervatio et inflorescentiae habitu, sed praecipue androecio breviore et androphoro apicem versus angustato statim dignoscenda.

Tree 20–25 m tall, branchlets robust, subterete, darkly ferruginous tomentose when young (hairs usually sessile or short-stalked, stellate, few-branched, up to 0.5 mm long), soon glabrescent; petioles canaliculate, stout, 3–6 mm long, 1.5–2 mm diam., darkly ferruginous tomentose; leaf blades chartaceous, oblong-lanceolate, 5–12 cm long, 1.8–4.0 cm broad, obtuse at base, acute at apex, glabrescent or sparsely and minutely puberulent beneath (hairs sessile or subsessile, stellate, 4–5-branched); costa shallowly grooved and glabrous above, prominent and tomentellous beneath, secondary nerves 22–26 per side, straight, impressed above, raised-tomentellous beneath, tertiary nerves subparallel, impressed above, obscure beneath. Male inflorescences narrow, once-branched, 6.5–7.5 cm long, peduncle conspicuously flattened, 2.5–3.5 cm long, rachis 5–7 branched, each branch 5–8 mm long; branchlets few, short, with flower clusters sessile toward the apex; vestiture of branchlets and flowers darkly ferruginous tomentose; bracts not seen; flowers arranged in clusters of about 25, pedicels slender, up to 3 mm long. Perianth of male flowers thin, 1.5–3 mm long, 3-lobed nearly to base, the lobes obtuse; androecium 1.2–1.3 mm long, androphore 0.7–0.8 mm long, carnose, slightly narrowed towards the apex, the anthers 3, 0.4–0.5 mm long, obtuse at apex, rounded and abruptly cuneate at base. Female inflorescences and fruits not seen.

Virola steyermarkii has a close affinity with the allopatric *V. officinalis*, particularly in the numerous, close secondary nerves and in the narrow, once-branched male inflorescence, but differs mainly by having a shorter androecium and androphore narrowed from the bottom toward the apex. Further, *V. steyermarkii* is known only from the type locality in Venezuela, very far from the restricted distribution of *V. officinalis* in the Brazilian states of Bahia and Minas Gerais.

The new species is named in honor of the late Julian A. Steyermark for his valuable contributions to the study of the neotropical flora.

I am grateful to the John Simon Guggenheim Memorial Foundation for the fellowship awarded to me in 1982 for continuation of my taxonomic studies of Myristicaceae, to William Leite for drawing the plate, and to Bruce Walker Nelson for reviewing the English translation.

—*William A. Rodrigues, Instituto Nacional de Pesquisas da Amazônia, Caixa Postal 478, 69083 Manaus, Amazonas, Brasil.*

A NEW SPECIES OF *CLITORIA* (LEGUMINOSAE) FROM VENEZUELAN GUAYANA

Two recent collections of a distinctive species of *Clitoria* L. (Leguminosae) were discovered while preparing a treatment of the genus for the *Flora of the Venezuelan Guayana*. This species is assigned to subg. *Bractearia* (Mart. ex Benth.) Fantz sect. *Brachycalyx* Fantz.

Clitoria comprises 60 species distributed primarily within the pantropical–subtropical belt; 49 species are native to the Neotropics. The genus is characterized by showy, resupinate, papilionaceous flowers; infundibular calyx with persistent bracteoles at the base; persistent stipules and stipels; and stalked ovaries with a geniculate, bearded style. Members commonly bear a pubescence of microscopic uncinate (hooked) trichomes best viewed at 20–30×.

Fantz (1979) circumscribed sect. *Brachycalyx* and in 1980 added three new species. Members are characterized by short tubular calyces with minute lobes, inflorescences cauliflorous emerging from denuded nodes preceding the leaves, erect habits (trees or shrubs), and fruits that become weakly convex around the seeds and that are conspicuously depressed transversely between the seeds. Species of this section are distributed from Guyana to central Panama to Ecuador with isolated collections of *Clitoria glaberrima* Pitt. collected as far north as southern Mexico.

Clitoria steyermarkii Fantz, sp. nov. TYPE. Venezuela. Bolívar: cumbre de Cerro Guaiquinima, Salto Río Szczerbanari (Río Carapo), 1–2 km rio arriba del Salto Szczerbanari, 5°44′4″N, 63°41′8″W, 750 m, 20–25 Jan. 1977, *Steyermark et al. 113464* (holotype, F 1878216; isotypes, F 1878213, MO 2769908, US 2821976, VEN).

Frutex ad 2 m altus. Folia trifoliata, foliola coriacea, oblonga-elliptica vel lancea-elliptica, subter pallida, cerifera; stipulae et stipelae lineares, persistentes. Inflorescentia cauliflora, brevissima. Bracteae et bracteolae lineares. Flores parvi, resupinati, albi, margine purpurea. Calyx breviter infundibularis, lobi breves. Stylus ovario duplo longior. Legumen incognitum.

Slender shrub to 2 m tall. Branches 2–5 mm diam., microscopically uncinate and sparsely strigose, becoming glabrous with age; pith hollow. *Leaves* 3-foliate, coriaceous, adaxial surface dull green to bluish green and glabrous, abaxial surface pale green to gray green, ceriferous, glabrous to sparsely strigose on veins; leaflets oblong-elliptic to lance-elliptic, apex with short acumen 0.5–1 cm long, mucronate, base broadly cuneate to nearly rotund, primary lateral veins 7–9 pairs, lamina 5–11 cm long, 2.5–6 cm wide. Petioles 5–8 cm long, subquadrangular, striate to slightly canaliculate at apex, microuncinate and sparsely strigose; rachis 1.5–3 cm long; petiolules subquadrangular, rugose, dark colored, sparsely pubescent, 4–6 mm long. Stipules persistent, linear, acute, striate, strigose apically, 3–4 mm long, 1 mm wide; stipels persistent, shorter than petiolules, linear-subulate, striate, 3–4 mm long, ca. 0.3–0.5 mm wide. *Inflorescences* cauliferous (1–3-fascicled) to 5 mm long, pseudoracemose, nodose, with 4–8 flowers, these paired at nodes, axes microuncinate; pedicels 3–4 mm long. Bracts in 3 series, striate, microuncinate, strigose-pilose apically; inner and middle ones inconspicuous, ovate, acute, ca. 0.4–0.6 mm long, 0.2–0.4 mm wide, outer ones linear, 2–3 mm long, ca. 0.3–0.5 mm wide. Bracteoles linear, acute, striate, microuncinate, 3–5 mm long, ca. 0.3–0.5 mm wide, inserted 1–2 mm below calyx base. *Flowers* resupinate, small, 2.5–3.5 cm long, white with purplish margin and purple venation. Calyx infundibular, 10-nerved, uncinate (trichomes conspicuous at 10–12×), tube 9–11 mm long, 2–3 mm wide at base expanding to 4–6 mm wide at throat, lobes acuminate-deltoid, 2–3 mm long, 1.5–2 mm wide basally, ventral lobe 3–4 mm long. Vexillum microuncinate toward apex and margins, blade complicate, obovate, emarginate, 1.5–3 cm wide, claw 4–6 mm long. Alae extended beyond carina 3–4 mm, blade 9–10 mm long, 4–5 mm wide, claw 12–14 mm long. Carina falcate, blade 6–8 mm long, 3 mm wide, claw 15–18 mm long. Staminal tube falcate apically, 18–21 mm long, free filaments 1–2 mm long; anthers linear, ca.

1.5 mm long, 0.4–0.5 mm wide. Gynophore ca. 2–3 mm long; ovary linear, 7–9 mm long, sericeous with tawny trichomes ca. 0.6–0.8 mm long masking dense uncinate microtrichomes beneath; style dark colored, ca. twice the ovary length, 14–17 mm long, bearded, geniculate 7–8 mm from distal end. *Legume* unknown.

Paratypes. VENEZUELA. BOLÍVAR: cumbre de Cerro Guaiquinima, Salto Río Szczerbanari (Río Carapo), 1–2 km río arriba del Salto Szczerbanari, 5°44′4″N, 63°41′8″W, 750 m, 20–25 Jan. 1977, *Steyermark et al. 113282* (MO 2769907, US 2821975, VEN).

This species is named in honor of Julian A. Steyermark who collected the species and who established the *Flora of the Venezuelan Guayana* project.

KEY TO SPECIES OF SECTION *BRACHYCALYX*

1a. Flowers 4–6 cm long; legume 10–15 mm wide; bracteoles 2–3 mm long.
  2a. Inflorescence 5–22 cm long; staminal tube 27 33 mm long, glabrous; leaflets glabrous above; shrub or treelet, 2–8 m tall (Ecuador) ..... *C. brachystegia* Benth.
  2b. Inflorescence to 2 cm long; staminal tube 23–26 mm long, microuncinate; leaflets hispidulous above; shrub to 2 m tall (Colombia) ..... *C. hermannii* Fantz
1b. Flowers 2.5–4 cm long; legume 16–30 mm wide; bracteoles 3–5 mm long.
  3a. Inflorescence to 0.5 cm long; leaves glabrous or glabrate below; anthers 1–1.5 mm long.
    4a. Leaves membranous, concolorous, nonceriferous; style 11–13 mm long, subequal ovary length; stipules & stipels caducous, 4–7 mm long; tree (Central America to northern Venezuela) ..... *C. glaberrima* Pitt.
    4b. Leaves coriaceous, pale green to gray green and ceriferous below; style 14–17 mm long, ca. twice the ovary length; stipules & stipels persistent, both 3–4 mm long; small shrub (southeastern Venezuela) ..... *C. steyermarkii* Fantz
  3b. Inflorescence 1–7 cm long; leaves conspicuously pubescent below; anthers 1.5–3 mm long.
    5a. Liana; petiolules 5–7 mm long; bracteoles 3–4 mm long; anthers 2.5–3 mm long; leaflets pilose below (western Brazil) ..... *C. froesii* Fantz
    5b. Tree or shrub; petiolules 7–10 mm long; bracteoles 1.5 3 mm long; anthers 1.5 2 mm long; leaflets strigose or velutinous below.
      6a. Calyx cup-shaped, 8–12 mm wide at throat; flowers white; gynophore 6–7 mm long; style geniculate 6–8 mm from distal end (western Guyana and adjacent Brazil) ..... *C. brachycalyx* Harms
      6b. Calyx narrowly infundibular, 5–7 mm wide at throat; flowers dull purple; gynophore 1–3 mm long; style geniculate 3–6 mm from distal end.
        7a. Calyx tube 7–11 mm long, lobes 2–3 mm long; staminal tube 16–22 mm long; keel blade 7–9 mm long, 2–3.5 mm wide; leaflets velutinous below; tree (Venezuela, Colombia) ..... *C. dendrina* Pitt.
        7b. Calyx tube 13–15 mm long, lobes 3–4 mm long; staminal tube 24–28 mm long; keel blade 14–16 mm long, 4–5 mm wide; leaflets strigose below; shrub (Venezuela) ..... *C. canescens* Pitt. ex Fantz

I am grateful to the curators of the herbaria (F, MO, US, VEN) for the loan of specimens and to Julian A. Steyermark and Bruce Holst for assistance on the *Flora of the Venezuelan Guayana* project. Paper No. 11981 of the *Journal Series of the North Carolina Agricultural Research Service*, Raleigh, North Carolina 27695-7643, U.S.A.

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—Paul R. Fantz, North Carolina State University. Mailing address: Dept. of Horticultural Science, Box 7609, North Carolina State University, Raleigh, North Carolina 27695-7609, U.S.A.

A NEW SPECIES OF *CABOMBA* (CABOMBACEAE) FROM TROPICAL AMERICA

The genus *Cabomba* is restricted to the Western Hemisphere, ranging from the eastern United States through Central America and the Caribbean to Argentina. Species of this genus are quite similar in habit, and few morphological characters are useful for distinguishing among them. The only complete taxonomic treatment of *Cabomba*, by Norman Fassett (1953), separated species primarily using characteristics of the perianth and leaf segments. From my fieldwork in tropical America and an examination of much of the material that has been collected from this region, some taxonomically significant characters not employed by Fassett have been discovered. Such characters are the number of leaves per node, stamen number, and seed size and shape. Other differences among taxa for the characters used by Fassett have also been noted.

In applying this enhanced scrutiny to the material included by Fassett in *C. piauhyensis* Gardner (= *C. furcata*[1]), I have become convinced of the existence of two distinct taxa within this entity. Typical *C. piauhyensis* always has whorled leaves at most or all nodes, commonly six (occasionally four or five) stamens, and subglobose seeds. This has been verified using an isotype of Gardner's original collection (*Gardner 2478* US) and is also readily apparent from the original illustration (Gardner, 1844). The distribution of *C. piauhyensis* (*C. furcata*) includes Brazil, northern Bolivia, Venezuela, eastern Colombia, the Guianas, Trinidad, and outlying populations are known from Cuba and Costa Rica as well. A second taxon, which Fassett failed to recognize, has opposite leaves, often three stamens (sometimes four or five or rarely six), and slightly larger subglobose to oval seeds. This taxon occurs from Honduras to western Ecuador and northern Venezuela and in the Greater Antilles. The principal area of sympatry for the two species is northern Venezuela. The second taxon is here described, and a key to all members of *Cabomba* that occur within its range is provided.

Cabomba haynesii Wiersema, sp. nov. TYPE: Panama. Canal Zone: Gamboa, Chagres River, ca. ¼ mi. up river from hyacinth control building near dock, 8 Feb. 1973, *H. Kennedy, C. von Chong & J. Steiner 2323* (holotype, MO; isotypes, UNA, Z).

Folia natantia laminis simplicibus linearibus usque 1.5 cm longis et 1 mm latis; folia submersa opposita dissecta (divisionibus secundariis dichotomis et trichotomis) segmentis terminalibus 0.1–0.4 mm latis; flores plerumque 6–8 mm longi ubi clausi; stamina saepe 3, interdum 4 vel 5, raro 6; carpella 1–3, plerumque 2; semina 1–3, 1.8–2.5 mm longa, 1.2–1.9 mm lata, 1.1–2× longiora quam lata.

Aquatic herbs with creeping rhizomes rooted in substrate and with elongate, distally floating, leafy stems. Floating leaves alternate, opposite or borne opposite submerged leaves, with petioles to 3.5 cm long, the laminae simple, linear, to 1.5 cm long, to 1 mm wide, peltate, entire. Submersed leaves opposite (rarely whorled at some nodes), with petioles to 2.5 cm long, palmately dissected into usually 5–7 primary segments, these with 1–3 additional and mostly dichotomous divisions, except the central 2–3 segments with secondary and often tertiary divisions trichotomous, terminal segments 0.1–0.4 mm wide. Flowers solitary, axillary from the upper nodes, bisexual, radially symmetrical, mostly 6–8 mm long when closed, borne at or above the water surface on peduncles to 5 cm long; sepals 3, white to pink-purple; petals 3, coloration as in sepals, with protruding auricles near base; stamens often 3, sometimes 4 or 5 or rarely 6; carpels 1–3, mostly 2, each tapering to a short style and a spherical terminal stigma, the ovaries superior, the ovules (1?)2–3. Fruits indehiscent, coriaceous, achenelike, or folliclelike; seeds 1–3, 1.8–2.5 mm long, 1.2–1.9 mm broad, 1.1–2 times as long as broad, with longitudinal rows of papillae at maturity.

[1] Communication with Niels Jacobsen and Marian Ørgaard of the Royal Veterinary and Agricultural University, Frederiksberg, Denmark, who have examined the type of *Cabomba furcata* Schultes & Schultes f. (Roemer & Schultes, Syst. Veg. 7(2): 1379. 1830.), indicates that *C. furcata* is the correct name for the species previously known as *C. piauhyensis*.

Habitat and distribution. Submersed in stagnant or gently flowing water to 1 m deep in ditches, ponds, swamps, marshes, rivers, or streams to 1,000 m of altitude. Honduras to western Ecuador and northern Venezuela, and the Greater Antilles.

Additional specimens examined. EL SALVADOR. LA UNIÓN: Laguna Maquigua, 18 km W of La Unión, *Fassett 28633* (WIS), *Standley 20955* (US). HONDURAS. CORTÉS: Lake Yojoa, near Agua Azul, *Williams & Molina 17872a* (US); Lake Yojoa, Cienaga section, *Howard et al. 682* (US). NICARAGUA. CHONTALES: 12.5 km SE of Santo Tomás, *Haynes 8635* (MO, UNA); 1 km NW of Puerto Díaz, *Haynes 8324* (MO, UNA). JINOTEGA: Presa El Mancotal, *Haynes 8274* (MO, UNA). RÍO SAN JUAN: San Juan del Norte, *Seymour 5301* (MO, UNA), *Stevens 20849* (MO, UNA). ZELAYA: Santa Marta, *Haynes 8417* (MO, UNA). PANAMA. CANAL ZONE: Madden Lake, *Woodson & Schery 951* (US). DARIÉN: Río Pirre, *Duke & Bristan 8309* (US). COLOMBIA. CAUCA: across Río Naya from El Pastico, *Gentry & Juncosa 40602* (MO, UNA). ECUADOR. GUAYAS 18 km S of Balzar, *Davenport et al. 2090* (UNA, USF). LOS RÍOS: Juaneche forest, Canton Vinces, *Gentry et al. 30760* (SEL, UNA). VENEZUELA. ARAGUA: 1.6 km down road to Emo. Camatagua, *Haynes 7645* (UNA); La Victoria, *Palacios 79* (VEN). BOLÍVAR: Embalse between Upata and Villa Lola, *Trujillo 11498* (MY). COJEDES: 15 km S of San Carlos, *Trujillo 13812, 14435* (MY). GUÁRICO: 32 km SSE of Calabozo, *Davidse 3799* (MO, US). PORTUGUESA: Laguna Las Junquitos near Acarigua, *Salazar 24* (VEN). ZULIA: Caño La Maroma near Santa Barbara, *Trujillo 12044* (MY). CUBA: Herredura, *Cook 135* (US); unspecified locality, *Wright 1861* (US). JAMAICA: lake at Dromilly, *Proctor 24494* (NY). PUERTO RICO. Añasco, *Sintenis 5601* (Z); Aguadilla, *Sintenis 5766* (Z).

Named in honor of Robert R. Haynes, who played an important role in the collection and recognition of this species.

KEY TO *CABOMBA* OF CENTRAL AMERICA, WEST INDIES, AND NORTHERN SOUTH AMERICA

1a. Floating leaves broadly elliptic, flowers yellow ..... *C. aquatica* Aublet
1b. Floating leaves linear to narrowly elliptic, flowers white to pink-purple.
  2a. Submersed leaves mostly whorled ..... *C. furcata* Schultes & Schultes f. (including *C. warmingii* Caspary and *C. piauhyensis* Gardner)
  2b. Submersed leaves opposite.
    3a. Carpel 1, blades of petals abruptly narrowed to base (rarely auricled) ..... *C. palaeformis* Fassett
    3b. Carpels (1)2–4, blades of petals auricled toward base.
      4a. Stamens usually 6, floating leaves more than 1 mm wide ..... *C. caroliniana* A. Gray (including *C. pulcherrima* (Harper) Fassett)
      4b. Stamens usually 3, sometimes 4 or 5, rarely 6; floating leaves up to 1 mm wide ..... *C. haynesii* Wiersema

I thank Steven R. Hill for the Latin description, Lauritz B. Holm-Nielsen for supplying information on the type of *C. warmingii*, Niels Jacobsen and Marian Ørgaard for providing information on the nomenclature of *C. piauhyensis* and the curatorial staff at MO, NY, UNA, US, WIS, and Z for providing access to their specimens.

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A NEW SPECIES OF *HYPTIS* (LAMIACEAE) FROM THE VENEZUELAN GUAYANA

While examining collections of Lamiaceae for the *Flora of the Venezuelan Guayana*, I encountered a single gathering of a *Hyptis* species that was unfamiliar to me. It was surprising to find a new *Hyptis* species at an altitude of 120–150 m in northern South America.

Although clearly belonging to sect. *Hyptis*, it differs from all other known species in its elongate, interrupted, pseudospicate inflorescences composed of small sessile capitula and situated in the axils of much-reduced bracts. The new species is also remarkable for its almost sessile leaves, the petiole apparently never more than 2 mm long. In this respect, it recalls *H. vilis* Kunth & Bouché, from Central America and northern Venezuela but differs in floral characters and in leaf shape, and by having sessile rather than long-pedunculate capitula. The lack of a ring of hairs in the calyx tube places *H. guanchezii* in subsect. *Marrubiastrae* Benth., along with *H. parkeri* Benth., which is also found in the Territorio Federal Amazonas.

Hyptis guanchezii is named for the collector and discoverer Francisco Guánchez.

Hyptis guanchezii *R. Harley*, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Atures, bosque-laja en Cerro Uchonhua (lengua Piaroa), a unos 5 km N del casério San Pedro de Cataniapo (en lugar quemado durante la sequia de 1979), a unos 60 km al SE de Puerto Ayacucho, 05°41′N, 67°11′W, 120–150 m, 9 Nov. 1980, *Guánchez 365* (holotype, VEN; isotypes, K, TFAV). Figure 1.

Ab aliis speciebus sectionis Hyptidis foliis subsessilibus vel petiolis usque 2 mm longis, lamina basim truncata vel leniter subcordata, inflorescentia spiciformi interrupta capitulis sessilibus in axillis bracteis deminutis subtentis, differt.

Erect herb to 80 cm high, with slender purple-tinged stems branching from a central rootstock. Stems quadrangular with coarse, spreading villous hairs below, these sparser and more slender above, the nodes densely tufted with whitish, antrorse hairs. Leaves 3.5–7.5 × 2.0–3.2 cm, markedly decreasing in size above and often shorter than the internodes, ovate-lanceolate to narrowly ovate with acute apex and narrowing to a truncate or weakly cordate base; upper surface of lamina appearing dark green, villous with scattered rather broad-based hairs, the veins weakly impressed; lower surface paler, villous with weak hairs restricted to the rather prominent veins and margin, glabrous between the veins and with sunken sessile glands; margin coarsely and bluntly serrate; petioles 1–2 mm, the upper leaves often appearing almost sessile. Inflorescence spiciform, 10–15 cm long, composed of opposite sessile capitula in the axils of inconspicuous bracts, the lower internodes usually 5–6 cm long. Bracts up to 4–6 mm long (the upper bracts shorter), lanceolate to ovate-acuminate, with broadened base and somewhat recurved margin, midrib prominent abaxially. Capitula 10–12 mm diam., with an involucre of narrowly lanceolate, curved bracteoles up to 5 × 1 mm, these glabrous with the midrib prominent beneath. Flowers subsessile, surrounded at base by dense tuft of long, silky, white (pale brown in herbarium material) hairs. Calyx tubular, at anthesis ca. 4 mm long, the tube 2–2.5 mm, glabrous throughout; calyx teeth 1.75–2 mm long, narrowly deltoid-lanceolate, ciliate with long-acuminate apex. Corolla 5–6 mm long, white, the tube ca. 4.5 mm long; stylopodium absent. Ripe nutlets not seen.

I acknowledge Julian Steyermark's vision in conceiving the idea of a *Flora of the Venezuelan Guayana*, which helped turn my attention to this floristically rich area with its particularly interesting phytogeographical patterns in the Lamiaceae.

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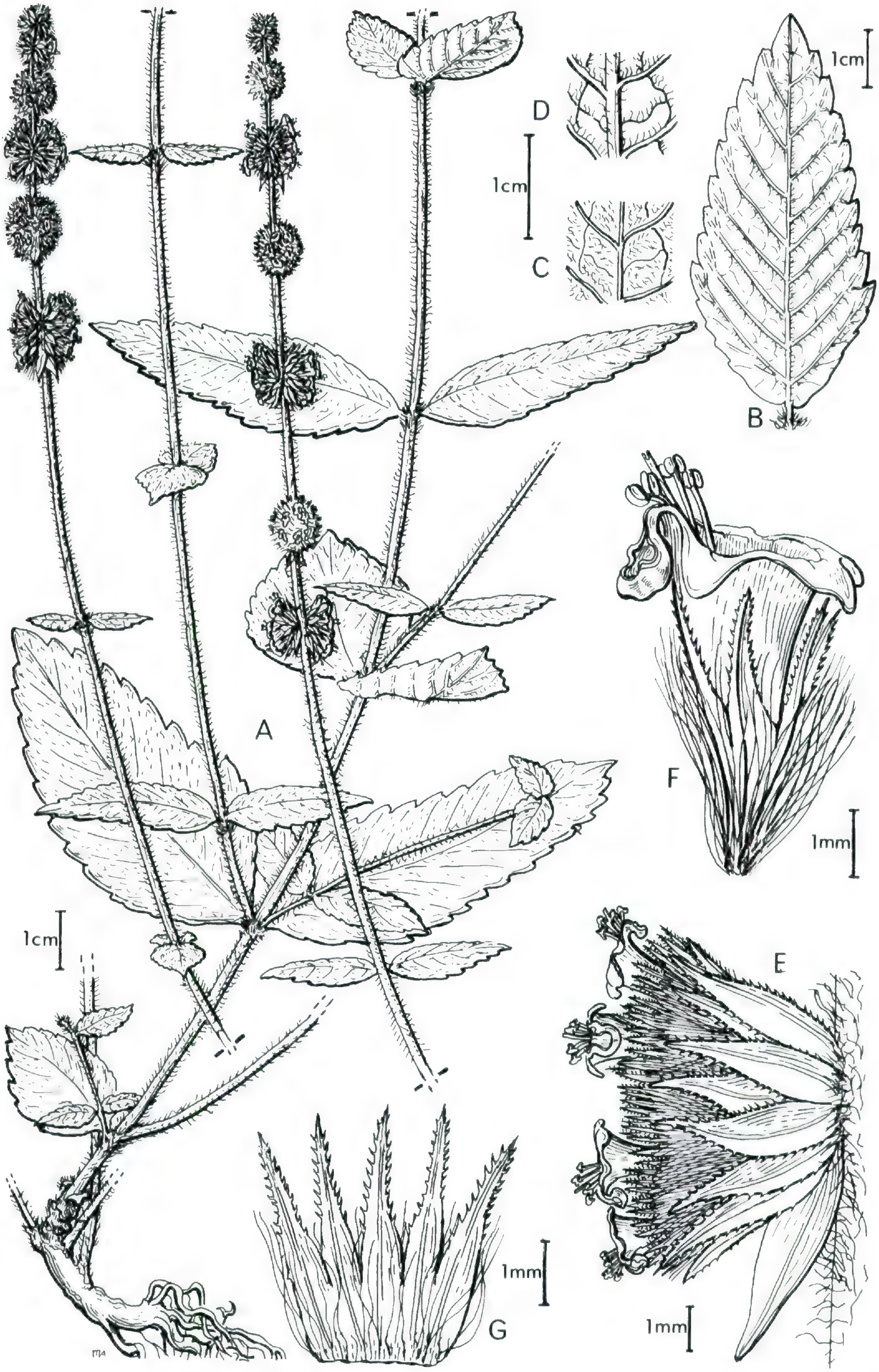

FIGURE 1. *Hyptis guanchezii.*—A. Habit.—B. Leaf, lower surface.—C. Leaf detail: upper surface.—D. Leaf detail: lower surface.—E. Sessile capitulum, side view.—F. Flower, side view.—G. Calyx, outer surface. (Drawn by Milton Andrews from *Guanchez 365.*)

NEW COMBINATIONS IN *SORGHASTRUM* (POACEAE: ANDROPOGONEAE)

Nash (1901:71) separated *Sorghastrum* from *Sorghum* Moench on the basis of the reduction of the pedicellate spikelets to simple pedicels in *Sorghastrum*. Morphological, anatomical, and cytological data (Davila, in prep.) support Nash's conclusion and reinforce the generic recognition of *Sorghastrum*. Davila (1988) recognized 15 American and two African species of *Sorghastrum*. Two new combinations in this genus are presented below.

Sorghastrum balansae (Hackel) Davila, comb. nov. *Sorghum balansae* Hackel, Fl. Bras. 2(3): 277. 1883. TYPE: Paraguay: *Balansa 209a* (holotype, P).

Sorghastrum incompletum (Presl) Nash var. **bipennatum** (Hackel) Davila, comb. nov. *Andropogon bipennatus* Hackel, Androp. Nov. Fl. 68(8): 142. 1885. TYPE: Central African Republic: Djur and Scriba ghattas, *Schweinfurth 2486* (holotype, US).

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PASSIFLORA MALLETII, A NEW SPECIES IN SECTION *DECALOBA* (PASSIFLORACEAE) FROM MESOAMERICA

A number of undescribed species of passionflower have been found during a revision of the Passifloraceae for the *Flora Mesoamericana* project (in press); most of them are in the small-flowered subgenus *Plectostemma* Masters. Newly described here is one such species; it is restricted to Panama and known from three recent collections.

Passiflora malletii J. MacDougal, sp. nov. TYPE: Panama. Panamá: near Cerro Jefe, 3 mi. along road past Alto Pacora toward Cerro Brewster, 9°15′N, 79°25′W, 700–750 m, 19 June 1988, *G. McPherson 12612A* (holotype, MO; isotype, PMA). Figure 1.

Passiflora pubescens scandens; petioli eglandulosi; folia eglandulosa integra acuta vel acuminata, vel raro trilobata, marginibus integris; bracteae lineares vel fusiformes vel obtrullatae, integrae vel trifidae, (3.5)4 7 × (0.3–) 0.7 2(3) mm; flores parvi subvirides vel pallido-viridiflavi, perianthiis ad basim purpurascentibus; coronae filamenta biseriata, filamentis exterioribus filiformibus 3.8–5 mm longis; operculum plicatum purpureum setulosum; androgynophorum 2.5(–3) mm longum; ovarium dense pubescens pilosum; bacca atropurpurea; semina 5–6(–7)-sulcata.

Vine 3–5 m, densely short-pubescent to pilosulous throughout. Stems subangulate or subflattened, substriate. Stipules (3–)5–8 × (0.3–)0.6–1 mm, linear to linear-lanceolate, sometimes slightly falcate; petioles eglandular; laminas (1.5–)4–10 × (0.8–)1.5–6 cm, entire, not variegated, ovate (rarely ovate-oblong), unlobed or occasionally 2–3 lobed (if lobed then usually unlobed leaves also present on the branch), the leaves of determinate axillary branches usually unlobed, the lateral lobes if present acute to acuminate, the central lobe acuminate (to acute); laminar nectaries absent. Inflorescence often present, of determinate, short, axillary shoots with reduced or no leaves. Peduncles 1(–2) per node, 0.6–1.4 cm long, uniflorous; bracts (3.5–)4–7 × (0.3–)0.7–2(–3) mm, linear, fusiform, oblanceolate, or obtrullate, entire or deeply 3-toothed to 3-cleft. Flowers pale to light yellow-green, slightly flushed purplish; floral stipe up to 0.5 mm long; sepals 8–10 × 4.2–5 mm, with no apical projection; petals 1–2 mm long (or obsolete?); coronal filaments in 2 series, the outer series 3.8–5 mm long, filiform, pale greenish yellow or greenish white, basally purplish?, the inner series ca. 3.5 mm long, capitellate, whitish with purplish apices; operculum 1.5 mm long, membranous, plicate, sparsely setose below the apex, purplish; staminal filaments connate 2.5(–3) mm along androgynophore, the free portions ca. 4 mm long; ovary densely pilose, dark green. Fruit 1.3–1.8 cm diam., subglobose, (dark green to) purplish black, estipitate; arils unknown; seeds 2.8–3.1(–3.3) × 1.9–2.1 mm, transversely sulcate with 5–6(–7) sulci, the ridges slightly rugulose.

Habitat and distribution. The one field observation by Mallet and the three collections are from 300–750 m at edges of tropical wet forest and premontane wet forest, within 25 km of each other in central Panama. The label on the type describes the locality as "Pacific slope near divide, rich wet forest."

Name. The specific epithet honors the ecologist Dr. James Mallet, whose specialty is the Heliconiine butterflies that feed on Passifloraceae. He observed this species along the Llano–Cartí road in March 1982, made field notes about the plant, sent living collections to the University of Texas at Austin for study (which died), and pointed out (in litt.) that it was apparently undescribed. He has made numerous and detailed observations on the Passifloraceae and realized that a number of species he encountered were new. By kindly allowing free access to his field books, his detailed notes have enhanced the accuracy of the revision for *Flora Mesoamericana* and contributed much to our understanding of *Passiflora*.

Additional specimens examined. PANAMA. PANAMÁ: El Llano to Cartí road, 9.3 km N of Panamerican Hwy., 8 June 1977, *Folsom 3601* (MO); El Llano–Cartí road, 9 mi. from Panamerican Hwy., 9°16′N, 78°57′W, ca. 300 m, 28 July 1983, *J. S. Miller et al. 851* (BM, MEXU, MO, PMA).

FIGURE 1. *Passiflora malletii*, composite drawing from *J. S. Miller et al. 851* and *Folsom 3601*.—A. Habit.—B. Bracts.—C. Stipule.—D. Seed.

Passiflora malletii is a member of subg. *Plectostemma* Masters sect. *Decaloba* DC. as revealed by the small flowers with biseriate filamentous corona and plicate operculum, small free bracts, narrow stipules, and transversely sulcate seeds. Within sect. *Decaloba* it belongs with the species group that includes *P. sexflora* A. L. Juss., *P. rugosissima* Killip, *P. porphyretica* Masters, and two new

species from Mexico. From these it is remarkably distinguished by its mostly unlobed, sharply pointed leaves, an evidently derived condition. Mallet's field notes describe the stem as strongly flattened, suggestive of an unusual phyllotaxy for the family, but the dried specimens of the other collectors appear to be subangulate to partially flattened. The phyllotaxy is not clear because of deformation of the stems in drying; both $\frac{2}{5}$ and $\frac{1}{2}$ are known in the related species of this group.

The flowers of the new species are notable for their short androgynophore and very reduced petals. The sparsely setulose operculum is also distinctive since the floral parts are only rarely pubescent in this genus. The peduncles are uniflorous and the flowers are generally crowded on determinate axillary branches, much like its close relative *P. porphyretica*.

The seeds of nearly all of the species of sect. *Decaloba* are probably bird dispersed, but observations are few. The label on *J. S. Miller et al. 851* notes "fruit green and being eaten by toucanettes." I believe the mature fruits to be purplish black because in this collection the pericarps turned black during the process of preparing the specimen, a phenomenon commonly seen with nearly mature fruits in this section. In most species of *Passiflora* the seeds and arils mature before the pericarp changes color (pers. obs.). It thus appears that the birds were eating submature fruit, probably with sweet mature arils.

The Missouri Botanical Garden, with a grant from the Jessie Smith Noyes Foundation, generously funded my postdoctoral research. John Myers prepared the illustration.

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A NEW COMBINATION IN *OCOTEA* (LAURACEAE)

Nees (1836) described *Nectandra arnottiana* in his *Systema Laurinarum* and cited only a specimen from the Arnott Herbarium which is now incorporated in the Herbarium of the Royal Botanic Garden, Edinburgh (E). This specimen has not been seen by later botanists working on Lauraceae, who treated the name incorrectly. Meissner (1864) treated *N. arnottiana* as a variety of *Nectandra laurel* Nees and stated that he did so only guided by Nees's description. Mez (1889) accepted *N. arnottiana* as a valid species and treated *Pleurothyrium chrysothyrsus* Meissner as a synonym of it. He cited only *Mathews 3031* (K, BM), the type of *P. chrysothyrsus*, under *N. arnottiana* and obviously had not seen the specimen from the Arnott Herbarium. I have now seen the Edinburgh specimen annotated by Nees as *N. arnottiana*. This specimen is *Mathews 1429*. Meissner (1864) recognized a duplicate of *Mathews 1429* in Kew as an undescribed species and made it the type of his *Pleurothyrium ferrugineum*, a species up to now known as *Ocotea ferruginea* (Meissner) Mez. But because the Nees epithet has priority, I transfer it to *Ocotea* and present the synonymy for the resulting combination, with the Meissner name in synonymy.

Ocotea arnottiana (Nees) van der Werff, comb. nov. BASIONYM: *Nectandra arnottiana* Nees, Syst. Laurin. 289. 1836; *Nectandra laurel* Nees var. *arnottiana* (Nees) Meissner, DC. Prodr. 15(1): 147. 1864. TYPE: *Mathews 1429* (holotype, E).

Pleurothyrium ferrugineum Meissner, DC. Prodr. 15(1): 169. 1864, superfluous name for *N. arnottiana*; typified by different specimen from same collection number; *Ocotea ferruginea* (Meissner) Mez, Jahrb. Bot. Garten Berlin 5: 265, 1889. TYPE: *Mathews 1429* (holotype, K).

Duplicates of *Mathews 1429* have also been reported from BM, G, OXF, and P; these are all isotypes of *Ocotea arnottiana* (Nees) van der Werff. Excluded from the synonymy is *Nectandra arnottiana* sensu Mez, non Nees, Jahrb. Bot. Garten Berlin 5: 402, 1889. Mez based his description on *Mathews 3031*, the only collection cited, and his description of leaves and flowers does not apply to *Ocotea arnottiana*.

Ocotea arnottiana is known to me from Andean cloud forests at 2,000–3,000 m in northern Peru and southern Ecuador. Bernardi (1975) placed *Ocotea steyermarkiana* Allen in synonymy under *O. ferruginea* and identified several collections from Venezuelan Guayana as *O. ferruginea*. However, I consider these Venezuelan collections distinct from *O. arnottiana*; their correct name is *Rhodostemonodaphne steyermarkiana* (Allen) van der Werff. Similar coriaceous leaves with raised reticulation and a dense tomentum on the lower leaf surface, which misled Bernardi, occur in several unrelated, montane species of Lauraceae and are probably a habitat adaptation. Meissner (1864) already noted the strong similarity between "*Pleurothyrium ferrugineum*" (= *Ocotea arnottiana*) and *Persea ferruginea* HBK; and an as yet undescribed species of *Ocotea* (not related to *O. arnottiana*) from high elevation cloud forests in Ecuador and Colombia also has these characteristics.

I thank the curator of E for the loan of neotropical Lauraceae.

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SISYMBRIUM AREQUIPANUM (BRASSICACEAE), A NEW SPECIES FROM PERU

The Brassicaceae (Cruciferae) of Peru were treated by Macbride (1938) more than half a century ago. Many new taxa and nomenclatural changes have since been proposed (see for example, Al-Shehbaz, 1989a, b; Khanna & Rollins, 1965). The family as represented in South America needs to be revised, and many undescribed taxa, particularly in the genera *Draba* L., *Lepidium* L., and *Sisymbrium* L., should be accounted for. The present writer is presently working on *Draba* in South America as a first step toward achieving that goal.

Sisymbrium arequipanum Al-Shehbaz, named after Depto. Arequipa (Peru), to which it is apparently endemic, is somewhat isolated morphologically from all of the Peruvian species of *Sisymbrium*. It is easily distinguished by having narrowly linear-lanceolate, remotely dentate basal leaves, auriculate linear-lanceolate cauline leaves, a few small flowers, and straight, terete fruits on short, ascending, straight pedicels. The species resembles superficially members of *Arabis* L., but this genus does not occur anywhere in Central and South America, and it always has flattened fruits.

Sisymbrium arequipanum Al-Shehbaz, sp. nov. TYPE: Peru. Depto. Arequipa: Pichu Pichu, sandy hillside, 5 Jan. 1937, 13,500 ft. [ca. 4,423 m], *Dora Stafford 674* (holotype, F; photo, GH). Figure 1.

Herba perenna, caulibus erectis glabris, 7–21 cm longis; folia basalia petiolata, angusti lineari-lanceolata, remoti dentata, ciliata, attenuata, 3.5–14 cm longa, 2–8 mm lata; folia caulina auriculata, lineari-lanceolata, integra; racemi ebracteati, pedicelli fructiferibus recti, crassi, adscendentibus, 2–6 mm longi; sepala erecta, oblonga, sparse hirsuta, 3–3.5 mm longa; petala alba, spathulata, 3.5–4.5 mm longa, 1.2–1.4 mm lata; siliquae teretae, linearae, 1.5–4 cm longae, ca. 1.5 mm latae; stylus 0.4–0.7 mm longis; semina immatura uniseriata.

Perrenial herbs with a slender to thick caudex covered with petiolar remains of previous years. Stems simple, erect, glabrous, 1 or few from the caudex, 7–21 cm high. Basal leaves petiolate, narrowly linear-lanceolate, 3.5–14 cm long, 2–8 mm wide, remotely dentate, ciliate, acute to acuminate at apex, attenuate at base, sparsely to densely hirsute on both surfaces, the trichomes simple, straight, 0.3–0.6 mm long; petioles slender, ciliate, flattened and broadened at base. Cauline leaves few, sessile, auriculate, linear-lanceolate, 1.5–3 cm long, 2–2.5 mm wide, entire, ciliate. Inflorescence an ebracteate, few-flowered, corymbose raceme, elongated considerably in fruit; fruiting pedicels thick, ascending, straight, sparsely pubescent, 2–6 mm long. Sepals erect, oblong, 3–3.5 mm long, 1–1.3 mm wide, nonsaccate at base, scarious at margin, sparsely hirsute. Petals white, spatulate, 3.5–4.5 mm long, 1.2–1.4 mm wide, rounded at apex, attenuate at base to a claw ca. 2 mm long. Filaments erect, white, ca. 3 mm long; anthers oblong, ca. 0.8 mm long. Nectar glands confluent, subtending the bases of filaments. Fruits ascending, linear, terete, obscurely torulose, 1.5–4 cm long, ca. 1.5 mm wide; valves glabrous, with a conspicuous midvein; septum complete; style 0.4–0.7 mm long; stigma slightly 2-lobed. Immature seeds uniseriate, ca. 2.4 × 1.2 mm.

Additional specimen examined. PERU. DEPTO. AREQUIPA: SW slope of Nevado Chachani, rocky quebrada with steep slopes, 3,950 m, 3 Nov. 1963, *Richard M. Straw 2326* (US).

The holotype of *Sisymbrium arequipanum* differs from the paratype in being sparsely instead of densely hirsute. The two collections are otherwise very similar.

I am most grateful to the directors and curators of the Field Museum and the Smithsonian Institution for the loan of specimens. I thank Neil A. Harriman for his critical review of the manuscript and Barbara Nimblett for typing the manuscript.

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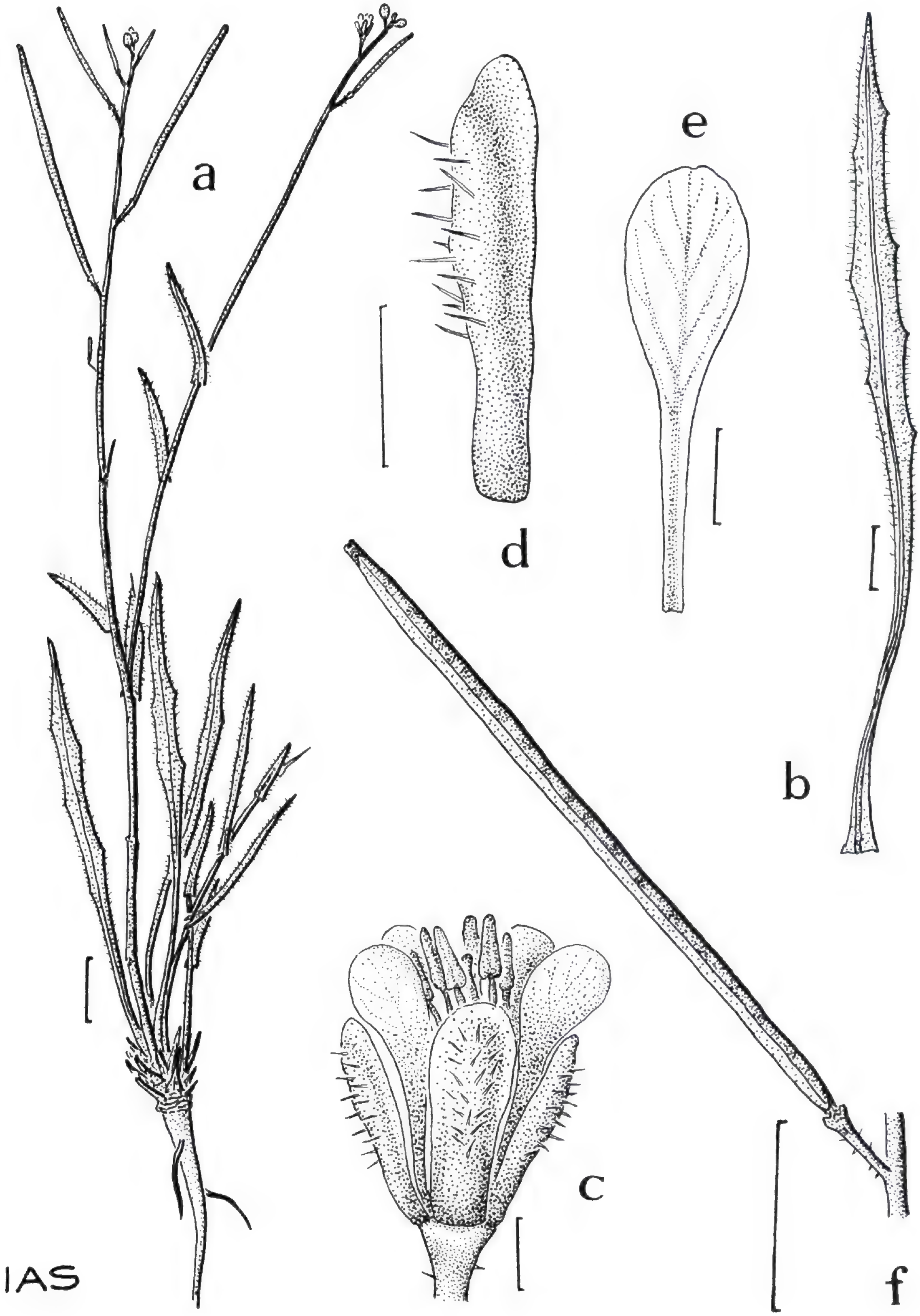
FIGURE 1. *Sisymbrium arequipanum*.—a. Plant.—b. Basal leaf.—c. Flower.—d. Sepal.—e. Petal.—f. Fruit. a and f from *Stafford 674*; b–e from *Straw 2326*. Scales: a, b, f = 1 cm; c–e = 1 mm. Illustrations by the author.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INGA NEBLINENSIS (LEGUMINOSAE–MIMOSOIDEAE), UNA NUEVA ESPECIE DEL SUR DE VENEZUELA

English Summary

Inga neblinensis (Leguminosae) is named and described from Venezuela.

Una serie de colecciones recientes de la base y las laderas de Cerro de la Neblina en Territorio Federal Amazonas, Venezuela, ha confirmado la presencia de una nueva especie de *Inga*, la cual se describe a continuación.

Inga neblinensis Cárdenas & De Martino, sp. nov. TIPO: Venezuela. Territorio Federal Amazonas: Departamento Río Negro; gravelly banks of large island in Río Mawarinuma just above Neblina Base Camp, ca. 160 m, 00°50′N, 66°10′W, small tree, flowers yellow, 3 Dec. 1984, *R. Kral 71954* (holotipo, MY). Figura 1.

Arbor ramis glabris, striatis vel costatis, fuscis. Foliorum rhachi alata; foliola plerumque 3-juga, elliptica, glabra vel subglabra, nitida, 2.6–20 cm longa, 1–6.5 cm lata, apice acuta, basi cuneato-rotundata. Flores magni, calyce tubuloso, 5-dentato, 5–11 mm longo; corolla tubulosa, 5-lobata, 1.3–2.2 cm longa; staminibus numerosis, 4–5.4 cm longis; pistillo 3.5–5.2 cm longo. Legumen compressum, nitidum, fuscum, nervis transversis praeditum, basi rotundatum, apice cuspidatum.

Arbusto o árbol pequeño 3–8 m alto. Ramas flexuosas, glabras, estriadas o costilladas, castaño-ennegrecidas; lenticelas dispuestas longitudinalmente, generalmente de color más claro que el resto de la superficie de la rama. Hojas con 2–4 pares de folíolos, más comúnmente 3 pares, el distal siempre más grande; estípulas subuladas o lanceoladas, estriadas, 3–6 mm largo, 1–1.5 mm ancho, glabras o las márgenes pubescentes; pecíolo desnudo o alado, pubescente, 4–17 mm largo (incluye el pulvínulo); raquis alado, 2–7.8 cm largo, ala 2–10 mm ancho (incluye el raquis), ancha y cordada en el ápice, angostada hacia la base; peciolulo antrorso-pubérulo, ennegrecido como el pulvínulo, 2–2.5 mm largo, 1–2 mm ancho, articulado con el raquis; folíolos elípticos, 2.6–20 cm largo, 1–6.5 cm ancho, glabros o subglabros, nítidos por ambas caras, arriba castaño-ennegrecidos, abajo pardos, nervadura pinnada sobresaliente, el envés conspicuamente reticulado, margen entero, ondulado, glabro o antrorso-aplicado, base cuneado-redondeada, ápice agudo o algo obtuso, a veces acuminado, la punta mucronulada; glándula entre cada par de folíolos, subglobular u ovoide, cupuliforme, levantada sobre la superficie, castaño-ennegrecida, adentro casi negra, 1.3–2.8 mm diámetro. Flores en racimos acortados corimbiformes; pedúnculos antrorso-pubérulos, 1–2 en las axilas de las hojas, 2–4.2 cm largo, 1 mm diámetro; brácteas caedizas, 2–6 mm largo, 0.1–1.5 mm ancho, pedicelos pubérulos, 1–2 mm largo, 0.5–1.5 mm diámetro; cáliz tubular, pubérulo, nervado, 5-dentado, 5–11 mm largo, 1.5–3 mm diámetro, dientes irregulares; corola tubulosa, tomentosa a escaso pubérula, nervada, 5-lobulada, 1.3–2.2 cm largo, 1–3 mm diámetro, abajo unida al tubo estaminal en una distancia de 2–4 mm, lóbulos 2–5 mm, profundos, márgenes involutos; estambres numerosos (más de 50), 4–5.4 cm largo, tubo estaminal exerto o incluso, 2–2.6 cm largo; granos de polen en políades; pistilo 3.5–5.2 cm largo, ovario sésil, glabro o corto pubérulo, 2–2.5 mm largo, 0.2–0.9 mm diámetro. Legumbre aplanada, 10–13.3 cm largo, 2.1–2.5 cm ancho, 2–3 mm grueso, base redondeada, ápice cuspidado, superficie brillante, castaño-ennegrecida, con numerosos nervios transversales.

Paratipos. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Departamento Río Negro, Neblina Base Camp, Río Mawarinuma, periodically flooded forest along river, 140 m, 00°50′N, 66°10′W, 21 Feb. 1985 (fr), *Boom & Weitzman 5930* (MY); Neblina Base Camp on the Río Mawarinuma, 00°50′N, 66°10′W, ca. 140 m, 17 July 1984 (fr inmaduro), *Davidse & Miller 27438* (MY);

FIGURA 1. *Inga neblinensis* (*Kral 71954*) –a. Rama florífera.—b. Flor, corte longitudinal.

margins of Río Mawarinuma below Cerro Neblina Base Camp, 140 m, 00°50′N, 66°11′W, frequently inundated bamboo swamp forest, 4 May 1984 (fl), *Gentry & Stein 47172* (MY); near Cerro de la Neblina, Base Camp, Río Mawarinuma, 140 m, 00°50′N, 66°55′W, 5 Feb. 1984, (fr inmaduro), *Liesner 15664* (MY); Cerro de la Neblina Camp IV, 15 km NNE of Pico Phelps, N branch of river in canyon, 780 m, 00°51′N, 65°57′W, 15–18 Mar. 1984 (fr inmaduro, restos de fl), *Liesner 16710* (MY); along Cañon Grande E of Cumbre Camp, Cerro de la Neblina, Río Yatua, 1,100 m, 24 Nov. 1957 (fl), *Maguire, Wurdack & Maguire 42223* (VEN); tropical lowland evergreen forest along gravelly and silty banks of river, along Río Baria (= Río Mawarinuma) just upstream from Base Camp, SW side of Cerro de la Neblina, 140 m, 00°49′50″N, 66°09′40″W, 16 Feb. 1985 (fr inmaduro), *Nee 30876*

(MY); ca. 2 km S of Base Camp, alluvial and upland forests along Mawarinuma River, 140 m, 00°50′N, 66°10′W, 11 Feb. 1984 (fl), *Thomas & Plowman 3008* (MY); along Río Mawarinuma, 2–6 km E of base camp, between base camp and "Puerto Chimo," 160 m 00°50′N, 66°08′W, 26 Apr. 1984 (fl), *Thomas 3212* (MY); along Río Mawarinuma, at "Puerto Chimo" camp, ca. 6 km E of base camp, 170 m, 00°50′N, 66°07′W, 23 April 1984 (fl), *Thomas 3224* (MY).

Inga neblinensis pertenece a la sección *Pseudinga* Benth. Se caracteriza por sus hojas glabras, nítidas, raquis alado, flores grandes amarillentas y por el color castaño-ennegrecido de la planta (en muestras de herbario). Solamente se ha localizado en el sur del Territorio Federal Amazonas, en el Cerro de la Neblina.

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REDISCOVERY OF *TETRAMOLOPIUM ARENARIUM* SUBSP. *ARENARIUM* VAR. *ARENARIUM* (ASTERACEAE: ASTEREAE) ON THE POHAKULOA TRAINING AREA, HAWAII

The initial step in the U.S. Army's Land Condition Trend Analysis Program (LCTA) is to conduct a comprehensive floristic and vegetation inventory of each installation. One of the first group of installations to be inventoried was the Pohakuloa Training Area (PTA) on the Island of Hawaii, Hawaii (Fig. 1). Pohakuloa Training Area is a 44,100-ha area located in the saddle between Mauna Loa and Mauna Kea. Approximately half of the installation is ordnance impact area. Because of the rough terrain and inaccessibility of much of the area, only about 4,100 ha are used for infantry, artillery, and tracked-vehicle maneuvers.

Three endangered plant species have been identified previously from PTA (Herbst & Fay, 1979): *Haplostachys haplostachya* (A. Gray) St. John var. *angustifolia* (Sherff) St. John (Lamiaceae), *Stenogyne angustifolia* A. Gray var. *angustifolia* (Lamiaceae), and *Lipochaeta venosa* Sherff (Asteraceae). The species of Lamiaceae were thought to be extinct until their rediscovery on PTA (Ayensu & DeFilipps, 1978; Herbst & Fay, 1979). All three of these species occur in a designated endangered plants habitat (approximately 1,600 ha) on the northwest side of PTA within Kipuka Kalawamauna (Fig. 1). This kipuka is a vegetated older lava flow isolated by newer, sparsely vegetated, or barren lava flows. The elevation of the area is approximately 1,545 m. The kipuka receives about 380 mm of precipitation annually.

During the LCTA survey of the vegetation at PTA, *Tetramolopium arenarium* (A. Gray) Hillebr. subsp. *arenarium* var. *arenarium* (Asteraceae: Astereae) was collected by P. Douglas (*Douglas 3191*) (Fig. 2). Ayensu & DeFilipps (1978) and Lowery (1986) reported this taxon as presumably extinct because no collections had been made since the late 1800s. The only previously known localities for this taxon were Puu Hualalai and Nohonao Hae (near Waimea) on Hawaii and Kula, East Maui (Lowery, 1986). A botanical survey conducted in 1977 as supporting documentation for an environmental impact statement for PTA listed *T. arenarium* (Lawrence Hirai, pers. comm.). We have been unable to locate any voucher specimens for this reported collection.

Douglas 3191 was collected in the endangered plants habitat, near the three endangered plant species. The population of *Tetramolopium* covers an area about 200 m by 60 m and is bisected by an unpaved road. One part of the population grows about 20 m east of the road. When last observed, it consisted of 33 robust individuals. The other portion, with 81 adult plants and 14 juvenile or seedling plants, occurs approximately 80 m west of the road. Consequently, the two portions are about 10 m apart. Fifteen dead individuals were found in the larger portion of the population. The cause of death of these plants is unknown. The occurrence of juvenile or seedling plants indicates that viable seed is being produced and that environmental conditions necessary for seed germination and seedling establishment occur periodically. Mature plants were observed flowering in January, April, and August.

The collection was made in a shrubland dominated by *Dodonaea viscosa* Jacq., *Dubautia linearis* (Gaud.) D. Keck, and *Sophora chrysophylla* (Salisb.) Seem. A weedy, introduced grass (*Pennisetum setaceum* (Forssk.) Chiov.) is aggressively expanding into the area. The *Tetramolopium* population occurs on a mesic ridge that runs west-northwest. The soil type at this site is rockland (rRO) (USDA, 1973).

Tetramolopium arenarium is a member of sect. *Sandwicense* Lowery, which is composed of gynomonoecious, upright shrubs with corymbose-paniculate heads, narrowly funnelform disk corollas, and fewer than 15 disk florets per head (Lowery & Crawford, 1985; Lowery, 1986). This section

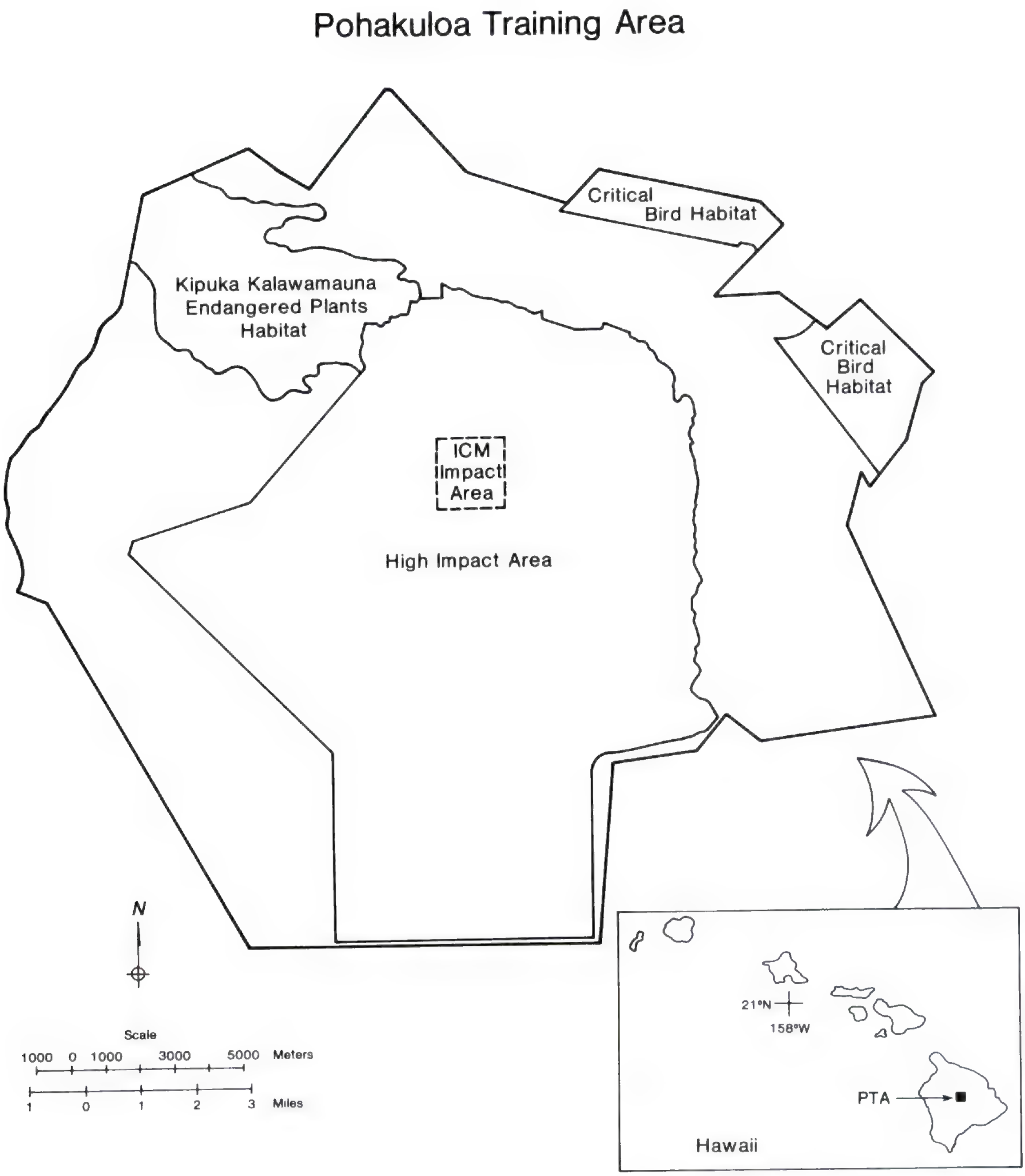

FIGURE 1. Map of Pohakuloa Training Area, Island of Hawaii, Hawaii, showing the extent of the ordnance impact area, and locations of the Kipuka Kalawamauna Endangered Plants Habitat and Critical Bird Habitat (Palila, *Loxioides bailleui* Oustalet).

also includes *T. consanguineum* (A. Gray) Hillebr., *T. conyzoides* (A. Gray) Hillebr., and *T. lepidotum* (Less.) Sherff. Of the four species in the sect. *Sandwicense*, two have been considered extinct: *T. arenarium* and *T. conyzoides* (Ayensu & DeFilipps, 1978; Lowery, 1986). The other two species have extinct infraspecific taxa (Lowery, 1986).

Tetramolopium consanguineum never has hirsute or pilose leaves (*Douglas 3191* has densely and evenly hirsute leaves). *Tetramolopium conyzoides* has 1–3 disk florets per head (*Douglas 3191* has 5–9 disk florets per head). *Tetramolopium lepidotum* has glandular punctate leaves (*Douglas 3191* has glandular but not punctate

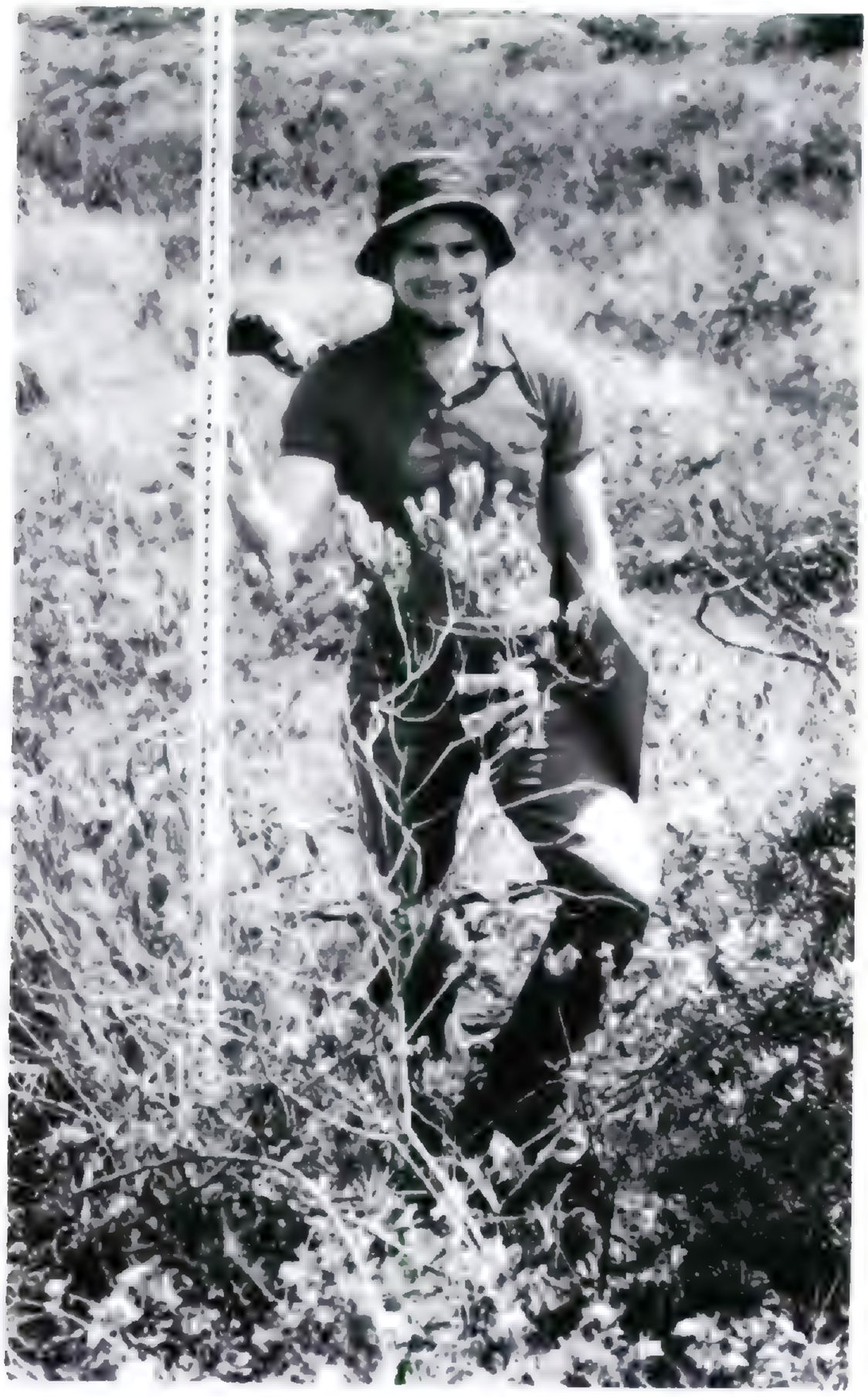

FIGURE 2. General habit of *Tetramolopium arenarium* subsp. *arenarium* var. *arenarium* within the Kipuka Kalawamauna Endangered Plants Habitat, Pohakuloa Training Area, Island of Hawaii, Hawaii. (Scale in decimeters.)

leaves). The only other member of sect. *Sandwicense* that occurs on PTA is *Tetramolopium consanguineum*.

Tetramolopium arenarium is composed of two subspecies, both presumably extinct: subsp. *arenarium* on Hawaii and Maui and subsp. *laxum* on Maui (Lowery, 1986). *Tetramolopium arenarium* subsp. *laxum* has open, lax inflorescences, flexuous pedicels, granuliferous-glandular achenes, and foliage that retains its yellow-green color when dried. In contrast, *T. arenarium* subsp. *arenarium* has compact inflorescences, densely strigose achenes, nonflexuous pedicels, and brown foliage upon drying. *Douglas 3191* has compact capitula, densely strigose achenes, nonflexuous pedicels, and brown dried foliage.

Tetramolopium arenarium subsp. *arenarium* is separated into two varieties: var. *arenarium* and var. *confertum*. *Tetramolopium arenarium* subsp. *arenarium* var. *confertum* has dentate leaf margins, and involucres 4–6 mm wide and 2–3 mm long. *Tetramolopium arenarium* subsp. *arenarium* var. *arenarium* has entire leaf margins, and involucres 6–9 mm wide and 3–5 mm long. *Douglas 3191* has entire leaves and involucres that are 6–7 mm wide and 4–5 mm long.

We verified our collection by comparing it with two specimens of *T. arenarium* subsp. *arenarium* var. *arenarium* at the U.S. National Herbarium (US): *Mann & Brigham 519*, collected at Puu Hualalai; and *Hillebrand 319*, which has no locality information. Both of these specimens were annotated by Lowery (1986) as *T. arenarium* subsp. *arenarium* var. *arenarium*. Lowery (1986) stated the lectotype for this taxon was "Hawaiian Islands: Hawaii: 1840, U.S. Exploring Expedition (US!, mixed collection with isotype of *T. arenarium* subsp. *laxum*)." The staff at US could not locate nor has any record of this specimen; thus, we were unable to compare our specimen with the lectotype.

Tetramolopium arenarium subsp. *arenarium* var. *arenarium* has no federal or state protection, because it has been listed as extinct by the U.S. Fish and Wildlife Service, Office of Endangered Species, Region 1 (Andy Robinson, pers. comm.). The U.S. Army, however, has begun a protection program for this taxon at PTA.

Herbst & Fay (1979) reported that grazing and browsing by feral animals, cutting for camouflage by military units, trampling by foot traffic or vehicles, and accidental fires set by hunters and/or military ordnances may adversely affect the three endangered plant species found at PTA. Our observations indicate that the most likely threats to the endangered plant species and the *Tetramolopium arenarium* population are from feral animals, fire, and competition from invading, introduced plants. We have observed numerous feral sheep, goats, and hogs in the endangered plants habitat. Also, the area has been burned (date unknown). We have not observed off-road vehicular traffic, foot traffic, or cutting of vegetation for camouflage. Fencing, removal of all feral animals, reduced use of the area for training, and continued efforts by the Army to control fires may help protect these plants.

We are researching the ecology and population biology of the endangered species and *Tetramolopium arenarium* with funding from the U.S. Army. Propagation of the species is being investigated as a means of ensuring its survival.

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MISCELLANEOUS CHROMOSOME COUNTS IN ASTERACEAE, BIGNONIACEAE, PROTEACEAE, AND FABACEAE

Since the publication of my review of the chromosome cytology of the Fabaceae (Goldblatt, 1981a) and the documentation of the original chromosome counts cited therein (Goldblatt, 1981b), I have made several more counts in the family. These are reported here with associated collection data (Table 1). Most of the counts are particularly noteworthy as they are either the first records for genera or the first for species.

Counts are also reported for species of Asteraceae, Bignoniaceae, and Proteaceae. The significance of the counts in relation to the existing cytological record is briefly discussed for each species.

Material and Methods

All counts were made from root tips of germinating seeds, grown in the greenhouse. All seeds were collected in the wild for this study. Tips were harvested in midmorning and pretreated in either 0.001 M aqueous hydroxyquinoline for 6–8 hr. at refrigerator temperature or in saturated aqueous M-bromonaphthalene for 4 hr. at room temperature. After rinsing in tap water, the tips were fixed for 2–3 min. in 3 : 1 absolute ethanol : glacial acetic acid, rinsed again in tap water, and then hydrolyzed in 10% HCl for 6 minutes at 60°C. Root apices were squashed in FLP orcein (Jackson, 1975). The species studied and collection data are listed in Table 1, in which the diploid numbers are presented.

Discussion

ASTERACEAE

Of the estimated 48 species of the Old World and predominantly African *Dicoma* (tribe Mutisieae), only an Indian species, *D. tomentosa* Cass., has been counted, Bhandari & Singh (1977) having reported $2n = 22$. The report here for the southern African *D. schinzii* provides additional support for assuming a base number of $x = 11$ for the genus, although $x = 9$ is almost certainly basic for the tribe Mutisieae as well as for the entire family (Raven, 1975; Goldblatt, 1987).

PROTEACEAE

Already counted as *Aulax cneorum*, the record here of $2n = 22$ in *A. umbellata*, confirms de Vos's (1943) report of $n = 11$ in *Aulax*. Other African Proteoideae have $x = 12$, except *Leucadendron*, which has $x = 13$ (de Vos, 1943; Williams, 1972). *Aulax* and *Leucadendron* are the only dioecious African Proteoideae, and the karyological data support the contention, based on other criteria (Rourke, 1987), that dioecism evolved independently in the two genera and that they are not closely allied.

BIGNONIACEAE

The count here of $2n = 40$ for *Parmentiera valerii*, the first record for this species, is consistent with the number reported for three other members of this neotropical genus of tribe Crescentieae (Goldblatt & Gentry, 1979).

FABACEAE

The count for *Zenia insignis*, a taxonomically isolated and apparently primitive member of Caesalpinieae–Cassieae, accords with the putatively basic chromosome number for the tribe, $x = 14$ (Goldblatt, 1981a).

In Papilionoideae, $2n = 20$ in the monotypic *Graziodendron* is consistent with other numbers recorded for Dalbergieae, including the closely related genus *Andira* (Goldblatt, 1981a). *Pterocarpus*, also considered closely related (de Lima, 1983) probably has $x = 11$, but at least two species also have $n = 10$ (Goldblatt, 1981a). The diploid numbers for the previously uncounted *Chadsia* and for *Lonchocarpus pycnophyllus*, $2n = 22$, accord

TABLE 1. Chromosome counts reported here for Asteraceae, Bignoniaceae, Proteaceae, and Fabaceae, with collection data.

Species	Diploid chromosome numbers $2n$	Collection data
		ASTERACEAE
		MUTISIEAE
Dicoma schinzii O. Hoffmg.	22	Namibia, Kupferberg Pass, *Goldblatt & Manning 8849* (MO)
		PROTEACEAE
Aulax umbellata (Thunb.) R. Br.	22	South Africa, Cape Prov., Vogelgat, Hermanus, *Williams s.n.* (no voucher)
		BIGNONIACEAE
Parmentiera valerii Standl.	40	Costa Rica, Volcán Miravalles, *Poveda 2478* (MO)
		FABACEAE–CAESALPINIOIDEAE
		CASSIEAE
Zenia insignis Chun	28	China, Kwangsi, *Yu s.n.* (PE)
		PAPILIONOIDEAE
		DALBERGIEAE
Graziodendron rio-docensis Lima	20	Brazil, Espírito Santo, Linhares, *de Lima 1928* (RB)
		TEPHROSIEAE
Chadsia grevei Drake	22	Madagascar, Fort Dauphin-Tulear, *Dorr et al. 4075* (MO)
Lonchocarpus pycnophyllus Urban	22	Dominican Republic, Peninsula de Barahana, *Zanoni & Pimentel 26349* (MO)
		ROBINIEAE
Poissonia hypoleuca (Speng.) Lillo	ca. 32	Argentina, Jujuy, Río San Lorenzo, *Vervoorst s.n.* (no voucher)
		DESMODIEAE
Brya buxifolia (Murr.) Urban	22	Dominican Republic, Prov. San Juan, *Zanoni & Mejía 19785* (MO)
		PHASEOLEAE–ERYTHRININAE
Neorudolphia volubilis (Willd.) Britton	22	Puerto Rico, *Vivaldi s.n.* (no voucher)
		PHASEOLEAE–PHASEOLINAE
Neorautanenia brachypus (Harms) C. A. Smith	22	Zimbabwe, Wedza, *Corby 727* (SRGH)
		AESCHYNOMENEAE
Pachecoa prismatica (Sesse & Moc.) Standley & Schubert	20	Mexico, near Vera Cruz, *Norman 801* (F, GH)

with the presumed base number for Tephrosieae, $x = 11$ (Goldblatt, 1981a). In the previously uncounted genus *Poissonia* (tribe Robinieae), *P. hypoleuca* has $2n = 32$, and this species appears to be tetraploid. Base number in Robinieae is either $x = 11$ or 10, but dysploidy is evident in the tribe, with $x = 9$, 8, and 6 recorded in some genera (Goldblatt, 1981a). A base number of $x = 8$ seems likely for *Poissonia*, a hypothesis consistent with the patterns of karyological variation in the tribe.

Basic chromosome number for Desmodieae is probably $x = 11$, but at least *Pycnospora* and the one species of *Brya* previously counted have $n = 10$ (Goldblatt, 1981a). This first count for *B. buxifolia* is consistent with the earlier record for the genus.

Basic number for Phaseoleae is $x = 11$, the number also probably basic for all eight subtribes (Goldblatt, 1981a). The counts here for *Neorudolphia* (Erythrininae), a monotypic genus previously uncounted, and *Neorautanenia brachypus* (Phaseolinae) are consistent with this pattern. The count for *Neorudolphia* is of interest in view of its possible relationship with the large genus *Erythrina*, which has $x = 21$. The chromosome number in *Neorudolphia* confirms data from other sources that it is probably not closely allied to *Erythrina*.

My count of $2n = 20$ in *Pachecoa prismatica* (Aeschynomeneae–Stylosanthinae), cited by Norman & Gunn (1985), accords with the base number of $x = 10$ in *Arachis* and *Stylosanthes*, two of the remaining four genera of the subtribe. *Arthrocarpum* is uncounted while *Chapmannia* has $x = 11$ (Goldblatt, 1981a, b). The last-mentioned two genera are most closely allied to *Pachecoa* (Norman & Gunn, 1985).

I extend my thanks to all those who provided the living material used in this study.

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LEPIDIUM BOELCKEI AND *L. JUJUYANUM* (BRASSICACEAE), NEW SPECIES FROM JUJUY, ARGENTINA

Several new taxa and nomenclatural changes have been published (Al-Shehbaz, 1986; Boelcke, 1964, 1984, 1986) following the treatments of Thellung (1906) and Hitchcock (1945) on the South American species of *Lepidium*. The genus, which is represented in South America by probably more than 50 species, is in need of a comprehensive study. Species boundaries within certain complexes are artificial, and the variation of many taxa is poorly understood.

The two novelties described below were initially sent to Professor Reed C. Rollins for identification. I am grateful to him for making them available for my study. Each of these is known only from the holotype.

Lepidium boelckei Al-Shehbaz, sp. nov. TYPE: Argentina. Jujuy: Depto. Humahuaca, Cerro La Soledad, 3,500 m; 23 Jan. 1929, *S. Venturi 8859* (holotype, US 1549309). Figure 1a–c.

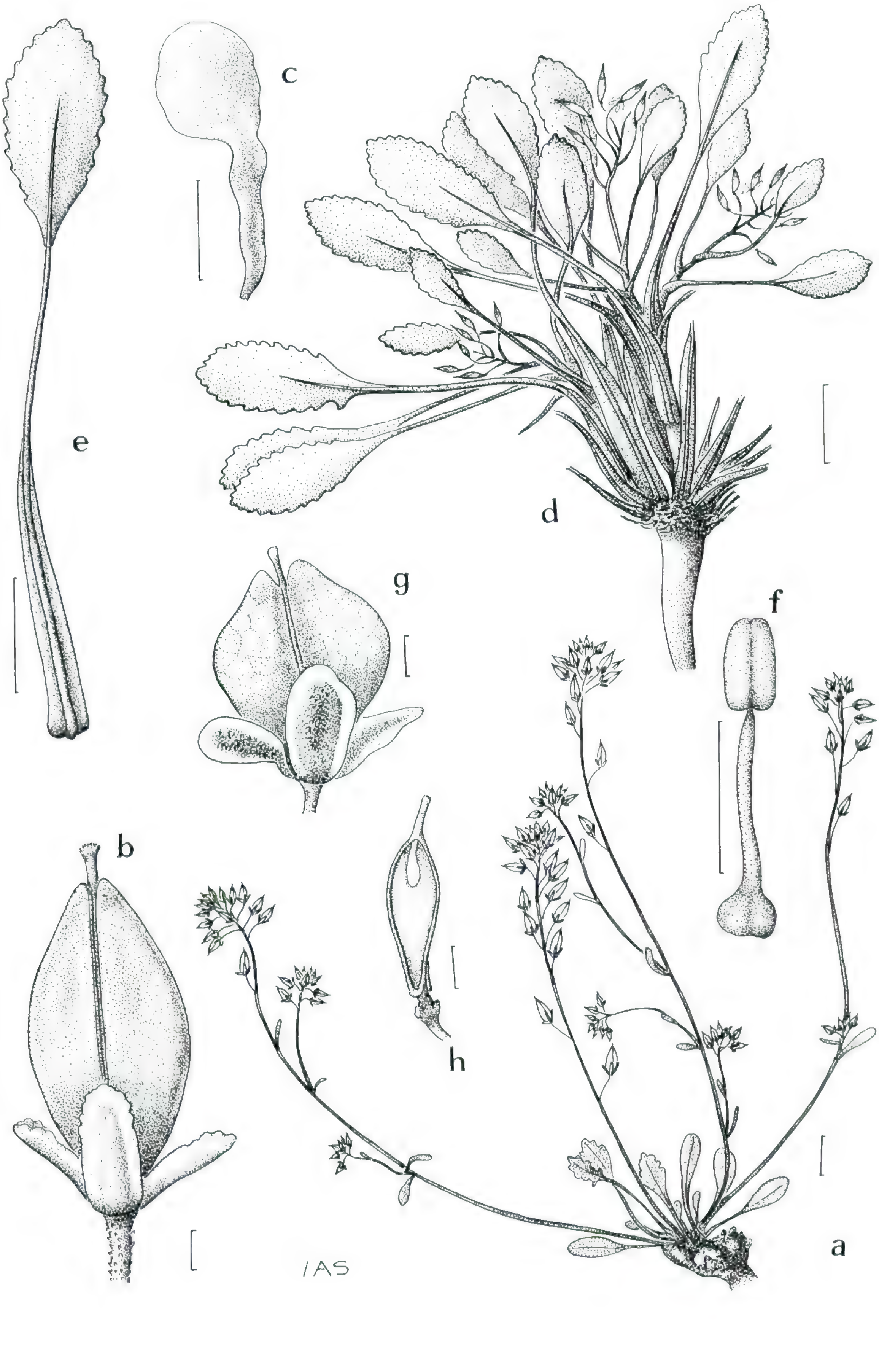
Herba perennis caudicibus lignosis simplicibus, 1–2 cm in diametro, caulibus villosis subdecumbentibus, 6 15 cm longis; folia basalia spathulata integra vel dentata; racemi floriferi subcorymbosi, fructiferi valde elongati; sepala oblonga glabra persistentia albo-marginata; petala alba; stamina 2; siliculae anguste ellipticae vel elliptico-oblongae, glabrae, obtusae vel retusae, 6–7 mm longae, 3–3.6 mm latae; styli exserti, 0.6–0.8 mm longi; semina oblonga, nigella, compressa, exalata, ca. 3 × 1.5 mm.

Perennial herbs, with a woody, unbranched caudex 1–2 cm diam. Stems few to several from the caudex, ascending to subdecumbent, villous, 6–15 cm long. Basal leaves spatulate, petiolate, obtuse to rounded at apex, attenuate at base, earlier ones entire, later ones dentate to subincised, 1.6–4 cm long, 3–8 mm wide, the blades glabrous or hirsute along the midrib; petioles flattened, densely hirsute, 1–2.5 cm long. Cauline leaves few, spatulate to oblanceolate, entire, attenuate and subsessile at base, 5–11 mm long, 1–3 mm wide. Inflorescences densely flowered, ebracteate, corymbose racemes, considerably elongated in fruit; fruiting pedicels ascending, densely puberulous to subhirsute, 5–7 mm long. Sepals oblong, persistent, glabrous, somewhat leathery, 2–2.5 mm long, 1.2–1.5 mm wide, with a conspicuous white margin 0.2–0.5 mm wide, repand to suberose in the distal half. Petals spatulate, white, rounded at apex, attenuate at base, 3–3.2 mm long, 0.7–0.9 mm wide. Stamens 2; filaments white, 2–2.5 mm long; anthers oblong, 0.7–0.8 mm long. Fruits narrowly elliptic to elliptic-oblong, conspicuously flattened, glabrous, wingless, obtuse to obscurely notched at apex, 6–7 mm long, 3–3.6 mm wide; style exserted, 0.6–0.8 mm long; stigma entire, wider than the style. Seeds oblong, blackish, wingless, flattened, ca. 3 × 1.5 mm.

Lepidium boelckei, which is named after Dr. Osvaldo Boelcke, authority on the Argentinian Brassicaceae and author of several species of *Lepidium*, is easily distinguished from all of the perennial South American species in having narrowly elliptic fruits 6–7 mm long, persistent sepals with a broad white margin, conspicuous styles well-exserted beyond the apical fruit notch, and subdecumbent stems from a thick woody caudex. The Brazilian *L. grandifructum* C. L. Hitchc. is the only other South American species with fruits as large as those of *L. boelckei*. However, the former is a robust, erect plant with caducous sepals, six stamens, and included styles. Evidently, the two species are unrelated, and *L. boelckei* has no close relatives.

Lepidium jujuyanum Al-Shehbaz, sp. nov. TYPE: Argentina. Jujuy: Depto. Humahuaca, Tres Cruces; 3,750 m; 6 Apr. 1973, *Barbara Ruthsatz 506/7* (holotype, GH). Figures 1d–h, 2.

Herba perennis caudicibus tenuibus simplicibus; folia basalia longe petiolata, oblonga vel oblongo-oblanceolata, laminis 13–23 mm longis, 6–10 mm latis, serrato-crenatis, superne villosis, petiolis persistentibus, 3–4 cm longis, in dimidio proximale stramineis, valde alatis, glabris, in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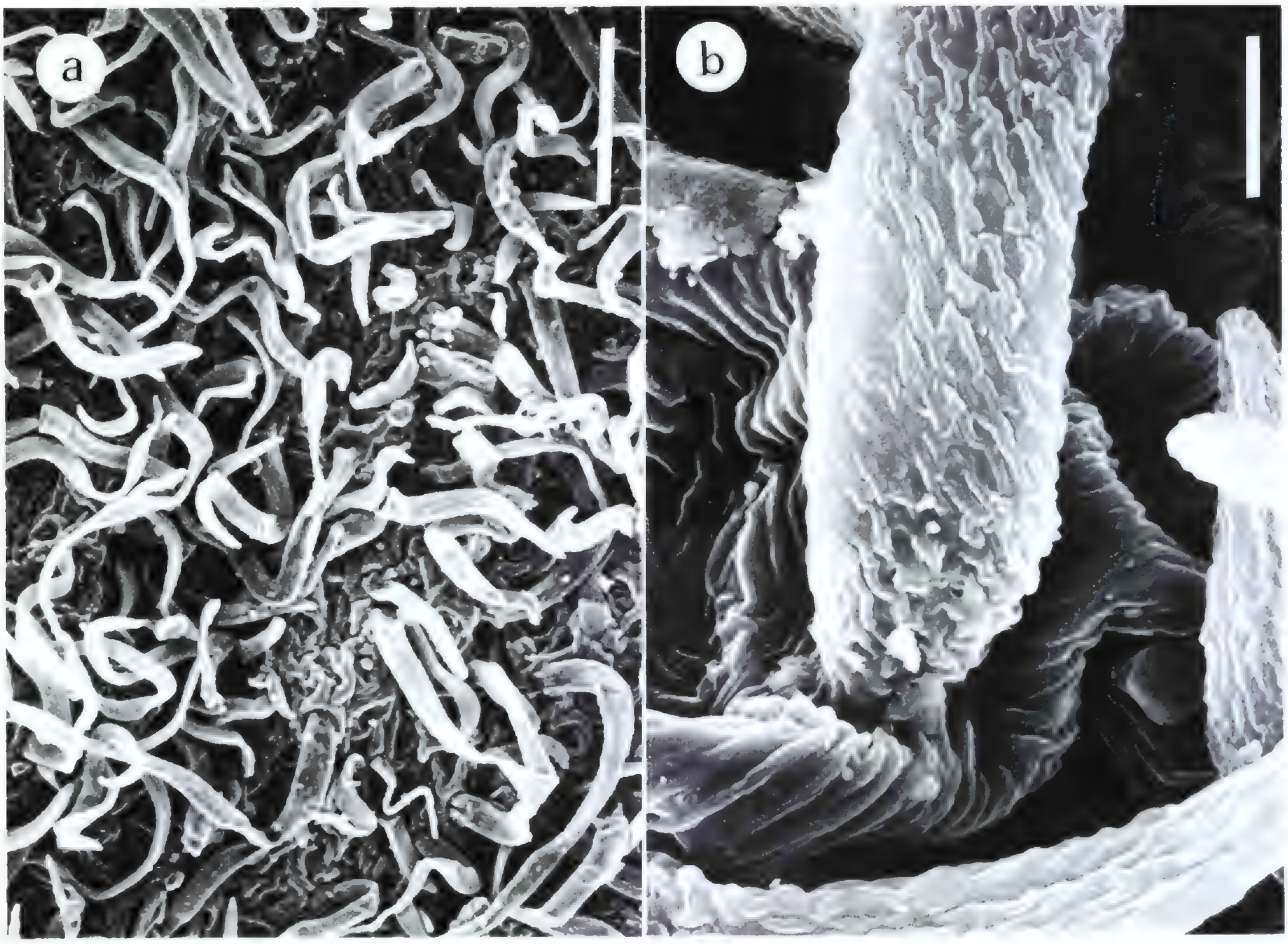

FIGURE 2. Leaf trichomes of *Lepidium jujuyanum*. Scales: a = 100 μm; b = 10 μm.

dimidio distale exalatis, villosis; sepala papyracea, persistentia, 2–3 mm longa; petala alba; stamina 2, filamentis basi valde dilatatis; siliculae rhomboideae, glabrae, emarginatae, 3.5–4.5 mm longae, 3–4 mm latae; septum in dimidio apicale peforatum; styli exserti, 0.6–0.8 mm longi; semina ovata exalata, 2–2.4 mm longa, 1.4–1.6 mm lata.

Cespitose perennial with an unbranched, slender caudex. Stems few, glabrous, 1.5–6 cm long, much shorter than the basal leaves. Basal leaves long-petiolate; blades oblong to oblong-oblanceolate, 13–23 mm long, 6–10 mm wide, serrate-crenate, obtuse at apex, cuneate at base, glabrescent below, villous above with crisped, subappressed, simple trichomes, the midrib prominent in the proximal half; petioles persistent, 3–4 cm long, the distal half green, villous, slender, wingless, the proximal straw-colored, glabrous, with 2 conspicuous lateral wings to 1.2 mm wide. Cauline leaves few to several, similar to the basal ones but gradually reduced in size upward. Inflorescences ebracteate, corymbose racemes, slightly elongated in fruit; fruiting pedicels divaricate, usually straight, densely villous, 4–7 mm long. Sepals oblong to slightly obovate, papery, persistent, spreading, membranaceous and entire to repand at margin, sparsely pubescent in the middle, 2–3 mm long, 1.5–1.8 mm wide. Petals spatulate, white, rounded at apex, 2–2.6 mm long, ca. 1 mm wide. Stamens 2; filaments white, 1.4–1.6 mm long, considerably dilated at base; anthers oblong, ca. 0.6 mm long. Fruits rhomboid, 3.5–4.5 mm long, 3–4 mm wide, with an apical notch

←

FIGURE 1. *Lepidium boelckei* and *L. jujuyanum*. a–c. *L. boelckei*. — a. Plant. —b. Fruit. —c. Petal. d–h. *L. jujuyanum*. —d. Plant. —e. Basal leaf. —f. Stamen. —g. Fruit. —h. Replum with perforated septum. Scale: a, d, and e = 1 cm; others = 1 mm. Illustrations by the author.

0.3–0.4 mm deep; valves glabrous, thin, obscurely veined; septum membranaceous, perforated at apex; replum 1–1.2 mm wide; style exserted from the apical notch, 0.6–0.8 mm long. Seeds ovate, flattened, dark brown, wingless, 2–2.4 mm long, 1.4–1.6 mm wide; cotyledons incumbent.

Lepidium jujuyanum, which is named after Province Jujuy, Argentina, belongs to the *L. meyenii* Walp. complex, of which the component species are perennials with exserted styles. The new species is easily distinguished from all the South American lepidiums in having long-petiolate leaves with villous, crenate-serrate blades and straw-colored, conspicuously winged, persistent petioles, strongly dilated filament bases, perforated septa, and rhomboid fruits with exserted styles.

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ERRATUM

This is an *erratum* for the R. J. Rodin volume, *The Ethnobotany of the Kwanyama Ovambos*, published in 1985 by the Missouri Botanical Garden. APONOGETONACEAE; *Aponogeton* (pp. 50, 147): the description given on p. 50 is for *A. junceus* Lehm. subsp. *junceus*, not *A. rehmannii* Oliv. See H. van Bruggen (1973) Bull. Jard. Bot. Nat. Belg. 43: 191–233.

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